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VARIATION IN THE IMPACT OF CLIMATE CHANGE ON FLOWERING PHENOLOGY AND ABUNDANCE: AN EXAMINATION OF TWO PAIRS OF CLOSELY RELATED WILDFLOWER SPECIES[1]

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Variability in plant phenological responses to climate change is likely to lead to changes in many ecological relationships as the climate continues to change. We used a 34-yr record of flowering times and flower abundance for four species (two *Delphinium* [Ranunculaceae] species and two *Mertensia* [Boraginaceae] species) from a subalpine plant community near the Rocky Mountain Biological Laboratory to test the hypothesis that the phenologies of early-flowering species change more rapidly in response to climatological and other abiotic cues than do late-flowering species, a pattern previously found in plant communities in North America and Europe. We also explored a related hypothesis, that flower abundance of late-flowering species is more responsive to changes in climate than that of early-flowering species. The *Delphinium* species did not support these hypotheses, but the *Mertensia* species did. The difference between the peak flowering times of the early and late *Mertensia* species is expanding, leading to a period of diminished resources for pollinators that specialize on this genus. *Mertensia ciliata* populations are already severely declining in our study area, possibly as a result of earlier snowmelt. Together, these results show that the reported differences between early- and late-flowering species may be widespread, but they are not ubiquitous.

Key words: Boraginaceae; climate change; *Delphinium*; flower abundance; flowering phenology; frost; global warming; *Mertensia*; Ranunculaceae; Rocky Mountain Biological Laboratory; snowmelt.

Recent changes in climate have influenced plant ecology worldwide (Parmesan, 2006). Most notably, plants are leafing out and flowering earlier in many locations as a response to warmer temperatures and earlier snowmelt (Cleland et al., 2007). However, climate change is also influencing the reproduction, growth, and other important traits of many species (e.g., Kudo, 1993; Inouye et al., 2002, 2003; Perfors et al., 2003). A critical component of the impact on plants is the large variability among species' responses to changes in climate (Menzel et al., 2006). For example, although most plant species are flowering earlier than they did in the past (Root et al., 2003), some are flowering much earlier while other species' flowering times are not changing or are even occurring later (Fitter et al., 1995; Miller-Rushing and Primack, 2008; Primack et al., 2009).

The consequences of variability among species' responses have received much recent attention (Inouye et al., 2000; Stenseth and Mysterud, 2002; Visser and Both, 2005). As species' traits shift in different ways, ecological relationships will change. Changes in the timing, duration, and abundance of flowering have the potential to disrupt ecological relationships among plants, pollinators, herbivores, and flower parasites and pathogens (Memmott et al., 2007). Changes in the timing of other plant life history traits, such as germination, fruiting, and senescence, could disrupt even more ecological interactions (Stenseth and Mysterud, 2002; Visser and Both, 2005). Shifts in growth and reproduction will likely alter demography, community composition, and competition (Inouye, 2008; Willis et al., 2008). Only by understanding the factors that underlie the variability in species' responses will we be able to predict how communities might respond to future climate change.

Despite the importance of understanding this variability, empirical analysis of the variation among plant responses to climate change has been limited. However, some broad patterns are emerging. Here, we focus on one in particular. Species that flower early in the growing season appear to flower earlier for each degree of warming or day earlier snowmelt than do those of later-flowering species (Price and Waser, 1998; Fitter and Fitter, 2002; Dunne et al., 2003; Menzel et al., 2006; Miller-Rushing and Primack, 2008). This pattern may occur because early-flowering species respond to climate or other variables that are changing more rapidly than those to which late-flowering species respond. For example, the flowering times of some plants are strongly correlated to spring temperatures or snowmelt, while others are correlated with temperatures in other months or with nontemperature factors such as precipitation or daylength (Inouye and McGuire, 1991; Fitter et al., 1995; Sparks and Carey, 1995; Sherry et al., 2007; Miller-Rushing and Primack, 2008). Thus, if spring temperatures rise quickly and summer temperatures do not change, the flowering times of spring-temperature-dependent species will shift, while those of summer-temperature-dependent species will remain constant. Alternatively, earlier- and

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later-flowering species may respond to the same climate variables, but flowering times of early species may change more rapidly for each change in climate than that of later-flowering species. In Japan, for example, the early bell-flowered cherry (*Cerasus campanulata*) flowers 5.7 d earlier for each 1°C increase in spring temperatures, whereas the later Korean mountain cherry (*C. verecunda*) flowers just 3.5 d earlier for each 1°C increase in spring temperatures (Miller-Rushing et al., 2007). As a result, the difference between the flowering times of the two species is larger in warm years and smaller in cool years. In addition, although the relatively rapid changes in early-flowering species' phenology is apparent at the community level, this kind of difference may or may not occur among closely related species, for which phenology and phenological responses to climate may be taxonomically conserved (but see Miller-Rushing et al., 2007).

We also explore a second hypothesis related to flower abundance in montane habitats. In alpine and subalpine meadow habitats, susceptibility to frost appears to reduce flower abundance in years with early snowmelt (Inouye, 2000). The flower buds of species that flower later in the growing season appear to be particularly susceptible to frost, incurring damage after they have formed but before they open (Inouye, 2008). Flower abundance of earlier-flowering species may be more resilient to frost than later-flowering species. However, we can only provide suggestive evidence for this hypothesis and cannot test it directly without physiological data.

To explore these two hypotheses—(1) the phenologies of early-flowering species change more rapidly in response to climatological and other abiotic cues than do late-flowering species, and (2) flower abundance of late-flowering species is more responsive to changes in climate than that of early-flowering species—and to describe the relationships among several abiotic factors and flowering phenology and abundance, we examined a 34-yr (1973–2006) record of flowering times and flower abundance for two pairs of herbaceous perennials growing in a subalpine meadow: two *Mertensia* species, *M. fusiformis* S. Wats. (dwarf bluebells) and *M. ciliata* (James) G. Don (tall bluebells); and two *Delphinium* species, *D. nuttallianum* Pritzel (dwarf larkspur, previously *D. nelsonii*) and *D. barbeyi* Huth (tall larkspur). *Mertensia fusiformis* and *D. nuttallianum* flower shortly after snowmelt, while *M. ciliata* and *D. barbeyi* flower later in the summer. By choosing two co-occurring species pairs from genera in two distinct families (Boraginaceae and Ranunculaceae), we are able to focus on the influence of flowering time and minimize the confounding influences of differences in habitat and taxonomy.

