

# Local environment, not local adaptation, drives leaf-out phenology in common gardens along an elevational gradient in Acadia National Park, Maine

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**PREMISE OF THE STUDY:** Climate-driven changes in phenology are substantially affecting ecological relationships and ecosystem processes. The role of variation among species has received particular attention; for example, variation among species' phenological responses to climate can disrupt trophic interactions and can influence plant performance. Variation within species in phenological responses to climate, however, has received much less attention, despite its potential role in ecological interactions and local adaptation to climate change.

**METHODS:** We constructed three common gardens across an elevation gradient on Cadillac Mountain in Acadia National Park, Maine, to test population-level responses in leaf-out phenology in a reciprocal transplant experiment. The experiment included three native species: low bush blueberry (*Vaccinium angustifolium*), sheep's laurel (*Kalmia angustifolia*), and three-toothed cinquefoil (*Sibbaldiopsis tridentata*).

**KEY RESULTS:** Evidence for local adaptation of phenological response to temperature varied among the species, but was weak for all three. Rather, variation in phenological response to temperature appeared to be driven by local microclimate at each garden site and year-to-year variation in temperature.

**CONCLUSIONS:** Population-level adaptations in leaf-out phenology appear to be relatively unimportant for these species in Acadia National Park, perhaps a reflection of strong genetic mixing across elevations, or weak differences in selection on phenological response to spring temperatures at different elevations. These results concur with other observational data in Acadia and highlight the utility of experimental approaches to understand the importance of annual and local site variation in affecting phenology both among and within plant species.

**KEY WORDS** Cadillac Mountain; common garden experiments; intraspecific variation; leaf phenology; local adaptation; reciprocal transplants; Ericaceae; Rosaceae.

Climate change is shifting the seasonal timing of spring greening. Shifts in plant phenology in response to warming temperatures have been recorded across the globe through observational studies and experimental manipulations (Root et al., 2003; Parmesan and Yohe, 2003; Wolkovich et al., 2012). Although spring phenology is advancing for most temperate plant species, leaf out and flowering responses to warming temperatures can vary substantially. Some species advance their phenology, some delay, and others exhibit no change as temperatures warm (Menzel et al., 2006; Miller-Rushing and Primack, 2008; Polgar and Primack, 2011; Polgar et al., 2014). This variation is due in part to variation in the environmental cues by which plants regulate their spring phenology, including

photoperiod, winter chilling, and spring warming requirements (Körner and Basler, 2010; Polgar et al., 2014). These interspecific differences in the importance of photoperiod, chilling, and spring warming lead to variation in the response of spring phenology to climate change: the most responsive species show greater plasticity in their spring phenology. Variation in phenological response to climate change is ecologically important because phenology is linked to many aspects of plant physiology, trophic interactions, and reproductive success (Memmott et al., 2007; Richardson et al., 2013; CaraDonna et al., 2014; Sakurai and Takahashi, 2016). In addition, phenological sensitivity to climate has been linked to performance: species that advance their phenology in response to

warming temperatures are likely to grow or reproduce more, and are less likely to decline in abundance (Willis et al., 2008; Cleland et al., 2012).

Intraspecific variation in phenological response is also widespread, but less widely noted. Variations in phenological response to temperature within species have been recorded across latitudinal gradients for reproductive (Weber and Schmid, 1998; Olsson and Agren, 2002; Panchen and Gorelick, 2016; Prev  y et al., 2017) and vegetative phenology (Rossi and Isabel, 2016; K  rner et al., 2016), and across elevation gradients for trees at different life history stages (McGee, 1974; Vitasse et al., 2009, 2010, 2013, 2017). Many of these studies have found intraspecific variation in phenological responses, but taken together, they show no consistent pattern to which populations are likely to display greater phenological plasticity across these latitudinal and elevation gradients, which generally represent gradients in climate. For example, a study of congeneric pairs of species found that high-elevation (colder) species were less plastic in their phenological responses relative to low-elevation (warmer) species (Gugger et al., 2015). In contrast, another analysis of temperature sensitivity across latitudinal gradients from 20 years of leaf emergence data across 18 high-latitude sites discovered greater temperature sensitivity at colder, higher latitude sites (Prev  y et al., 2017). Most studies of intraspecific phenological variation sample populations from across large latitudinal or altitudinal ranges, but it is possible that similar variation happens more locally across small elevation gradients or other short-distance climate gradients.

Local adaptation likely contributes to both inter- and intraspecific variation in phenology along these gradients (Weber and Schmid, 1998; Olsson and Agren, 2002; Panchen and Gorelick, 2016). For example, experiments and observational monitoring have demonstrated that taxa sensitive to early spring freezing leaf out later than more frost-tolerant taxa, leading to differences in the lengths of their growing seasons (Augspurger, 2009; K  rner et al., 2016; Muffler et al., 2016). The trade-off between growing season length and risk of frost damage may be more dramatic at high elevations and high latitudes, even within species, leading to later phenology and reduced temperature sensitivity among these cold-adapted plants (Inouye, 2008; Laube et al., 2014; Polgar et al., 2014). This trade-off may be reduced at lower elevations or latitudes where growing seasons are longer.

If local adaptations are contributing to intraspecific variation in phenological responses to local climate, monitoring approaches and interpretations of data should account for it. Data from one population of a species that spans gradients (e.g., latitude, elevation) in which different phenological responses may be advantageous in different parts of the gradient, could over- or underestimate the phenological responses for other populations. This intraspecific variation could have implications for pollination, competition, and management (Ostaf   et al., 2015). For example, Prev  y et al. (2017) suggest that intraspecific variation in flowering phenology at high latitudes, where plants at colder sites display greater temperature sensitivity, could lead to convergence in flowering times as temperatures warm, and thus increase the potential for gene flow across latitudes. Vitasse et al. (2017) report a similar pattern towards more uniform leaf-out phenology across elevations in Switzerland because of stronger phenological advances at higher elevation.

We used a common garden experiment to examine potential intraspecific variation in phenological responses to climate among populations growing across very local gradients—at different elevations on Cadillac Mountain in Acadia National Park, Maine.

Common gardens are a classic experimental method in ecology to study reaction norms (Clausen and Hiesey, 1958), and a particularly useful approach to studying plant responses to climate change (Wilczek et al., 2010; Woolbright et al., 2014; Elmendorf et al., 2015). Here, we were interested in disentangling the general pattern of temperature-induced shifts in spring leaf phenology—in which populations at cooler (presumably high-elevation) locations tend to leaf out later than populations at warmer (presumably low-elevation) locations—from population-level variation in phenological sensitivity. We focused on understory species, which are less well studied in experimental gardens than trees and seedlings (K  rner et al., 2016; Vitasse et al., 2017). The compressed environmental gradient in Acadia (the summit of Cadillac Mountain is 466 m elevation) allowed us to explore intraspecific variation in phenological sensitivity over a smaller elevation gradient than most other garden studies (Greene et al., 2005). This narrow elevation range may limit intraspecific variation in phenological responses if selection on phenological response is low, or if there is strong genetic mixing among these populations. However, it is currently not clear at what scale local adaptation in phenology might occur. We monitored leaf-out phenology in three gardens over three years to answer the following questions: (1) Is there evidence for intraspecific variation in phenological sensitivity to local climate across Cadillac Mountain's elevation gradient? (2) Do high-elevation populations display more plasticity in leaf out (as in Vitasse et al., 2017 and Prev  y et al., 2017) or less (as in Gugger et al., 2015) than low elevation populations? (3) How does phenological sensitivity measured in this experiment compare with sensitivity values calculated from local observational data?

