Ecology, 91(2), 2010, pp. 431–440
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Flowering phenology in subalpine meadows: Does climate variation influence community co-flowering patterns?

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Abstract. Climate change is expected to alter patterns of species co-occurrence, in both space and time. Species-specific shifts in reproductive phenology may alter the assemblages of plant species in flower at any given time during the growing season. Temporal overlap in the flowering periods (co-flowering) of animal-pollinated species may influence reproductive success if competitive or facilitative interactions between plant species affect pollinator services. We used a 33-year data set on flowering phenology in subalpine meadows in Colorado, USA, to determine whether interannual variation in snowmelt date, which marks the start of the growing season, affected co-flowering patterns. For two of four species considered, we found a significant relationship between snowmelt timing and composition of the assemblage of co-flowering plants. In years of early snowmelt, *Lathyrus lanszwertii* var. *leucanthus* (Fabaceae), the species we investigated in most detail, tended to overlap with earlier-flowering species and with fewer species overall. In particular, overlap with the flowering period of *Lupinus polyphyllus* var. *prunophilus*, with which *Lathyrus leucanthus* shares pollinators, was significantly reduced in early-snowmelt years. The observed association between timing of snowmelt and patterns of flowering overlap could not have been predicted simply by examining temporal trends in the dates of peak flowering of the dominant species in the community, as peak flowering dates have largely shifted in parallel with respect to snowmelt date. However, subtle interspecific differences in responsiveness of flowering time, duration, and intensity to interannual climate variation have likely contributed to the observed relationship. Although much of the year-to-year variation in flowering overlap remains unexplained by snowmelt date, our finding of a measurable signal of climate variation suggests that future climate change may lead to altered competitive environments for these wildflower species.

Key words: climate change; co-flowering; Heterotheca; Hymenoxys*;* Lathyrus; *long-term data;* Lupinus; Mertensia; *phenology; Rocky Mountain Biological Laboratory, Colorado, USA; snow; snowmelt*.

Introduction

Species are shifting their geographic distributions and seasonal timing of reproduction in response to climate warming (e.g., Parmesan and Yohe 2003, Root et al. 2003, Rosenzweig et al. 2007). Individualistic responses to climate change are expected to produce novel assemblages of interacting species or "ecological surprises" (Williams and Jackson 2007). There are now several examples of apparently growing phenological disjunctions between interacting organisms: for instance, between marmots and their plant foods in the Rocky Mountains (Inouye et al. 2000), between flycatchers and their caterpillar prey in Europe (Both et al. 2006), and among three trophic levels within the North Sea plankton community (Edwards and Richardson 2004). In all these examples, the increase in asynchrony in response to climate change supposedly arises because the seasonal activity patterns of different taxa respond to different kinds of cues. For example, timing of flycatcher migration is apparently dictated by an internal circannual clock, whereas the time of peak caterpillar biomass is determined by springtime temperatures (Both et al. 2006, Visser et al. 2006).

At present there are few examples of shifts in temporal overlap among more ecologically similar species. In the Rocky Mountains of the western United States, flowering phenology of subalpine plants is thought to be largely controlled by the timing of snowmelt (Inouye et al. 2002, 2003, Dunne et al. 2003). As a consequence, many species are expected to shift their dates of peak flowering more or less in parallel in response to climatic variation. However, the relationship between snowmelt and flowering onset is stronger for relatively early-flowering species than for later-flowering species (Dunne et al. 2003). Furthermore, variation in snowpack and snowmelt date has been shown to influence not only the timing but also the abundance and duration of flowering for certain species. For example, in the midsummer-

Manuscript received 19 January 2009; revised 22 April 2009; accepted 15 May 2009. Corresponding Editor: C. M. Herrera.
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blooming species *Delphinium barbeyi*, early snowmelt is associated with declines in inflorescence number, which in turn lead to reductions in the plot-level flowering period (Inouye et al. 2002). Early snowmelt also reduces the number of flowering *Delphinium nuttallianum* plants per plot and the number of flowers per plant, significantly reducing flower abundance at the population level (Saavedra et al. 2003); however, in this early-flowering species, warming lengthens the flowering period of individual plants (Dunne et al. 2003). It is unclear how temporal patterns of flowering overlap at the community level (co-flowering patterns) might be affected by such variation.