MATERIALS AND METHODS

Study species—*Mertensia fusiformis* and *M. ciliata* are long-lived herbaceous perennial plant species. *Mertensia fusiformis* is early flowering and occurs in a wide variety of soil types in the western United States (Warfa, 1998). *Mertensia ciliata* is relatively late-flowering and is found primarily along streamsides and wet meadows in subalpine and lower alpine zones of the Rocky Mountains and Sierra Nevadas (Pelton, 1961). Individual ramets of both species produce one flowering stem each year. *Mertensia ciliata* forms clonal colonies via rhizomes (Pelton, 1961). Bumble bees (*Bombus* spp.) are probably the most important pollinators of both species, with queens visiting *M. fusiformis* and workers visiting *M. ciliata* (Pelton, 1961; Geber, 1985; Suzuki, 1994). No other *Mertensia* species occur in or near our study area.

Delphinium nuttallianum and *D. barbeyi* are also long-lived herbaceous perennials. *Delphinium nuttallianum* is early flowering and is found in dry meadows throughout the western United States (Harrington, 1964). It preforms its flower buds during the fall and winter, flowers soon after snowmelt with just one inflorescence per plant, and is vegetatively active for only 3–5 wk (Waser and Price, 1994). *Delphinium barbeyi* is relatively late flowering and is found in wet meadows and bogs in montane and supalpine areas of Colorado, Wyoming, and Utah (Nelson, 1992). Each *D. barbeyi* plant produces multiple stems each year (Inouye et al., 2002). Both species provide important nectar resources for pollinating hummingbirds (*D. nuttallianum* for *Selasphorus platycercus* and *D. barbeyi* for *S. platycercus* and *S. rufus*) and bumble bees (*D. nuttallianum* for queens as they emerge from overwintering and *D. barbeyi* for workers) (Inouye, 1978; Waser, 1978).

Observations—A group of 2 m × 2 m plots was established in 1973 by D. W. Inouye near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado (38°57.5′N, 106°59.3′W, 2900 m a.s.l.) to initiate a study on floral phenology. The plots are in two distinct habitats, rocky meadow (8 plots) and wet meadow (12 plots), and consist of naturally occurring vegetation. The plots are all covered by snow throughout the winter (average of 159–185 d of snow cover in the three winters from 2006 to 2009) and have never been manipulated. The rocky meadow plots extend over a linear distance of 272 m and the wet meadow plots over 235 m, but some plots are as close as 1 m to each other. The closest rocky meadow and wet meadow plots are separated by 492 m, and the lowest rocky meadow plot is 57 m in elevation above the highest wet meadow plot.

The number of open flowers per ramet and the number of flowering ramets were counted approximately every other day during the flowering season (usually from late May to early September 1973–2006). Each ramet was counted as a single inflorescence. *Mertensia fusiformis* was observed in 16 plots, *M. ciliata* in 10 plots, *D. nuttallianum* in 8 plots, and *D. barbeyi* in 12 plots, but not in all plots in all years. When the same peak number of flowers was observed on multiple days in the same year, we calculated the mean date of peak flowering. Phenology and flower abundance in these plots were affected by occasional herbivory in addition to the climate variables mentioned later. Data were collected in all years since 1973, except 1990. Metadata for this study (aerial photographs and survey-grade global positioning system [GPS] coordinates for plots and description of census methods) are available at the RMBL website (http://www.rmbl.org), and the data are available at the RMBL website and the University of Maryland Digital Repository (https://drum.umd.edu/dspace/index.jsp).

Analysis—Analyses for this paper are based on annual means of flowering dates and flower abundance for each species averaged across all of the plots in which the species was observed. Each plot was included in calculations of the average flower abundance for each year regardless of whether plants flowered in that plot in that year (counting a zero for that plot-year). Before calculating changes in flowering dates, we transformed dates to days after the vernal equinox. This transformation avoided the bias present in calculations based on the day of the year, because the date of the vernal equinox becomes systematically earlier over time until it is reset at the end of most centuries (Sagarin, 2001). We used regression analysis to describe temporal trends in mean date of peak flowering (the mode of the flowering distribution in our study area in each year), duration of flowering (days between first and last flower), maximum flower abundance, and maximum number of flowers per inflorescence. We also used correlation and regression to test the relationships of these variables (as dependent variables) with several abiotic explanatory variables, including the timing of spring snowmelt, monthly temperatures, monthly precipitation, and incidence of frost. (For explanation of selection of variables, see *Climate.*) We tested for autocorrelation within each of the dependent variables, with lags of up to three years. We did not consider the total amount of snow received during the winter, the length of the growing season, or the length of snowpack in our analysis; these factors were all highly correlated with the timing of spring snowmelt ($|r| > 0.77$ for all correlations).

Several of the variables we did test were also correlated (e.g., incidence of frost and timing of snowmelt) and could not be included in the same multiple regression model. Thus, we prepared separate multiple regression models that included each of these variables. We proceeded in a stepwise fashion and selected the models that best explained flowering phenology and abundance for each species by choosing the models with the lowest Akaike information criterion (AIC) values (Akaike, 1973). AIC values balance reductions in the sum of squares with the addition of model parameters, allowing us to compare competing models with different numbers of parameters (Gotelli and Ellison, 2004; Johnson and Omland, 2004).

We tested for differences between the species in each genus by testing for a significant interaction between species and the independent variable(s) of interest in a multiple regression. We considered all results where $P < 0.05$ to be statistically significant.

Climate—We obtained weather data from the Crested Butte weather station, located ~9.5 km from the plots at 2704 m a.s.l. (data available from the National Climatic Data Center). Temperature data for some months in 1977, 1978, and 1979 were missing. We used snowpack data collected at RMBL from 1975–2006 by B. Barr (Inouye et al., 2000). The snowpack data were collected at a single site at RMBL, within 1 km of the plots. Snowmelt varied among plots in such a manner that some plots consistently experienced snowmelt before other plots, but the order of melt was consistent among years; the mean date of snowmelt for the rocky meadow plots was 4–7 d earlier than the wet meadow plots over the three winters from 2006 to 2009. From these weather and snowpack data, we calculated the first day of snowmelt, monthly temperatures, monthly precipitation, and incidence of frost (discussed later). Each of these variables has a known relationship with flowering phenology or abundance or both for some plant species. For example, early snowmelt and warm spring temperatures are linked with earlier flowering time of several plant species (e.g., Inouye and McGuire, 1991; Fitter and Fitter, 2002; Miller-Rushing and Primack, 2008). Precipitation can also affect flowering times, particularly in dry habitats (Inouye et al., 2003; Franks et al., 2007). Finally, the incidence of frost is a mechanism that links snowmelt and flower abundance in some plants (Inouye, 2008).