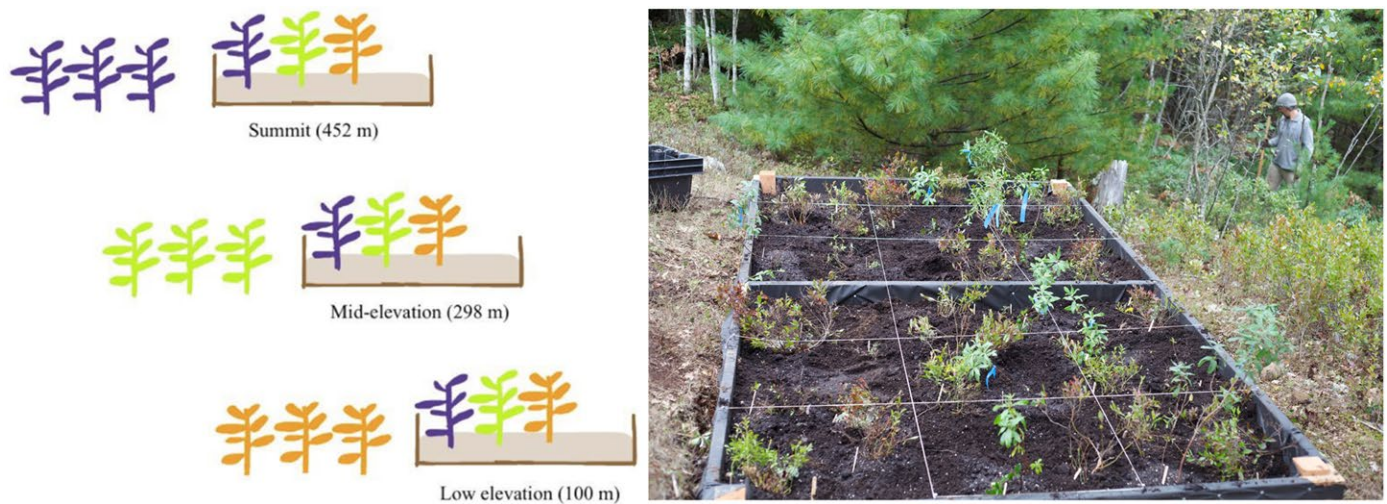
## MATERIALS AND METHODS

### Study site and experimental design

Our study took place on Cadillac Mountain in Acadia National Park, Maine (44.3526   N, 68.2251   W). Cadillac Mountain, the tallest mountain on the Atlantic seaboard of the United States, is located on Mount Desert Island. Its bald summit is relatively low (466 m), but hosts an open, unforested vegetative community of shrubs and low herbs typical of subalpine areas, because of poor soil conditions and exposure to coastal winds (Greene et al., 2005; Harris et al., 2012). The 30-year (1983–2013) mean annual temperature at Acadia National Park Headquarters in Bar Harbor (143 m elevation, 3.6 km from the summit of Cadillac Mountain) is 7.7  C (data from the U.S. National Oceanic and Atmospheric Association [NOAA]).

For our experiment, we chose three low perennial woody species that are abundant along the 350-m elevation gradient from the base to the summit of Cadillac Mountain: low bush blueberry (*Vaccinium angustifolium* Ait.), sheep's laurel (*Kalmia angustifolia* L.), and three-toothed cinquefoil (*Sibbaldiopsis tridentata* Ait.). We refer to these species by their genus names throughout this study. *Vaccinium* and *Kalmia* are low ericaceous shrubs (Ericaceae); *Sibbaldiopsis* is a cinquefoil with woody stems at ground level (Rosaceae). These species are among the most common plants on Cadillac Mountain and across Mount Desert Island; *V. angustifolium* in particular is an iconic Maine plant, important in both wild populations and among blueberry growers.

We established common gardens on Cadillac Mountain at 100, 300, and 450 m in elevation. At each elevation, we constructed one 1.8-m    3.7-m    0.3-m raised bed, which we lined with a weed



**FIGURE 1.** Left: A schematic of our experimental design. Each wild population is represented in different colors (summit = purple, mid-elevation = green, low elevation = orange). The raised beds were filled with transplants sourced from areas adjacent to the gardens at 100, 300, and 450-m elevations. Right: A photograph of the low elevation garden during transplanting in September 2013. Our flagged control plants are just outside the frame of the photograph; these represent the source populations of our transplants, but were not manipulated in our experiment.

barrier and filled with 2 m<sup>3</sup> of gardener's potting soil. We refer to the raised beds as “gardens” throughout this study. The approximate horizontal distance between the low elevation (100 m) site and the mid-elevation (300 m) site is 1.3 km; the approximate horizontal distance between the mid-elevation and summit (450 m) sites is 2.3 km. We collected mature plants from wild populations adjacent to the gardens at 100, 300, and 450 m elevations and transplanted them into each garden in September 2013 (Fig. 1). Each wild population was collected within 5 m of the garden; for *Kalmia* and *Vaccinium*, we suspect that many of the plants collected were clones as we separated “individuals” in roughly 10 cm<sup>2</sup> sections from larger blocks of shrubs. Wild populations were mature (average stem height in 2014: *Vaccinium* 16.4 cm, *Kalmia* 35.5 cm, and *Sibbaldiopsis* 5.9 cm) and transplanted with roots and soil intact.

We planted 10 individuals of each species from each elevation population in each garden, for a total of 90 plants per garden. Each garden was divided into a 3 × 6 grid of 18 60-cm × 60-cm blocks, and transplants were arranged five per block with a mix of all three species in each block. We labeled each plant with a random numeric code to blind observers to the source population of an individual during monitoring. The gardens were watered weekly for six weeks after transplanting in September 2013. We weeded gardens during the monitoring season and removed unmarked plants from the gardens to reduce competitive effects and make it easier to monitor the focal individuals. At each elevation, an additional 10 individuals of each species were flagged as controls, but not transplanted. The control plants were randomly selected from the same wild populations as our transplants, located within 5 m of the gardens. Light conditions were similar for the gardens and control plants.