Several authors (Price and Waser 1998, Dunne et al. 2003, Saavedra et al. 2003) have argued that climate-driven shifts in flowering patterns are likely to affect plant fecundity because of the potential for co-occurring species to attract and support populations of interacting animals, particularly pollinators (e.g., Lázaro et al. 2009), but also generalist seed predators or florivores. Such complex, indirect interactions are difficult to document in the field, but there is substantial evidence that they occur. For example, the co-flowering of other plants can reduce pollinator visitation to a focal species, as well as the quality of pollen delivered to its stigmas (Waser 1978, Kunin 1993, Brown et al. 2002). Competition for pollinators between simultaneously flowering species has been invoked to explain evolutionary divergence in flowering times in biotically pollinated plant lineages (Bolmgren et al. 2003). On the other hand, co-flowering plants can be mutually beneficial if the multispecies flowering display attracts more pollinators (Thomson 1981, 1982, Laverty and Plowright 1988, Moeller and Geber 2005), particularly if the spatial arrangement of the different species minimizes heterospecific pollen transfer (Thomson 1983). In any case, for an animal-pollinated species, the identity and abundance of other open flowers during (or before) its flowering period may influence its reproductive success (Waser and Real 1979, Gross and Werner 1983). Conversely, from the pollinators' perspective, changes in co-flowering patterns may mean that floral resources are scarce at certain times of the year (Memmott et al. 2007) or superabundant at others.

Here we use a unique long-term data set on flowering phenology in subalpine plant communities to determine whether interannual variation in climate affects co-flowering patterns. Specifically, we test whether the timing of snowmelt in a given year is related to temporal overlap in flowering in that growing season. Snowmelt timing is an informative variable because it integrates information on springtime temperatures and winter snow accumulation and determines both the start of the growing season and availability of soil moisture through the season, both of which are factors that may influence plant growth and flowering (Inouye and McGuire 1991, Inouye et al. 2002). Furthermore, despite pronounced interannual variability, there has been a trend toward earlier snowmelt in our study area since 1973, corresponding to a significant increase in springtime temperatures in the area (Miller-Rushing and Inouye 2009). This trend is expected to continue as the global climate warms. Over the last several decades, increases in winter and spring temperatures in the mountains of the western United States have led to a lower fraction of winter precipitation falling as snow and more rapid melting (Mote et al. 2005, Stewart et al. 2005, Knowles et al. 2006, Feng and Hu 2007). In most of the region, the effects of increasing temperatures are overriding any increases in snowfall, and, in consequence, the duration of the period of snow cover is projected to continue to decline (Christensen et al. 2007). Understanding community-level responses to variation in the timing of snowmelt is therefore particularly important.

Methods

Study area

Thirty 2×2 m permanent study plots were established beginning in 1973–1974 at the Rocky Mountain Biological Laboratory, in Gothic, Colorado, USA (38°57′30″ N, 106°59′18″ W, 2900 m above sea level) and have been monitored for flowering phenology every summer since (except 1978 and 1990). For analyses reported here, we considered data from 16 unmanipulated plots located in dry, rocky meadows, adjacent aspen forest, and more mesic meadow habitat. Approximately every second day throughout the growing season, typically late May through early September, the number of open flowers (or, for taxa in which counting individual flowers was impractical, such as Asteraceae and Apiaceae, the number of capitulae or flowering stems) of all non-graminoid plants was recorded for each plot. In total, 89 animal-pollinated species were recorded in these plots over the study period.

Total snow accumulation in each winter and the date of first bare ground in spring have been recorded since 1975 at a station located in Gothic within 1 km of the plots (data *available online*).[5] Snowmelt date varies among individual plots and differs from that recorded at the measurement station according to small-scale topographic and climatic conditions; on average, ground first becomes bare 9.3 days later at the station than at individual plots (SD = 8.9 d; data available from 2007 only; D. Inouye, *unpublished data*). However, interannual variation in timing of snowmelt is substantial (range = 21 April–18 June, SD = 14.8 d; Fig. 1) and exceeds among-plot spatial variation. In addition, there are air temperature data from the National Oceanic and Atmospheric Administration (NOAA) weather station in Crested Butte, ~10 km away and 200 m lower in