We calculated mean monthly temperatures and total monthly precipitation for individual months, and also as aggregate values from April, the earliest month of snowmelt, to the average month of flowering for each species. Previous studies have shown that the months immediately preceding flowering have the most influence on flowering times for most species, but that temperatures in other months in the fall can also affect flowering times (Fitter et al., 1995; Sparks and Carey, 1995; Miller-Rushing and Primack, 2008). We calculated frost days as the number of days with minimum temperatures below −3.5°C after the snow had melted at RMBL. We chose −3.5°C based on our observation that plants show visible responses to frost (e.g., damaged leaves or flower buds) after temperatures have dropped below that temperature.

RESULTS

Changes in climate—During the 34 years of study (1973–2006), mean spring (April–June) temperatures warmed by 2.0°C, as determined by linear regression ($P = 0.007$) (Fig. 1A). Over the same period, mean temperatures in April and May warmed by 2.3°C ($P = 0.006$). Snowmelt was highly variable and had a weak, nonsignificant trend toward earlier occurrence in recent years, as determined by linear regression (slope = 4.7 d earlier/decade, $P = 0.090$) (Fig. 1B). Since 1975, the number of frost days has not changed significantly ($P = 0.362$) (Fig. 1C). The date of snowmelt, mean temperatures averaged across April, May, and June, and the number of frost days were all significantly correlated with one another (snowmelt-temperature: $r = -0.786$; snowmelt-frost: $r = -0.794$; temperature-frost: $r = 0.533$; $P < 0.003$ in all cases).

Changes in flowering phenology—Peak flowering dates were all approximately normally distributed among years, as determined by Jarque–Bera tests ($P > 0.47$ in all cases; H_0 is normal distribution). The mean peak flowering date for *M. fusiformis* was June 7 ± 2 d (±SE), and was July 11 ± 2 d for *M. ciliata*. The mean peak flowering date for *D. nuttallianum* was June 17 ± 2 d, and was July 22 ± 2 d for *D. barbeyi*.

Mertensia fusiformis, *M. ciliata*, and *D. nuttallianum* all flowered significantly earlier over time during the study, as determined by linear regression (Fig. 2, Table 1). The peak flowering date of *M. fusiformis*, an early-flowering species, changed most quickly (5.0 d earlier/decade, $P = 0.020$). *Del-*

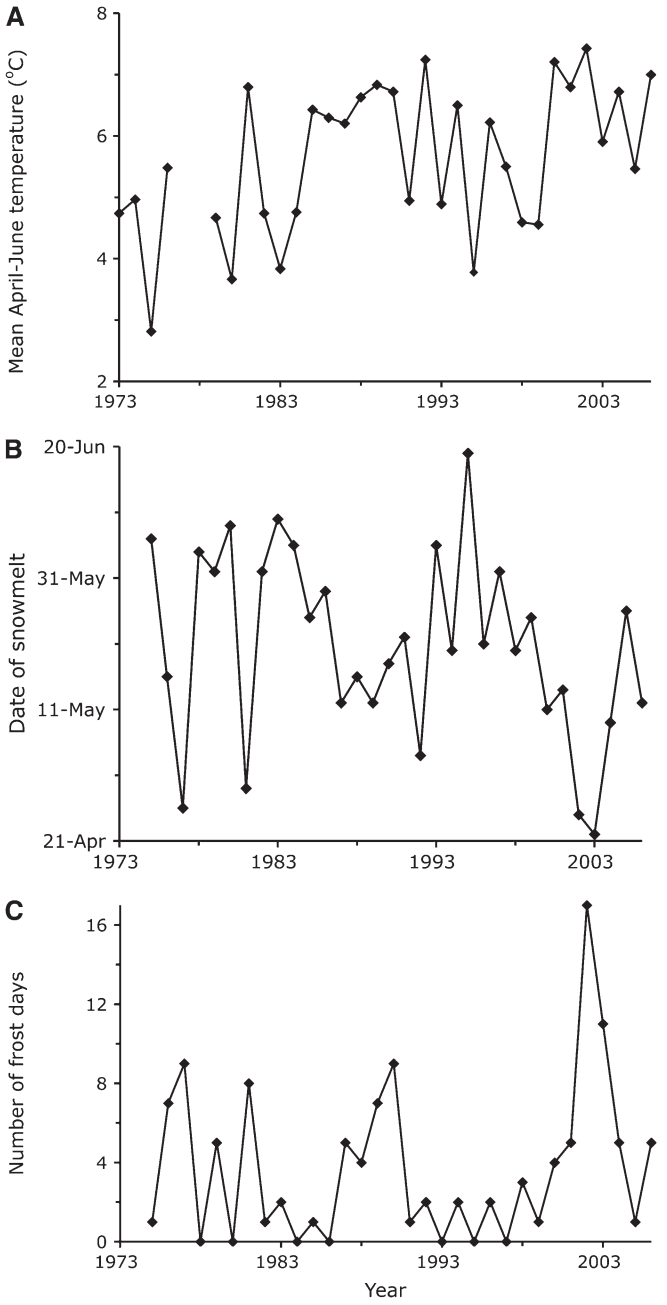

Fig. 1. Variation in (A) mean April–June temperatures, (B) snowmelt, and (C) number of frost days during the study (1973–2006). Temperatures for (A) and (C) are from the Crested Butte weather station, approximately 9.5 km from Rocky Mountain Biological Laboratory (RMBL). Snowmelt observations were made at RMBL starting in 1975. Frost days were calculated as the number of days in April, May, and June with minimum temperatures below −3.5°C after the snow had melted at RMBL. Mean monthly temperature data were not complete for 1977 and 1978 and have been omitted from (A). Over the time periods shown, mean April–June temperatures warmed by 0.6°C/decade ($P = 0.007$), the date of snowmelt occurred earlier by 4.7 d/decade, although the change was not significant ($P = 0.090$), and the number of frost days did not change significantly ($P = 0.36$).