### Abiotic measurements

We recorded hourly soil temperature (at a depth of 5 cm) and air temperature (2 cm above the soil) in each garden and in the control plots adjacent to each garden, because local temperature loggers are recommended over downscaled weather station data (Körner and Hiltbrunner, 2017). Each garden and control plot was outfitted with

a single air and soil temperature logger located in the center of the garden or control plot. Air temperature at 2 cm is just below “plant height” for our species; we modeled our logger set up on Kimball et al. (2014) from similar phenology research and plant communities in the White Mountains of New Hampshire; high winds at our summit site made taller temperature logger sticks untenable. HOBO temperature loggers (Onset, Bourne, Massachusetts, USA), which had been deployed at each site in November 2013, suffered water damage in March 2014 and their data was not recovered. We replaced these loggers with iButton dataloggers (model number DS1922L) housed in weatherproof capsules (model number DS9107); both the loggers and capsules are manufactured by Maxim Integrated, San Jose, California, USA in November 2014. In spring 2016, the iButton at the summit recording air temperature in the garden malfunctioned; all other iButtons recorded air and soil temperature from 2015 and 2016. These data were used to calculate mean March and April temperatures from each site and year for our analyses (Clark et al., 2013). We used mean spring temperatures rather than mean annual temperatures because early spring temperatures have been experimentally and observationally shown to be more highly correlated with spring phenology in temperate ecosystems (Miller-Rushing and Primack, 2008; Clark et al., 2013).

Soil moisture was measured in each garden and recorded during each spring monitoring day with a General (Secaucus New Jersey, USA) DSMM500 Precision Digital Soil Moisture Meter with a 203-mm probe. Soil moisture was recorded once per visit from the center of each garden; for our analyses, we used the mean soil moisture for each site and year.

### Phenology monitoring

The gardens were monitored twice per week from April through July in 2014, 2015, and 2016. At the beginning of the growing season (early April), we recorded the presence of snow and frozen soil at each garden.

We recorded leaf-out phenology for the gardens and control plots following the USA National Phenology Network's definitions



for phenophases (Denny et al., 2014). At each visit, we inspected each plant for signs of new leaves (*Kalmia* and *Sibbaldiopsis* have evergreen leaves). First leaf-out day (FLD) was recorded if a plant had at least one unfolded leaf with a visible petiole.

In May 2015, after leaf out was recorded for *Sibbaldiopsis*, the control plot of *Sibbaldiopsis* at the lowest elevation garden was accidentally destroyed in a prescribed fire facilitated by National Park Service staff. The control plots for *Kalmia* and *Vaccinium* at this site were unaffected, and the garden itself was covered with fire-proof fabric to reduce heating and prevent ashes from falling in the garden.

### Mortality

At the end of each monitoring season, we recorded mortality in the gardens and control plots. Over the course of the study, some plants appeared dead in 2014 or 2015, only to resprout in following years. For each combination of species, year, garden, and source population, our experimental design had a maximum  $n = 10$ ; ultimately our mean was  $n = 9.1$  plants per species-year-garden-source population, with a minimum of  $n = 6$  for the 2016 *Sibbaldiopsis tridentata* in the mid-elevation garden sourced from the low-elevation garden.

### Statistical analyses

We used Fisher's exact tests (`fisher.test`) to assess whether there were differences in mortality among species or among gardens. Then, within each species, we assessed whether there were differences in mortality among gardens. We also used Fisher's exact tests at the species level to assess patterns of mortality in individuals transplanted above or below their source population versus those that were locally transplanted. Here, we included plants that were marked 'dead' in one year and then resprouted in the subsequent year. However, each individual was only counted once, even if it was marked 'dead' in multiple years. By this metric, 16 *Kalmia angustifolia*, 4 *Vaccinium angustifolium*, and 16 *Sibbaldiopsis tridentata* were excluded from monitoring for at least one year because of perceived mortality.

We assessed the effect of our experimental transplanting on leaf-out phenology by comparing the mean FLD for local transplants (sourced from the same elevation as each garden) to the mean FLD of the flagged control individuals located outside of the gardens at each site ( $n = 10$  local transplants per species per garden and  $n = 10$  controls per species per garden site, before accounting for mortality). These local transplants and controls were from the same source population. We used Welch two sample t-tests (`t.test`) for each combination of species, elevation (low, mid, summit), and year (2014, 2015, 2016) for a total of nine garden-year combinations.

We evaluated the environmental differences among gardens with ANOVA for mean March and April air temperatures ( $n = 2926$  hourly temperature readings per March–April period each year) and mean soil moisture ( $n = 15$ – $20$  measurements per garden per year depending on early season snow and frost conditions) for each growing season. We then used Tukey multiple comparisons of means (Tukey's Honestly Significant Difference [HSD]) for post-hoc comparisons; we report the  $P$  adj from Tukey HSD, which corrects for multiple tests. Within each elevation, we used Welch two sample t-tests to assess the differences between March and April air temperatures in the gardens and in the control plots for each year.

We compared the population-level differences in leaf-out phenology for our three species with ANOVA for our reciprocal transplants. The response variable in this set of analyses was FLD, and the main effects were the categorical variables site (garden), source, and year, as well as all two-way and three-way interactions. This analysis allowed us to utilize all three years of phenology data (2014, 2015, and 2016), even when temperature data were missing (*Kalmia*  $n = 235$ , *Vaccinium*  $n = 264$ , *Sibbaldiopsis*  $n = 242$ ). The site variable explained variation caused by the local microclimate of each garden, and represented the importance of local spring climate in cueing leaf out. The source variable explained variation caused by population-level, local adaptations that influenced leaf out. We ran separate ANOVA tests for each species, then used Akaike information criterion (AIC) backwards selection (step) to determine the best model.

We calculated the relationship between spring temperature and FLD for each source population with linear models; this facilitated comparisons of phenological plasticity (days/°C) among source populations ( $n = 30$  plants from each source population before accounting for mortality) of the same species. This analysis was limited to the two years (2015 and 2016) with air temperature data at the gardens, and excluded the summit garden in 2016 ( $n = 5$  mean spring temperature values).

Finally, we compared the linear regressions of phenological plasticity (days/°C) found in this garden experiment with local field observations that were recorded during the same field seasons in Acadia National Park (McDonough MacKenzie, unpublished data). For this analysis, we calculated the days/°C advance of FLD for our three species in the common gardens and compared these results to the days/°C calculated from field observations along three elevational gradients on Cadillac, Sargent, and Pemetic mountains (McDonough MacKenzie, unpublished data). To calculate the sensitivity from our garden experiment, we considered the subset of local transplants and control plants from years and sites with mean spring temperature data, excluding individuals transplanted to new elevations (*Kalmia*  $n = 103$ , *Vaccinium*  $n = 108$ , *Sibbaldiopsis*  $n = 100$ ). The field observations were a part of a separate study during 2014–2016 (*Kalmia*  $n = 43$ , *Vaccinium*  $n = 71$ , *Sibbaldiopsis*  $n = 60$ ). We ran a generalized linear model (GLM) for each species with a dummy variable for observational versus garden data; a model with a significant interaction term for data type and spring temperatures would provide evidence for different temperature responses between the gardens and observational datasets.

All analyses were performed in R version 3.3.3 (R Core Team, 2017).

## RESULTS

### Mortality as a result of transplanting

The mortality rate among transplants was low and evenly distributed across sites and source populations. Over the three years of this experiment, 24 of the original 270 transplanted individuals died: 12 *Kalmia*, 2 *Vaccinium*, and 10 *Sibbaldiopsis* (Appendix S1; see the Supplemental Data with this article). Mortality varied by species ( $P = 0.014$ ) with *Vaccinium* experiencing lower mortality than *Kalmia* and *Sibbaldiopsis*. In contrast, mortality did not vary among gardens ( $P = 0.098$ ) across all species. Within *Kalmia* and *Sibbaldiopsis*, mortality did not vary by garden ( $P = 0.084$  and  $P = 0.328$ , respectively) or source population ( $P = 0.925$  and  $P = 0.070$ ,

respectively). That is, there was no detectable difference in mortality rates among gardens or where the plants came from.

We found no difference in perceived mortality among plants transplanted to higher elevations, lower elevations, or their local (same elevation) gardens (Appendix S2, *Kalmia*  $P = 0.47$ , *Vaccinium*  $P = 1$ , *Sibbaldiopsis*  $P = 0.16$ ).

### Effect of transplanting on leaf out

The effect of transplanting on FLD phenology varied by species, site, and year, however the direction of bias (gardens or controls leafing out first) was not consistent. There was no systematic effect of transplantation on leaf out phenology for any of our study species (Table 1). For the years and gardens with temperature data, the gardens experienced significantly warmer spring air temperatures (between 0.6°C and 1.3°C warmer) than the control plots ( $P < 0.001$ ) in four garden-year combinations (2015 Low-Elevation  $t = -10.42$ ,  $df = 1783$ ,  $p < 0.001$ ; 2015 Summit  $t = -11.60$ ,  $df = 1544.4$ ,  $p < 0.001$ ; 2016 Low-Elevation  $t = -4.23$ ,  $df = 1960.8$ ,  $p < 0.001$ ; 2016 Mid-Elevation  $t = -3.67$ ,  $df = 2707$ ,  $p < 0.001$ ). At the mid-elevation garden in 2015, the control plot was significantly warmer (0.4 °C warmer) than the garden ( $t = 3.66$ ,  $df = 2876.7$ ,  $p < 0.001$ ; Table 1).

*Vaccinium* FLD in the gardens was significantly later than in the control plots in four garden-years. In 2014, this was true in all three elevations (Low Elevation  $t = -3.43$ ,  $df = 8.48$ ,  $p = 0.008$ ; Mid-Elevation  $t = -3.83$ ,  $df = 10.562$ ,  $p = 0.003$ ; Summit  $t = -2.79$ ,  $df = 11.44$ ,  $p = 0.017$ ), as well as 2015 at the Mid-Elevation site ( $t = -2.82$ ,  $df = 11.72$ ,  $p = 0.016$ ). *Vaccinium* never leafed out significantly earlier than the control plots, however in five of the nine garden-years there was no significant difference between control and garden FLD (Table 1).

**TABLE 1.** Pairwise comparisons of temperature and leaf out in gardens and control plots and among locally transplanted individuals.

Species	Year	Garden Elevation		
		Low	Mid	Summit
<i>Kalmia angustifolia</i>	2014		•	
	2015		*	*
	2016	*	*	
<i>Vaccinium angustifolium</i>	2014	•	•	•
	2015		•	
	2016			
<i>Sibbaldiopsis tridentata</i>	2014			
	2015			*
	2016	n/a		

Notes: In all garden-years for which we have temperature data, there was a significant difference between the mean spring air temperatures at the control plots and the gardens at each site ( $P < 0.001$ ). The grey shading indicated warmer temperature in the gardens, while the blue shading indicated warmer temperatures in the control plots. In locations where leaf out was significantly different ( $P < 0.05$ ) between controls and gardens, • = Control earlier leaf out, \* = Garden earlier leaf out.

**TABLE 2.** Spring environmental conditions at each garden.

Site	2014	2015			2016		
	Soil moisture (%)	Air temp (°C)	Soil temp (°C)	Soil moisture (%)	Air temp (°C)	Soil temp (°C)	Soil moisture (%)
Low elevation	11.9	4.6	2.3	9.2	4.3	7.0	9.1
Mid elevation	11.3	1.0	1.2	10.2	3.7	7.3	9.6
Summit	9.0	0.6	0.0	8.0	n/a	4.3	8.3

Notes: Air Temp and Soil Temp reflect mean March and April temperatures (°C) from aboveground and belowground iButtons; Soil moisture was averaged across the monitoring season 10 April–30 June), beginning when the gardens thaw. There is no temperature data from 2014 because the HOBs malfunctioned; the summit garden air temperature iButton also malfunctioned in 2016.

Among *Kalmia*, the garden FLD was significantly different from control FLD in five of nine garden-years. At the mid-elevation garden, FLD was significantly different in all three years (2014:  $t = -4.42$ ,  $df = 17.95$ ,  $p < 0.001$ ; 2015:  $t = 8.12$ ,  $df = 13.88$ ,  $p < 0.001$ ; 2016:  $t = 4.58$ ,  $df = 9$ ,  $p = 0.001$ ), but in 2014 the controls FLD was earlier than the garden plants, while the reverse occurred in 2015 and 2016 (Table 1). FLD was also significantly earlier in the gardens in 2015 at the summit ( $t = 4.28$ ,  $df = 8.52$ ,  $p = 0.002$ ) and 2016 at the low elevation site ( $t = 3.19$ ,  $df = 13.65$ ,  $p = 0.007$ ).

Among *Sibbaldiopsis*, the garden FLD was only significantly different from control FLD in one of eight garden-years; in 2015, the garden leafed out earlier than the control plot at the summit ( $t = 7.69$ ,  $df = 9$ ,  $p < 0.001$ ; Table 1).

### Environmental differences between elevations

Mean March–April air temperatures across the control plots adjacent to the gardens varied by 2.2°C in 2015 (warmest at lowest elevation and coolest at the summit) and 1.9°C in 2016 (warmest at summit and coolest at middle elevation; a pattern that does not match the garden air temperature data for low and mid elevations from 2016, Table 2).

In 2015, mean spring air temperatures were significantly different among the three gardens (ANOVA,  $F_{2,4386} = 255.06$ ,  $P < 0.0001$ ). Post-hoc Tukey's HSD tests for multiple comparisons revealed that only the mid-elevation garden and the summit garden were not significantly different from each other ( $P_{adj} = 0.083$ ) (Table 2). In 2016, mean spring air temperatures were significantly different between the low-elevation and mid-elevation gardens (the iButton recording air temperature in the summit garden malfunctioned) ( $t$ -test,  $t = 8.58$ ,  $df = 1462$ ,  $P < 0.001$ ) (Table 2).

Mean spring soil moisture varied by year and site: the summit was consistently drier than the other gardens. The soil thawed at all three gardens by 29 April in 2014. In 2015, the low elevation garden was thawed by 24 April, mid-elevation by 28 April, and summit by 1 May. In 2016, the low elevation was thawed by 14 April and the mid-elevation and summit gardens thawed by 18 April. In 2015, the summit garden was not snow free until 1 May, and the summit control plants were still snowbound through 12 May. In 2014 and 2016, all gardens and control plots were snow free by 18 April. At the summit garden, soil moisture was not significantly related to year (ANOVA,  $F_{2,50} = 2.544$ ,  $P = 0.089$ ) (Table 2). At the mid-elevation garden, soil moisture was significantly related to year (ANOVA,  $F_{2,51} = 5.051$ ,  $P = 0.01$ ). Post-hoc Tukey's HSD tests for multiple comparisons revealed that at this garden, soil moisture was significantly different between 2014 and 2016 ( $P_{adj} = 0.007$ ) (Table 2). At the low-elevation garden, soil moisture was significantly related to year (ANOVA  $F_{2,51} = 13.12$ ,  $P < 0.001$ ). Post-hoc Tukey's HSD tests for multiple comparisons revealed that at this garden, soil moisture was significantly

different between 2014 and 2015 ( $P_{\text{adj}} < 0.001$ ), and 2014 and 2016 ( $P_{\text{adj}} < 0.001$ ) (Table 2).