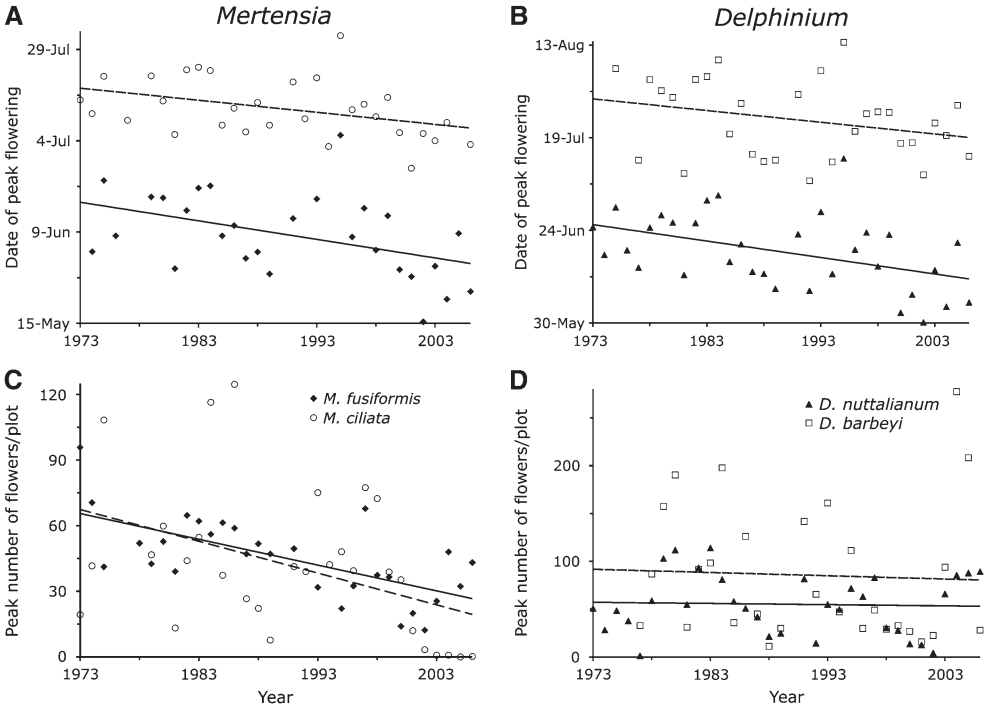

Fig. 2. Variation in (A, B) peak flowering date and (C, D) peak number of flowers over time for *Mertensia* and *Delphinium*. *M. fusiformis* is shown by solid diamonds and solid lines; *M. ciliata* by open circles and dashed lines; *D. nuttallianum* by solid triangles and solid lines; and *D. barbeyi* by open squares and dashed lines. Lines show least squares best fit. See Table 1 for regression statistics.

phinium nuttallianum, the other early-flowering species, flowered 4.4 d earlier each decade ($P = 0.011$), and *M. ciliata* flowered 3.3 d earlier each decade ($P = 0.028$). The peak flowering date of *D. barbeyi* did not change significantly over time ($P = 0.14$). Within each genus, however, the rate of change in peak flowering date was not significantly faster for the earlier-flowering species than for the later-flowering one, as determined by species × year interaction terms in multiple regression analyses (*Mertensia*: $P = 0.49$; *Delphinium*: $P = 0.51$)

All species tended to flower earlier in springs with early snowmelt ($P < 0.001$ in each case), as determined by simple linear regression (Fig. 3). However, alternate models provided better explanatory power and lower AIC values for the two *Delphinium* species (Table 2). Peak flowering of *D. nuttallianum* was best explained by mean April–May temperatures, with flowering occurring 6.1 d earlier for each 1°C increase in temperature ($R^2 = 0.75$, $P < 0.001$). Peak flowering of *D. barbeyi* was best explained by mean April–June temperatures, with flowering 7.1 d earlier for each 1°C increase in temperature ($R^2 = 0.76$, $P < 0.001$). The peak flowering times of *Mertensia* species, meanwhile, were best explained by the timing of snowmelt. They flowered 0.73 and 0.42 d earlier for each day earlier that snow melted, respectively (*M. fusiformis*: $R^2 = 0.83$, $P < 0.001$; *M. ciliata*: $R^2 = 0.60$, $P < 0.001$). *Mertensia fusiformis* flowered significantly earlier for each day earlier snowmelt than did *M. ciliata*, as determined by the species × snowmelt interaction in a multiple regression with both species considered together ($P = 0.002$). In addition, the period of time between *M. fusiformis* and *M. ciliata* peak flowering times was longer in years with earlier snowmelts, as determined by simple linear regression (slope = 0.27 d longer/day earlier snowmelt, $P < 0.001$). However, the responses of the *Delphinium* species to changes in temperature were not statistically distinguishable ($P = 0.68$), nor was the difference between their flowering times dependent on temperature ($P = 0.83$), as determined by multiple regression.

The distribution of flowering duration among years was not significantly different from a normal distribution, as determined by Jarque–Bera tests, for the early-flowering *M. fusiformis* (mean = 18 ± 1 d) and *D. nuttallianum* (mean = 18 ± 1 d), nor for the late-flowering *D. barbeyi* (mean = 22 ± 1 d). The flowering durations of *M. ciliata*, however, were negatively skewed ($P = 0.020$) with a mean duration of 29 ± 1 d and a median of 31 d.

The duration of flowering did not change significantly over time for any of the species examined, as determined by simple linear regression (Table 1). Moreover, the duration of flowering for *M. fusiformis* was not significantly related to any of the weather variables we examined, as determined by multiple regression. The duration of flowering for *M. ciliata* was best explained by the number of frost events during May; the flowering duration was 0.96 d shorter for each frost event ($R^2 = 0.24$, $P = 0.034$) (Table 2). The durations of flowering for the *Delphinium* species were best explained by the number of inflorescences, with both species flowering for longer periods in years with more inflorescences (*D. nuttallianum*: 2.5 d longer/10 inflorescences/plot, $R^2 = 0.36$, $P < 0.001$; *D. barbeyi*: 7.1 d longer/10 inflorescences/plot, $R^2 = 0.66$, $P < 0.001$) (Table 2).

TABLE 1. Change in flowering time, duration, and abundance over time in *Mertensia fusiformis, M. ciliata, Delphinium nuttalianum,* and *D. barbeyi*. Units for change are: days/decade for peak flowering date and flowering duration, and flowers/decade for peak flower abundance/plot and flowers/inflorescence. Significant *P*-values are given in boldface.