In all three years, soil moisture varied by garden (ANOVAS, 2014:  $F_{2,44} = 9.479$ ,  $P = 0.0003$ ; 2015:  $F_{2,51} = 6.7$ ,  $P = 0.002$ ; 2016:  $F_{2,57} = 8.13$ ,  $P = 0.0007$ ). These differences are driven by low soil moisture at the summit garden. Post-hoc Tukey's HSD tests for multiple comparisons revealed that in 2014, the low-elevation and mid-elevation gardens were not significantly different from each other ( $P_{\text{adj}} = 0.67$ ); in 2015, the low-elevation garden was not significantly different from the mid-elevation ( $P_{\text{adj}} = 0.17$ ) or summit ( $P_{\text{adj}} = 0.15$ ) gardens; in 2016, the low-elevation and mid-elevation gardens were not significantly different from each other ( $P_{\text{adj}} = 0.30$ ) (Table 2).

### Relative effects of environment and source population on leaf-out phenology

For *Kalmia*, *Vaccinium*, and *Sibbaldiopsis*, the garden site and year were the most important factors related to FLD (Table 3). Across all species and years, the low-elevation garden leafed out earlier than the mid-elevation and summit gardens. Post-hoc Tukey HSD comparisons from all three of our species models revealed that FLD at the summit gardens was consistently significantly ( $P_{\text{adj}} < 0.05$ ) later than the mid-elevation (*Kalmia* 2.4 days later, *Vaccinium* 7.2 days later, and *Sibbaldiopsis* 4.2 days later) and low-elevation gardens (*Kalmia* 4.3 days later, *Vaccinium* 7.3 days later, and *Sibbaldiopsis* 6.0 days later).

Comparing AIC among the ANOVA models also revealed that FLD for each species was best explained by a different combination of factors and interaction effects (Appendix S3).

For *Kalmia*, the full model with all interactions provided the lowest AIC score. While the source population on its own was not a significant factor, the two-way interaction between Source and Year and the three-way interaction between Source, Year, and Garden were significant (Appendix S3). There was no trend in source population and order of leaf out: transplants from the low-elevation source population leafed out, on average, earlier than other source populations across all three gardens in 2014, but later than other source populations across all three gardens in 2015, and earlier in 2016 at two of the three gardens. Post-hoc Tukey HSD tests for multiple comparisons within each year found only one significant difference in leaf-out dates by source population: in 2014, the low-elevation source population was 5.5 days earlier than the summit source population ( $P_{\text{adj}} = 0.002$ ). In 2015 and 2016, there were no significant differences in leaf-out dates between source populations.

For *Vaccinium*, the best model included the three main terms and the interaction between year and garden (Appendix S3). Post-hoc

Tukey's HSD tests for multiple comparisons revealed that the low-elevation source population leafed out 2.7 days earlier than the mid-elevation source population ( $P_{\text{adj}} = 0.02$ ), but there was no significant difference between the summit and mid-elevation or summit and low-elevation source populations. As in *Kalmia*, there was no trend in source population and order of leaf out: transplants from the summit source population leafed out, on average, earlier than other source populations in two out of three gardens in 2014, while transplants from the low-elevation source population leafed out earlier than other source populations in all three gardens in both 2015 and 2016.

For *Sibbaldiopsis*, like *Kalmia*, source population on its own was not a significant factor, although the interaction effect between Source and Garden was significant (Appendix S3). Post-hoc Tukey's HSD tests for multiple comparisons revealed that the combination of summit source population at the summit garden was significantly late to leaf out compared to other garden-source population combinations; the low-elevation source population at the mid-elevation garden was also relatively late to leaf out. The mid-elevation source population at the low-elevation garden leafed out significantly earlier than both of these garden-source population combinations. As in *Kalmia* and *Vaccinium*, there was no trend in source population and order of leaf out.

The best model for each species explained more than one-third to more than one-half of the variation in FLD recorded (*Kalmia*  $R^2 = 0.53$ ; *Vaccinium*  $R^2 = 0.41$ , *Sibbaldiopsis*  $R^2 = 0.37$ ).

### Phenological sensitivity of the source populations of each species

Only two source populations (*Kalmia* mid-elevation, *Vaccinium* mid-elevation) showed significant relationships between FLD and mean March–April temperatures in the common gardens, as determined by linear regression (Figure 2). *Kalmia* from mid-elevation advanced 1.1 days/°C in the gardens, while *Vaccinium* from mid-elevation advanced 2.2 days/°C in the gardens. However, when the populations for each species were grouped, the species-level FLD were strongly related to mean March–April temperatures (*Kalmia*  $F_{1,13} = 10.18$ ,  $p < 0.001$ , *Vaccinium*  $F_{1,13} = 8.637$ ,  $p < 0.001$ , *Sibbaldiopsis*  $F_{1,13} = 22.77$ ,  $p < 0.001$ ) (Table 4). The population-level analysis was likely limited by the small sample size ( $n = 5$  garden-year combinations for spring temperature data), and the range of temperatures experienced during the study (0.6–4.6°C).

### Comparison of phenological sensitivity in common garden and field observations

In our common garden experiment, we pooled the local transplant and control plot data to calculate species-level FLD

**TABLE 3.** ANOVA results for each species for the response of leaf out to year (2014, 2015, 2016), garden (low, mid, summit elevations), and source populations (low, mid, summit elevations), and their respective interactions.

	<i>Kalmia angustifolia</i>			<i>Vaccinium angustifolium</i>			<i>Sibbaldiopsis tridentata</i>		
	df	F	P	df	F	P	df	F	P
Year	2	75.80	<0.001	2	43.26	<0.001	2	45.95	<0.001
Garden	2	13.86	<0.001	2	34.41	<0.001	2	12.57	<0.001
Source	2	2.33	0.100	2	4.18	0.017	2	2.63	0.074
Year * Garden	4	2.62	0.036	4	2.90	0.023	4	0.50	0.734
Year * Source	4	4.89	<0.001	4	1.26	0.286	4	1.40	0.236
Garden * Source	4	1.68	0.157	4	1.35	0.251	4	2.79	0.027
Year * Garden * Source	8	2.07	0.041	8	1.24	0.274	8	1.24	0.277

Note: Significant P-values are indicated in bold.

sensitivity to spring temperatures. We found that *Sibbaldiopsis* ( $-3.5$  days/ $^{\circ}\text{C}$ ), *Vaccinium* ( $-2.3$  days/ $^{\circ}\text{C}$ ), and *Kalmia* ( $-1.2$  days/ $^{\circ}\text{C}$ ) are all advancing FLD; all linear regressions were significant ( $P < 0.05$ ) (Table 4). We compared this to the sensitivity of each species calculated from observational monitoring along transects of wild-occurring plants in Acadia National Park. We used species-level GLMs of all FLD data from Acadia to further investigate this comparison. The GLMs for *Kalmia* and *Vaccinium* included significant interaction terms between the type of data (observational vs. experimental) and the mean spring temperatures, indicating different temperature responses between garden plants and plants along observational transects (Table 4). Although the limited data from two years of garden monitoring may have reduced the utility of this comparison, there is strong agreement in the direction (i.e., advancing leaf out in warmer temperatures) of phenological response in Acadia National Park across all three species and in both experimental and observational studies.