Trait and species	Mean	Change	SE	R^2	*P*
Peak flowering date					
M. fusiformis	June 7	−4.97	2.01	0.19	**0.020**
M. ciliata	July 11	−3.27	1.42	0.16	**0.028**
D. nuttallianum	Jun 17	−4.38	1.61	0.19	**0.011**
D. barbeyi	July 22	−3.08	2.02	0.08	0.138
Flowering duration					
M. fusiformis	18	0.03	0.47	<0.01	0.944
M. ciliata	29	−1.58	1.11	0.07	0.163
D. nuttallianum	18	0.31	0.78	0.01	0.690
D. barbeyi	22	−0.76	0.93	0.02	0.418
Peak flower abundance/ plot					
M. fusiformis	45	−11.8	2.63	0.43	**<0.001**
M. ciliata	42	−14.5	5.95	0.18	**0.021**
D. nuttallianum	55	−1.23	5.58	<0.01	0.827
D. barbeyi	85	−3.40	15.10	<0.01	0.824
Flowers/inflorescence					
M. fusiformis	5.8	−0.30	0.29	0.04	0.302
M. ciliata	2.9	0.09	0.18	0.01	0.606
D. nuttallianum	2.4	−0.13	0.07	0.09	0.085
D. barbeyi	9.7	0.09	0.38	<0.01	0.819

Changes in flower abundance—The distributions of peak flower abundance among years were not significantly different from normal for the two early-flowering species, as determined by Jarque–Bera tests ($P > 0.48$ in each case). The distribution of *M. ciliata* peak flower abundance was also not significantly different from normal ($P = 0.100$). However, peak flower abundance was positively skewed for *D. barbeyi* ($P = 0.022$), with abnormally high flower abundance in a few years. *Mertensia fusiformis* averaged 45 ± 3 flowers and 8 ± 0.4 inflorescences per plot, *M. ciliata* averaged 42 ± 6 flowers and 14 ± 2 inflorescences, *D. nuttallianum* 55 ± 6 flowers and 22 ± 2 inflorescences, and *D. barbeyi* 85 ± 13 flowers and 9 ± 1 inflorescences per plot.

Peak flower abundance declined over time for both of the *Mertensia* species (*M. fusiformis*: 11 fewer flowers/decade, $R^2 = 0.43$, $P < 0.001$; *M. ciliata*: 15 fewer flowers/decade, $R^2 = 0.18$, $P = 0.021$), but not for either of the *Delphinium* species, as indicated by simple linear regression (Fig. 2, Table 1). There were no significant differences between the changes in flower abundance in the early- and late-flowering species within each genus, as determined by year × species interaction terms in multiple regression models (*Mertensia*: $P = 0.67$; *Delphinium*: $P = 0.88$). The peak number of flowers for *M. fusiformis* was best explained (determined by AIC value) by the peak number of flowers in the previous year (0.47 flowers/flower in the previous year, $R^2 = 0.33$, $P = 0.003$). For *M. ciliata*, the peak number of flowers was most related to the date of snowmelt (1.6 flowers/day later snowmelt, $R^2 = 0.43$, $P < 0.001$). The peak number of flowers for *D. nuttallianum* was related to both the peak number of flowers in the previous year (coefficient = 0.42 flowers/flower in the previous year) and the date of snowmelt (coefficient = 1.1 flowers/day later snowmelt), as determined by multiple regression ($R^2 = 0.50$, $P < 0.001$). For *D. barbeyi*, the peak number of flowers was best explained by the date of snowmelt (1.9 flowers/day later snowmelt, $R^2 = 0.16$, $P = 0.032$). Changes in peak inflorescence abundance largely followed those of peak flower abundance, thus those results are not shown.

The ratio of flowers to inflorescences did not change significantly over time for any of the species ($P > 0.08$ in each case) (Table 1). No weather variables were associated with the number of flowers per inflorescence for *M. fusiformis*, *D. nuttallianum*, or *D. barbeyi* (Table 2). However, *M. ciliata* had 0.04 more flowers per inflorescence for each day later that snow melted ($R^2 = 0.41$, $P < 0.001$).

DISCUSSION

Data from the *Mertensia* species supported our hypotheses that relative to late-flowering species, flowering times for early-flowering species change more rapidly in response in climate. The flower abundance of the earlier-flowering *Mertensia* may also be less susceptible to frost. Specifically, the early-flowering *M. fusiformis* flowered earlier for each advance in snowmelt than did the late-flowering *M. ciliata* (Fig. 3, Table 2). Also, the decline in floral abundance of *M. ciliata* was explained by progressively earlier snowmelts, whereas the floral abundance of *M. fusiformis* was not related to snowmelt or frost (Table 2). However, the *Delphinium* species provided a counter-example in which the early- and late-flowering species had very few measurable differences in how they responded to climate variability. Thus, the previously reported differences between early- and late-flowering species (Fitter and Fitter, 2002; Dunne et al., 2003; Menzel et al., 2006; Miller-Rushing and Primack, 2008) may exist among some species pairs, but clearly not for all of them.

These two patterns of change will have substantially different consequences for pollinators and other species that rely on these plants. For example, the difference between the peak flowering dates for the *Delphinium* species is relatively constant, regardless of snowmelt or temperature. This consistency is important for hummingbirds and other pollinators that depend on the sequential flowering of *Delphinium* and *Ipomopsis* species (Waser and Real, 1979). However, the flowering times of the *Mertensia* species diverge in years when snowmelt occurs early (Fig. 4). This pattern is due to changes in both flower phenology and abundance. *M. fusiformis* flowers earlier relative to *M. ciliata* in years with early snowmelt. In addition, *M. ciliata* floral abundance declines in years with early snowmelt, leading to a shortened duration of flowering (Miller-Rushing et al., 2008). Species that rely on *Mertensia* for nectar resources have experienced progressively longer periods with limited or no flower availability because the date of snowmelt has occurred earlier.

In addition to *M. ciliata*, both *Delphinium* species had lower flower abundance in years with early snowmelt (Fig. 3, Table 2). We believe that increased frost damage to *D. barbeyi* flower buds in years with early snowmelt was probably responsible for the observed relationship, despite the lack of a correlation between incidence of frost and flower abundance. In years with early snowmelt, we have observed significant (sometimes total) frost damage to *D. barbeyi* flower buds (data not shown). Our estimate of incidence of frost came from a weather station 9.5 km from (and almost 300 m lower than) our study plots, which provided a reasonable estimate of air temperature in the area but probably underestimated actual

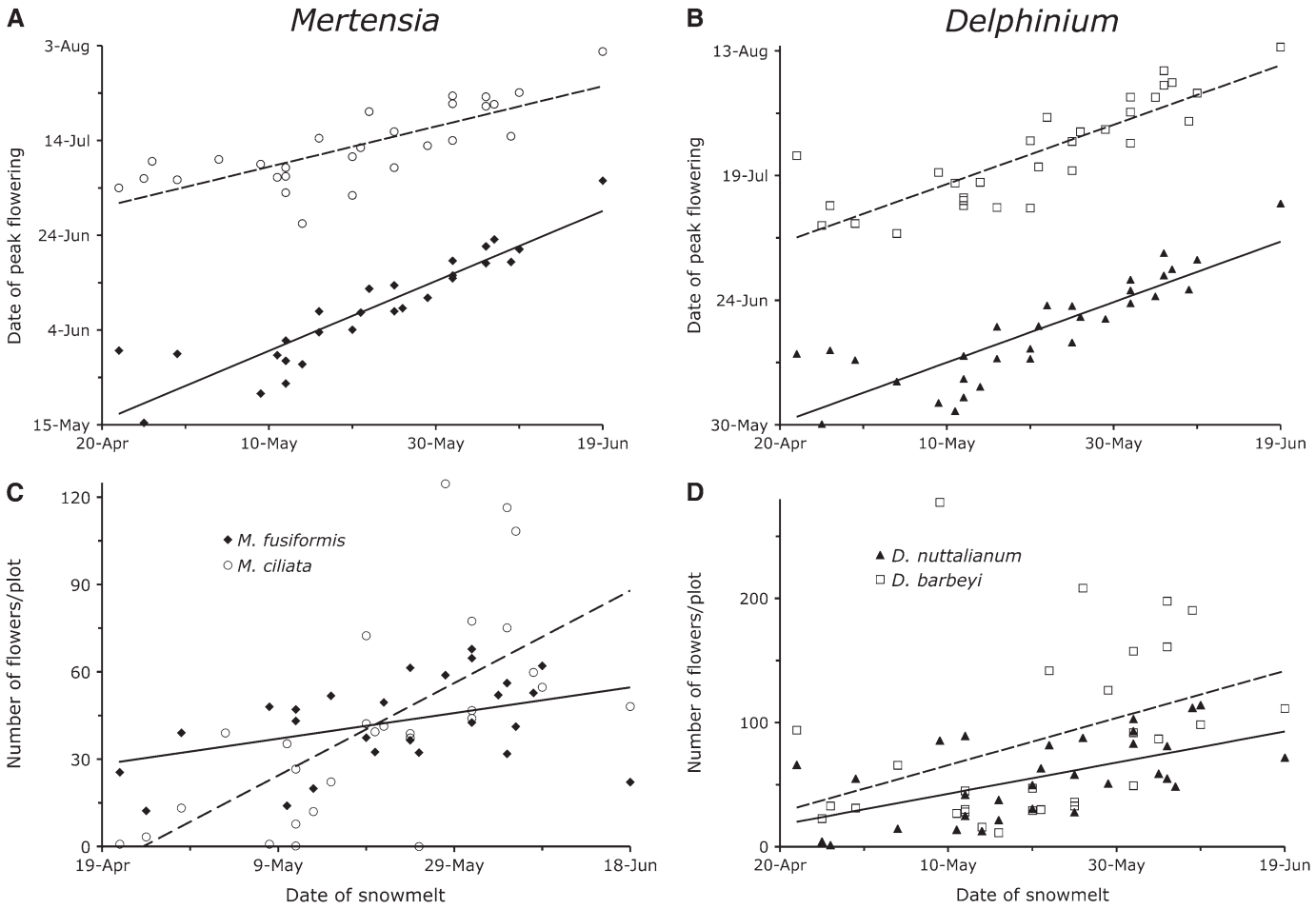

Fig. 3. Variation in (A, B) peak flowering date and (C, D) peak number of flowers in relation to the date of snowmelt for *Mertensia* and *Delphinium*. *M. fusiformis* is shown by solid diamonds and solid lines; *M. ciliata* by open circles and dashed lines; *D. nuttallianum* by solid triangles and solid lines; and *D. barbeyi* by open squares and dashed lines. Lines show least squares best fit. Regression results for peak flowering date: *M. fusiformis*: slope = 0.74 d/day later snowmelt, $R^2 = 0.83$, $P < 0.001$; *M. ciliata*: slope = 0.42 d/day later snowmelt, $R^2 = 0.60$, $P < 0.001$; *D. nuttallianum*: slope = 0.61 d/day later snowmelt, $R^2 = 0.72$, $P < 0.001$; *D. barbeyi*: slope = 0.59 d/day later snowmelt, $R^2 = 0.72$, $P < 0.001$. Regression results for peak number of flowers: *M. fusiformis*: slope = 0.44 flowers/day later snowmelt, $R^2 = 0.17$, $P = 0.031$; *M. ciliata*: slope = 1.59 d/day later snowmelt, $R^2 = 0.43$, $P < 0.001$; *D. nuttallianum*: slope = 1.25 d/day later snowmelt, $R^2 = 0.33$, $P < 0.001$; *D. barbeyi*: slope = 1.90 d/day later snowmelt, $R^2 = 0.16$, $P = 0.032$.

frost damage. In cases of cold air drainage or long wave radiative cooling (loss of heat to the cold night sky), frost can occur even if air temperatures in the area do not drop below freezing (radiation frost; Inouye, 2000). In years with earlier snowmelt, plants are probably exposed to more of these frost events. In addition to frost, early snowmelt is also correlated with earlier, longer dry seasons in this region (Westerling et al., 2006), which may lead to drought stress in plants in years with early snowmelt. Thus, even if frost is not the mechanism involved (perhaps in *D. nuttallianum* and *M. ciliata*), the link between early snowmelt and decreased floral abundance suggests that floral abundance may decline if snowmelt continues to occur earlier in the spring. In fact, the date of snowmelt in the area is predicted to advance increasingly faster over the next 100 years (Stewart et al., 2004). Declines in floral abundance may in turn lead to declines in recruitment and species' persistence in the area (Inouye, 2008).

This process may already be occurring with *M. ciliata*. The species has disappeared from several of our study plots in recent years (Fig. 2C), suggesting that it may completely disappear from our study area in the near future. Other researchers have also noted its disappearance from their study plots around RMBL (G. Pyke, Australian Museum, personal communication). Based on our personal observations, it is still abundant at higher elevations, but not at lower elevations. It is not clear what mechanism is responsible for this decline. On the basis of the relationship observed between time of snowmelt and flower abundance and the strong correlation between flower abundance and number of flowering individuals in our plots (data not shown), we suspect that changes in the timing of snowmelt may play a role, perhaps through drought stress. This point deserves further investigation.