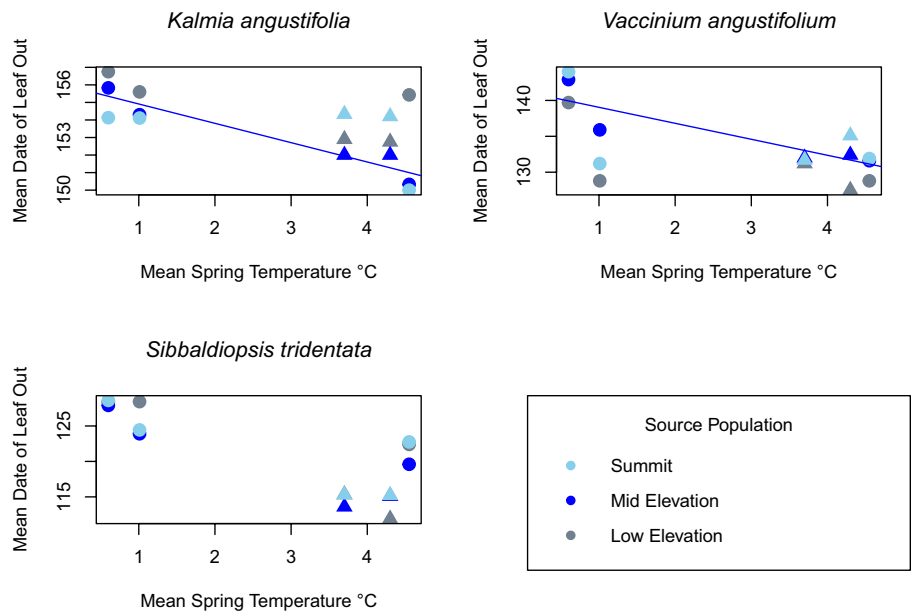
## DISCUSSION

Transplanting three perennial species across a 350-m elevation gradient led to shifts in the timing of first leaf-out phenology associated with garden microclimates. The source populations for these transplants were relatively unimportant in determining leaf-out phenology. For all three species, leaf out occurred earlier in response to warmer springs. We saw this general pattern in our transplant gardens as the plants in the warmer low-elevation garden leafed out before the cooler summit garden in all three years of our study.

### Utility and limitations of experimental design

Our common garden experiment demonstrated the utility of reciprocal transplants of adult plants to study the environmental and genetic components responsible for leaf-out phenology in two ericaceous shrubs and one cinquefoil. We report low rates of mortality (13.3% of transplants for *Kalmia*, 2.2% for *Vaccinium*, 11.1% for *Sibbaldiopsis*) despite sparse scientific literature to identify species robust to transplantation, and a dearth of standard practices for transplanting in common garden methods. In some cases, plants that appeared to be dead later resprouted and could be included in the study (Appendices S1, S2).

Our study design also compared local garden transplants to unmanipulated control plants adjacent to our common gardens. Despite some differences in soils and temperature between plants growing in gardens and control areas, we did not detect a systematic effect of transplantation on leaf-out phenology for any of our study species. These types of transplant experiments provide a time-efficient and cost-effective alternative for studies on the effects of microclimate and climatic variation on the phenology of long-lived



**FIGURE 2.** Relationships between mean spring temperatures (March and April) and leaf out for the three source populations of the three species. Mean spring temperatures correspond to the mean March and April temperatures at each garden in each year of monitoring (Circles = 2015, Triangles = 2016) with recorded temperature data. The summit garden from 2016 is excluded here, because of a broken iButton at that site. Within each garden, we show the mean date of leaf out for each source population. Regression lines are included for the two source populations (mid-elevation populations of both *Kalmia* and *Vaccinium*) where we found statistically significant relationships ( $P < 0.05$ ) between leaf-out date and temperature. *Kalmia* from mid-elevation advanced leaf out 1.1 days/ $^{\circ}\text{C}$  in the gardens ( $y = -1.1x + 156.0$ ,  $F_{1,3} = 32.94$ ,  $P = 0.012$ ), while *Vaccinium* from mid-elevation advanced leaf out 2.2 days/ $^{\circ}\text{C}$  in the gardens ( $y = -2.2x + 141.3$ ,  $F_{1,3} = 10.37$ ,  $P = 0.049$ ).

perennials (Reader, 1982; Weber and Schmid, 1998; Stinson, 2005; Vitasse et al., 2010; Alexander et al., 2015; Ostaff et al., 2015).

### Local adaptation vs. microclimate

We examined the potential for local adaptations in phenology between populations located across a 350-m elevation gradient. We found that transplants leafed out earlier in the low-elevation garden and later in the summit garden regardless of source population, indicating the importance of local microclimate for leaf-out phenology.

**TABLE 4.** Regression coefficients (days/ $^{\circ}\text{C}$ ) for each species calculated from the garden data and field observations and the interaction coefficient for data type and spring temperature from the generalized linear model for all observational and experimental FLD data. Significant interaction terms indicate a different temperature response between the observational and experimental studies.

Species	Sensitivity (days/ $^{\circ}\text{C}$ ) for garden FLD	Sensitivity (days/ $^{\circ}\text{C}$ ) for field FLD	Data Type*Temperature interaction coefficient from GLM
<i>Sibbaldiopsis</i>	$-3.5$ (0.3)	$-2.3$ (0.8)	1.2
<i>Vaccinium</i>	$-2.3$ (0.4)	$-4.3$ (0.7)	$-2.0$
<i>Kalmia</i>	$-1.2$ (0.3)	$-3.3$ (0.4)	$-2.3$

Notes: All linear regressions were significant ( $P < 0.05$ ). Spring temperatures (mean March and April temperatures) recorded by iButtons in the gardens and control plots (in 2015 and 2016; only 2015 for the summit garden), and by HOBO pendant loggers along the field observation transects (2014–2016). Standard error for regression coefficients is reported in parentheses. Significant interaction coefficients from the GLM are noted in bold; observational data was coded as '1' and experimental data was coded as '0' in this analysis.