Our results also yield several other insights into plant responses to climate change. For example, two species within the same genus can have traits tightly linked to different climate variables. *Delphinium nuttallianum* flowering times were linked with April–May temperatures, while *D. barbeyi* flowering times were linked with April–June temperatures. The difference be-

TABLE 2. Factors that explain significant amounts of variation in flowering time, duration, and abundance in *Mertensia fusiformis, M. ciliata, Delphinium nuttalianum,* and *D. barbeyi*. Units for slope: days (flowering date and duration), flowers (peak flower abundance), or inflorescences (peak inflorescence abundance) per day (date of snowmelt), 1°C (temperatures), frost event, inflorescence (number of inflorescences, previous year's inflorescence abundance), or flower (previous year's flower abundance). Negative slopes indicate earlier flowering, shorter flower duration, or lower inflorescence abundance per 1°C or frost event. For *D. nuttallianum*, peak flower abundance, results shown are from a multiple regression in which both the previous year's flower abundance and date of snowmelt explained significant portions of the variation in abundance. For all other results shown, only one factor explained significant amounts of variation in the dependent variable.

Trait and species	Factor	Slope	SE	*P*	R^2
Peak flowering date					
M. fusiformis	Date of snowmelt	0.734	0.07	<0.001	0.83
M. ciliata	Date of snowmelt	0.421	0.07	<0.001	0.60
D. nuttallianum	April–May temperatures	−6.14	0.65	<0.001	0.75
D. barbeyi	April–June temperatures	−7.07	0.79	<0.001	0.76
Flowering duration					
M. fusiformis	None				
M. ciliata	May frost events	−0.962	0.42	0.034	0.24
D. nuttallianum	No. of inflorescences	0.248	0.06	<0.001	0.36
D. barbeyi	No. of inflorescences	0.713	0.09	<0.001	0.66
Peak flower abundance					
M. fusiformis	Previous year's flower abundance	0.469	0.14	0.003	0.33
M. ciliata	Date of snowmelt	1.588	0.36	<0.001	0.43
D. nuttallianum	Previous year's flower abundance	0.338	0.15	0.033	0.51
	Date of snowmelt	0.960	0.26	0.001	
D. barbeyi	Date of snowmelt	1.899	0.84	0.032	0.16
Flowers/inflorescence					
M. fusiformis	None				
M. ciliata	Date of snowmelt	0.036	0.01	<0.001	0.41
D. nuttallianum	None				
D. barbeyi	None				

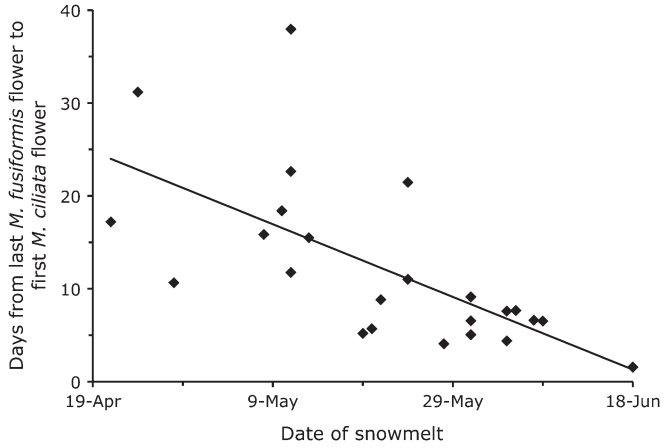

Fig. 4. The number of days between the last *M. fusiformis* flower and the first *M. ciliata* flower explained by the date of snowmelt. The least squares best-fit line is shown (slope = 0.35 d longer for each day earlier snowmelt, $R^2 = 0.58$, $P < 0.001$).

tween the climate variables is small, indicating that the relationship between the flowering dates of these two species will remain relatively constant. However, if June temperatures were to change in the opposite direction of April and May temperatures, the flowering times of the two species could change in different directions. Also, *M. fusiformis* flowering duration was relatively constant among years, while *M. ciliata* flowering duration declined in years with a high incidence of frost. These findings suggest that closely related species might respond quite differently to future climate change, depending on how climate variables change relative to one another. In addition, changes in *Mertensia* flowering times showed early-flowering species in some cases respond to the same climate variables as late-flowering species, but change more rapidly. Although our findings are based on correlation rather than causation and may be subject to some spurious results, they suggest that responses to climate change can be species-specific. They support the hypothesis that species' responses may differ for two reasons: (1) they might respond to different climate variables, each of which is changing at different rate, or (2) they might respond to the same variable, with some species responding faster than the others. Currently, there is no obvious way to distinguish species that respond to similar climate variables from those that respond to different ones, making it difficult to predict how particular species' phenologies will change relative to one another in the future.

We also found that *Delphinium* flowering durations depend on the number of inflorescences. This may result, at least in part, from early-developing inflorescences being particularly susceptible to frost in years with early snowmelt, so that only the later-flowering buds escape frost damage. This finding suggests that first flowering dates can be affected by changes in the number of inflorescences (an estimate of population size). This point is important because many studies of changes in flowering times rely on first flowering times to characterize changes in flowering for entire populations (e.g., Sparks and Carey, 1995; Fitter and Fitter, 2002; Inouye et al., 2002; Miller-Rushing and Primack, 2008). If first flowering times are affected by changes in population size or the impact of climate on flowering duration, it may be difficult or impossible to disentangle the relative contributions of changes in population size and climate change to changes in flowering times. Ideally, researchers should rely on the mean or peak flowering dates to estimate variation in flowering dates over time, because the mean and the mode are not affected by population size (Miller-Rushing et al., 2008).

Finally, we found that the flower abundance of both of the early-flowering species was positively correlated with the previous year's abundance (Table 2). The mechanism behind this correlation is unknown, but it may have been caused by unmeasured environmental variables that were also autocorrelated or changed directionally over time, leading to declines in flower abundance. Smaller, early-flowering species might be hypothesized to have a higher cost of reproduction (Obeso, 2002) compared to larger, later-flowering species, but this hypothesis would predict a negative relationship between flower abundance in one year and the next. In fact, *Delphinium nuttallianum* plants that flower and fruit in one year often do not flower for the next one or two years (N. Waser, University of Arizona, personal communication). However, we found that the slope of the autocorrelative term was positive. The value of the autocorrelative term was less than one, signifying a decline in flower abundance over time—on average, each year's abundance was lower than the previous year's whether the abundance was high or low.