At the species-level, we know FLD for *Kalmia*, *Vaccinium*, and *Sibbaldiopsis* are responsive to temperature: the three species in this experiment were also monitored in observational transects in Acadia National Park, where FLD advanced at 3.3, 4.3, and 2.3 days/°C for *Kalmia*, *Vaccinium*, and *Sibbaldiopsis*, respectively (Table 4). In our common garden study, we did not find evidence for intraspecific (population-level) differences in FLD phenology for these three species, suggesting that they do not have local adaptation in FLD response to spring temperatures. Rather, the microclimate at garden sites and year-to-year variability were the most important factors driving leaf-out phenology for all three species. Species varied in which models best described the factors determining FLD, but the role of source population was always eclipsed by the importance of garden site (Table 3).

Leaf-out phenology in our gardens was most responsive to the garden and year, both factors that represented environmental conditions. The three gardens varied in soil moisture, soil temperature, and air temperature, while our experimental design used potting soil to control for differences in soil and nutrient availability at each site (Table 2). In 2015, it is likely that the anomalous snowpack affected phenology, especially at the summit site. While our local temperature records were limited, we can see the strong effect of environmental factors cuing leaf-out phenology through the importance of garden and year as factors in every species' model (Table 3).

Other common garden experiments examining intraspecific variation in spring phenological response to climate at local or regional scales have highlighted the importance of local climate. For example, Vitasse et al. (2013) found that the significance of environmental effects, genetic effects, and interaction effects varied by species for seven deciduous trees in the Swiss Alps. As in our experiment, elevation (microclimate) was always a significant factor, but the importance of genetic effects (local adaptation) and interactions among factors differed from species to species; overall, environmental effects tended to be much stronger than genetic effects (Vitasse et al., 2013). In the Rocky Mountains, local microclimate determined the growth of *Potentilla diversifolia* transplanted into low-elevation (warmer) conditions regardless of the elevation of the source population, just as the local microclimate determined leaf-out phenology in our gardens (Stinson, 2005). In the Pyrenees, as in our study, warmer temperatures at low-elevation gardens advanced leaf unfolding dates in temperate tree species with no difference in the magnitude of phenological plasticity among populations from different elevations (Vitasse et al., 2010).

For common garden studies that have reported genetic effects on intraspecific variation in phenology, populations from colder source populations (higher elevation or higher latitude) were nearly always less sensitive to temperature cues than populations from warmer source populations. This was true for leaf unfolding in the Swiss Alps (Vitasse et al., 2013; Körner et al., 2016), budding and flowering in the Swiss Alps (Gugger et al., 2015), and leaf unfolding in the Pyrenees (Vitasse et al., 2009). Spruce trees (*Picea mariana*) in eastern Canada showed the opposite pattern in budbreak—trees from latitudes with warmer annual temperatures had later budbreaks than trees from latitudes with cooler annual temperatures (Rossi and Isabel, 2016). In observational studies with no experimental component, both Prevey et al. (2017) and Panchen and Gorelick (2016) report that high latitude plants have greater temperature sensitivity in their leaf-out and flowering phenologies than conspecific populations from lower latitudes (Panchen and Gorelick, 2016; Prevey et al., 2017). In contrast to these studies, we

found no consistent differences in leaf-out phenology across populations from different elevations.

Our comparison of the phenological response to temperature across source populations appeared to be limited by sample size of individual plants and a relatively small range of spring temperatures experienced across the sites and years. A similar analysis in the Swiss Alps found significant relationships between spring temperatures and leaf unfolding for all source populations of seven studied tree species, but the mean temperatures at these gardens ranged from 4–15°C (Vitasse et al., 2013), compared to 0.6–4.6°C in our study.

The species we examined are common across all elevations included in our study, and it is possible that there is strong genetic mixing along the 350-m elevational gradient, and that the effects of any selection for slower phenological development at the summit is weakened by this genetic mixing. It is also possible that selection for slower phenological development on the summit of Cadillac Mountain is weak, possibly because interannual variation in temperature (and late frosts) is strong throughout the elevational gradient. Most other elevation-gradient common garden studies tend to be located on much taller mountains—e.g., the Alps, Pyrenees, and Rocky Mountains—which allow for greater differences in climate conditions and more genetic isolation among populations. The change in altitude for transplants among these studies ranged from 950 m (Gugger et al., 2015) to 1500 m (Vitasse et al., 2010) between the lowest and highest sites. The Vitasse et al. (2010) experiment included five gardens along an elevational gradient from 100–1600 m above sea level; each step between gardens in that study is equivalent to the entire range of elevation in our Acadia gardens.

### Ecological and conservation implications, challenges, and future studies

If the lack of local adaptation (at relatively local scales) in phenological response to climate is widespread, it would suggest that studies of phenology at a particular location could be generalized over a reasonable scale. However, more research is needed to determine the scale at which local adaptation does become meaningful.

We had expected to find differences in leaf-out phenology between source populations. However, our results suggest that there may be high levels of genetic mixing along Cadillac Mountain's environmental gradients. Here, we may have a large pool of genetic variation and evolutionary potential, which could help species evolve in response to changing climate conditions. This also implies that conservation managers may not need to worry about exactly where they source plants (at least common species, like those included in our study) for restoration projects as long as they are reasonably local. For example, a restoration project on the summit of Cadillac Mountain—which is currently happening—could source plants from lower elevations with minimal effects on leaf-out phenology and mortality.

Comparing results across common garden studies is currently limited by the lack of standard practices. Even within general approaches (i.e., seed collection or transplanting mature individuals), a range of methods is applied at each step: potted individuals vs. arrays planted directly into soil, or local soil prepared manually (tilling) vs. commercial potting soil. These variable methods make it even more important for common garden experiments to be placed in a context of observational studies (Wilczek et al., 2010; Woolbright et al., 2014; Elmendorf et al., 2015). In Acadia National Park, we used observations of control (not transplanted) plants and



recent field observations of leaf-out phenology to provide this context for our common garden experiment. Although methodological constraints currently limit our ability to quantitatively integrate information on inter- and intraspecific variation in phenological responses across studies and sites, broad patterns illustrate the potential for variation across elevation and latitudinal gradients. With extended longevity of common garden experiments and standard protocols for this methodology, future research on local adaptation to climate-driven changes in phenology will provide new insights into the effects of climate change on plants.

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## DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.7s6vh7p> (McDonough MacKenzie et al., 2018).

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

## LITERATURE CITED

- Alexander, J. M., J. M. Diez, and J. M. Levine. 2015. Novel competitors shape species' responses to climate change. *Nature* 525: 515–518.
- Augsburger, C. K. 2009. Spring 2007 warmth and frost: phenology, damage and refoiling in a temperate deciduous forest. *Functional Ecology* 23: 1031–1039.
- 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 of the United States of America* 111: 4916–4921.
- Clark, J. S., J. Melillo, J. Mohan, and C. Salk. 2013. The seasonal timing of warming that controls onset of the growing season. *Global Change Biology* 20: 1136–1145.
- Clausen, J., and W. M. Hiesey. 1958. Experimental studies on the nature of species. IV. Genetic structure of ecological races. Carnegie Institution of Washington, Washington, D.C.
- 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: 1765–1771.
- Denny, E. G., K. L. Gerst, A. J. Miller-Rushing, G. L. Tierney, T. M. Crimmins, C. A. F. Enquist, P. Guertin, et al. 2014. Standardized phenology monitoring methods to track plant and animal activity for science and resource management applications. *International Journal of Biometeorology* 58: 591–601.
- Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, A. M. Fosaa, W. A. Gould, L. Hermanutz, A. Hofgaard, et al. 2015. Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. *Proceedings of the National Academy of Sciences* 112: 448–452.
- Greene, C. W., L. L. Gregory, G. H. Mittelhauser, S. C. Rooney, and J. E. Weber. 2005. Vascular flora of the Acadia National Park region, Maine. *Rhodora* 107: 117–185.
- Gugger, S., H. Kesselring, J. Stöcklin, and E. Hamann. 2015. Lower plasticity exhibited by high- versus mid-elevation species in their phenological responses to manipulated temperature and drought. *Annals of Botany* 116: 953–962.
- Harris, T. B., N. Rajakaruna, S. J. Nelson, and P. D. Vaux. 2012. Stressors and threats to the flora of Acadia National Park, Maine: Current knowledge, information gaps, and future directions 1. *The Journal of the Torrey Botanical Society* 139: 323–344.
- Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89: 353–362.
- Kimball, K. D., M. L. Davis, D. M. Weihrauch, G. L. D. Murray, and K. Rancourt. 2014. Limited alpine climatic warming and modeled phenology advancement for three alpine species in the Northeast United States. *American Journal of Botany* 101: 1437–1446.
- Körner, C., and D. Basler. 2010. Response—Warming, Photoperiods, and Tree Phenology. *Science* 329: 278.
- Körner, C., and E. Hiltbrunner. 2017. The 90 ways to describe plant temperature. *Perspectives in Plant Ecology, Evolution and Systematics* 30: 16–21.
- Körner, C., D. Basler, G. Hoch, C. Kollas, A. Lenz, C. F. Randin, Y. Vitasse, and N. E. Zimmermann. 2016. Where, why and how? Explaining the low-temperature range limits of temperate tree species M. Turnbull [ed.], *Journal of Ecology* 104: 1076–1088.
- Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* 20: 170–182.
- McDonough MacKenzie, C., R. B. Primack, and A. J. Miller-Rushing. 2018. Data from: Local environment, not local adaptation, drives leaf-out phenology in common gardens along an elevational gradient in Acadia National Park, Maine. Dryad Digital Repository. <https://doi.org/10.5061/dryad.7s6vh7p>.
- McGee, C. E. 1974. Elevation of Seed Sources and Planting Sites Affects Phenology and Development of Red Oak Seedlings. *Forest Science* 20: 160–164.
- Memmott, J., P. G. Craze, N. M. Waser, and M. V. Price. 2007. Global warming and the disruption of plant–pollinator interactions. *Ecology Letters* 10: 710–717.
- Menzel, A., T. H. Sparks, N. Estrella, and E. Koch. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12: 1969–1976.
- Miller-Rushing, A. J., and R. B. Primack. 2008. Global warming and flowering times in Thoreau's Concord: a community perspective. *Ecology* 89: 332–341.
- Mueller, L., C. Beierkuhnlein, G. Aas, A. Jentsch, A. H. Schweiger, C. Zohner, and J. Kreyling. 2016. Distribution ranges and spring phenology explain late frost sensitivity in 170 woody plants from the Northern Hemisphere. *Global Ecology and Biogeography* 25: 1061–1071.
- Olsson, K., and J. Agren. 2002. Latitudinal population differentiation in phenology, life history and flower morphology in the perennial herb *Lythrum salicaria*. *Journal of Evolutionary Biology* 15: 983–996.
- Ostaf, D. P., A. Mosseler, R. C. Johns, S. Javorek, J. Klymko, and J. S. Ascher. 2015. Willows (*Salix* spp.) as pollen and nectar sources for sustaining fruit and berry pollinating insects. *Canadian Journal of Plant Science* 95: 505–516.
- Panchen, Z. A., and R. Gorelick. 2016. Canadian Arctic Archipelago Conspecifics Flower Earlier in the High Arctic than the Mid-Arctic. *International Journal of Plant Sciences* 177: 661–670.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.

- Polgar, C., A. Gallinat, and R. B. Primack. 2014. Drivers of leaf-out phenology and their implications for species invasions: insights from Thoreau's Concord. *New Phytologist* 202: 106–115.
- Polgar, C. A., and R. B. Primack. 2011. Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist* 191: 926–941.
- Prev  y, J., M. Vellend, N. R  ger, R. D. Hollister, A. D. Bjorkman, I. H. Myers-Smith, S. C. Elmendorf, et al. 2017. Greater temperature sensitivity of plant phenology at colder sites: implications for convergence across northern latitudes. *Global Change Biology* 23: 2660–2671.
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Reader, R. J. 1982. Variation in the Flowering Date of Transplanted Ericaceous Shrubs in Relation to Their Flowering Season. *Journal of Biogeography* 9: 397.
- Richardson, A. D., T. F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag, and M. Toomey. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* 169: 156–173.
- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57–60.
- Rossi, S., and N. Isabel. 2016. Bud break responds more strongly to daytime than night-time temperature under asymmetric experimental warming. *Global Change Biology* 23: 446–454.
- Sakurai, A., and K. Takahashi. 2016. Flowering phenology and reproduction of the *Solidago virgaurea* L. complex along an elevational gradient on Mt Norikura, central Japan. *Plant Species Biology* 32: 270–278.
- Stinson, K. A. 2005. Effects of Snowmelt Timing and Neighbor Density on the Altitudinal Distribution of *Potentilla diversifolia* in Western Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research* 37: 379–386.
- Vitasse, Y., C. C. Bresson, A. Kremer, R. Michalet, and S. Delzon. 2010. Quantifying phenological plasticity to temperature in two temperate tree species. *Functional Ecology* 24: 1211–1218.
- Vitasse, Y., S. Delzon, C. C. Bresson, R. Michalet, and A. Kremer. 2009. Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Canadian Journal of Forest Research* 39: 1259–1269.
- Vitasse, Y., G. Hoch, C. F. Randin, A. Lenz, C. Kollas, J. F. Scheepens, and C. K  rner. 2013. Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species. *Oecologia* 171: 663–678.
- Vitasse, Y., C. Signarbieux, and Y. H. Fu. 2017. Global warming leads to more uniform spring phenology across elevations. *Proceedings of the National Academy of Sciences* 9: 201717342–5.
- Weber, E., and B. Schmid. 1998. Latitudinal Population Differentiation in Two Species of *Solidago* (Asteraceae) Introduced into Europe. *American Journal of Botany* 85: 1110–1121.
- Wilczek, A. M., L. T. Burghardt, A. R. Cobb, M. D. Cooper, S. M. Welch, and J. Schmitt. 2010. Genetic and physiological bases for phenological responses to current and predicted climates. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 365: 3129–3147.
- 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* 105: 17029–17033.
- Wolkovich, E. M., B. I. Cook, J. M. Allen, and T. M. Crimmins. 2012. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485: 494.
- Woolbright, S. A., T. G. Whitham, C. A. Gehring, G. J. Allan, and J. K. Bailey. 2014. Climate relicts and their associated communities as natural ecology and evolution laboratories. *Trends in Ecology & Evolution* 29: 406–416.