In conclusion, we found that the differences between early- and late-flowering species' responses to climate change depend on the particular species involved. Widespread patterns may exist, which allow us to make generalized predictions of how plant communities might respond to future climate change. For example, the flowering times of early-flowering plants appear to be changing more quickly than late-flowering plants in response to warming temperatures (Fitter and Fitter, 2002; Dunne et al., 2003, Menzel et al., 2006; Miller-Rushing and Primack, 2008), and late-flowering plants are more susceptible to frost at high elevations compared to early-flowering ones. However, exceptions to these rules clearly exist, as we have shown here. Thus, specific case studies are required to predict how a particular species or genus will respond to future climate change.

LITERATURE CITED

AKAIKE, H. 1973. Information theory as an extension of the maximum likelihood principle. *In* B. N. Petrov and F. F. Csaki, [eds.], Second International Symposium on Information Theory, 267–281. Akademiai Kiado, Budapest, Hungary.

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: 357–365.

DUNNE, J. A., J. HARTE, AND K. J. TAYLOR. 2003. Subalpine meadow flowering phenology responses to climate change: Integrating experimental and gradient methods. *Ecological Monographs* 73: 69–86.

FITTER, A. H., AND R. S. R. FITTER. 2002. Rapid changes in flowering time in British plants. *Science* 296: 1689–1691.

FITTER, A. H., R. S. R. FITTER, I. T. B. HARRIS, AND M. H. WILLIAMSON. 1995. Relationships between first flowering date and temperature in the flora or a locality in central England. *Functional Ecology* 9: 55–60.

FRANKS, S. J., S. SIM, AND A. E. WEIS. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences, USA* 104: 1278–1282.

GEBER, M. 1985. The relationship of plant size to self-pollination in *Mertensia ciliata. Ecology* 66: 762–772.

GOTELLI, N. J., AND A. M. ELLISON. 2004. A primer of ecological statistics. Sinauer, Sunderland, Massachusetts, USA.

HARRINGTON, H. D. 1964. Manual of the plants of Colorado. Sage Books, Denver, Colorado, USA.

INOUYE, D. W. 1978. Resource partitioning in bumblebees: Experimental studies of foraging behavior. *Ecology* 59: 672–678.

INOUYE, D. W. 2000. The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters* 3: 457–463.

INOUYE, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89: 353–362.

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: 1630–1633.

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.

INOUYE, D. W., M. A. MORALES, AND G. J. DODGE. 2002. Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): The roles of snowpack, frost, and La Niña, in the context of climate change. *Oecologia* 130: 543–550.

INOUYE, D. W., F. SAAVEDRA, AND W. LEE-YANG. 2003. Environmental influences on the phenology and abundance of flowering by *Androsace septentrionalis* (Primulaceae). *American Journal of Botany* 90: 905–910.

JOHNSON, J. B., AND K. S. OMLAND. 2004. Model selection in ecology and evolution. *Trends in Ecology & Evolution* 19: 101–108.

KUDO, G. 1993. Relationship between flowering time and fruit-set of the entomophilous alpine shrub, *Rhododendron aureum* (Ericaceae), inhabiting snow patches. *American Journal of Botany* 80: 1300–1304.

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, AND D. B. ROY. 2006. Altered geographic and temporal variability in phenology in response to climate change. *Global Ecology and Biogeography* 15: 498–504.

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: 1289–1296.

MILLER-RUSHING, A. J., T. KATSUKI, R. B. PRIMACK, Y. ISHII, S. D. LEE, AND H. HIGUCHI. 2007. Impact of global warming on a group of related species and their hybrids: Cherry tree (Rosaceae) flowering at Mt. Takao, Japan. *American Journal of Botany* 94: 1470–1478.

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.

NELSON, R. A. 1992. Handbook of Rocky Mountain plants. Roberts Rinehart, Niwot, Colorado, USA.

OBESO, J. R. 2002. The costs of reproduction in plants. *New Phytologist* 155: 321–348.

PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37: 637–669.

PELTON, J. 1961. An investigation of the ecology of *Mertensia ciliata* in Colorado. *Ecology* 42: 38–52.

PERFORS, T., J. HARTE, AND S. E. ALTER. 2003. Enhanced growth of sagebrush (*Artemisia tridentata*) in response to manipulated ecosystem warming. *Global Change Biology* 9: 736–742.

PRICE, M. V., AND N. M. WASER. 1998. Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology* 79: 1261–1271.

PRIMACK, R. B., I. IBÁÑEZ, H. HIGUCHI, S. D. LEE, A. J. MILLER-RUSHING, A. M. WILSON, AND J. A. SILANDER JR. 2009. Spatial and interspecific variability in phenological responses to warming temperatures. *Biological Conservation* .

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.

SAGARIN, R. 2001. Phenology: False estimates of the advance of spring. *Nature* 414: 600.

SHERRY, R. A., X. ZHOU, S. GU, J. A. ARNONE, D. S. SCHIMEL, P. S. VERBURG, L. L. WALLACE, AND Y. LUO. 2007. Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences, USA* 104: 198–202.

SPARKS, T. H., AND P. D. CAREY. 1995. The responses of species to climate over two centuries: An analysis of the Marsham phenological record 1736–1947. *Journal of Ecology* 83: 321–329.

STENSETH, N. C., AND A. MYSTERUD. 2002. Climate, changing phenology, and other life history traits: Nonlinearity and match-mismatch to the environment. *Proceedings of the National Academy of Sciences, USA* 99: 13379–13381.

STEWART, I. T., D. R. CAYAN, AND M. D. DETTINGER. 2004. Changes in snowmelt runoff timing in western North America under a 'business as usual' climate change scenario. *Climatic Change* 62: 217–232.

SUZUKI, K. 1994. Pollinator restriction in the narrow-tube flower type of *Mertensia ciliata* (James) G. Don (Boraginaceae). *Plant Species Biology* 9: 69–73.

VISSER, M. E., AND C. BOTH. 2005. Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society of London, B, Biological Sciences* 272: 2561–2569.

WARFA, A. M. 1998. Identity of *Mertensia oblongifolia* (Nutt.) G. Don (Boraginaceae) and its allies in western North America. *Great Basin Naturalist* 58: 38–44.

WASER, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* 59: 934–944.

WASER, N. M., AND M. V. PRICE. 1994. Cross-distance effects in *Delpinium nelsonii*: Outbreeding and inbreeding depression in progeny fitness. *Evolution* 48: 842–852.

WASER, N. M., AND L. A. REAL. 1979. Effective mutualism between sequentially flowering plant species. *Nature* 281: 670–672.

WESTERLING, A. L., H. G. HIDALGO, D. R. CAYAN, AND T. W. SWETNAM. 2006. Warming and earlier spring increase in western U.S. forest wildfire activity. *Science* 313: 940–943.

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: 17029–17033.