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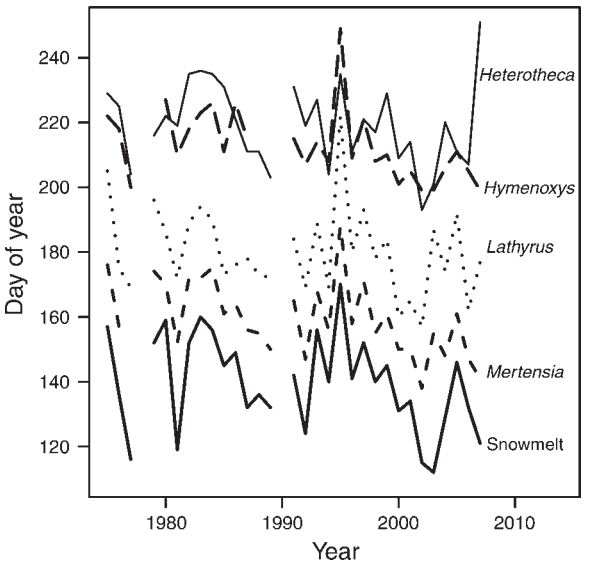


FIG. 1. Time series of peak flowering dates of the four focal species and snowmelt date for the period 1975–2007 (data were not collected in 1978 and 1990). Study plots were established beginning in 1973–1974 at the Rocky Mountain Biological Laboratory, in Gothic, Colorado, USA.

elevation. We use snowmelt date at the Gothic station as our primary explanatory variable, for reasons mentioned previously. As a check, we also ran analyses using monthly mean temperatures for April, May, and June, but because the inclusion of these variables did not significantly improve our predictive power, we present results based on snowmelt date alone.

Focal species

Plant nomenclature follows Hartman and Nelson (2001); to ease comparisons to older literature from this region, obsolete generic names are given in parentheses. To assess interannual changes in flowering overlap, we considered one particular focal species at a time and asked how the assemblage of species that co-flowered with that focal species varied across years with the timing of flowering onset. To determine the generality of any effect, we examined four focal species whose flowering periods collectively spanned most of the growing season. These species were selected, a priori, according to the following criteria: (1) they are native, (2) they are primarily bee-pollinated, based on our observations, (3) they are well represented in the data set, throughout the time series, in terms of both number of years in which flowering occurred and number of plots in which the species was found, and (4) their peak flowering dates are spread through the season (Table 1, Fig. 1) such that the flowering period of each focal species reflects a distinct segment of the whole-community flowering season and, therefore, a more or less independent test of the hypothesis. We did not select species that have frost-sensitive buds (e.g., *Delphinium barbeyi*, *Erigeron speciosus*) and therefore show marked reductions in flower number in early-snowmelt years (Inouye 2008). Even though these species were otherwise suitable for analysis, they might be particularly likely to show a change in overlap patterns in response to snowmelt date owing to this frost sensitivity. These criteria led us to select the earliest- (*Mertensia fusiformis*) and latest-flowering species (*Heterotheca* [= *Chrysopsis*] *villosa*) for which we had reasonably complete data (i.e., we had missed the flowering peak in 4 of 31 years, at most), as well as two species with intermediate flowering dates (*Lathyrus lanszwertii* var. *leucanthus* [henceforth *L. leucanthus*] and *Hymenoxys* [= *Helenium*, = *Dugaldia*] *hoopesii*). *Hymenoxys hoopesii* and *Heterotheca villosa* have more similar flowering periods than the other pairs of species but occur in different plots (wetter sites for the former, drier sites for the latter).

Of the four focal species, *L. leucanthus* is the one for which we have the most complete data (i.e., it occurs in a relatively large number of plots [10], and the beginning of its flowering period was rarely missed by censuses, something that occurred more often for the more abundant but earlier-flowering *M. fusiformis*). We therefore analyzed patterns of flowering overlap for this species in more detail. Furthermore, *L. leucanthus* is one of three legume species that occur commonly in the study area and that show partial overlap in flowering times. Like *L. leucanthus*, *Lupinus polyphyllus* var. *prunophilus* ("*Lupinus argenteus*" in some previous work from the Rocky Mountain Biological Laboratory [RMBL]) and *Vicia americana* Muhl. ex Willd. are visited by species of *Megachile*, *Osmia*, and *Bombus* (J. Forrest, *personal observation*; also Pyke 1982, Gori

TABLE 1. Focal species used in analyses and Mantel statistics.

Species	Family	Peak flowering date	No. plots	Mantel *r*	*P*	*N* (years)
Mertensia fusiformis Greene	Boraginaceae	8 June	14	0.15	0.109	27
Lathyrus lanszwertii Kellogg var. *leucanthus* (Rydb.) Dorn	Fabaceae	28 June	10	0.22	0.007	30
Hymenoxys (=*Helenium*) *hoopesii* (Gray) Bierner	Asteraceae	30 July	4	0.14	0.022	28
Heterotheca (=*Chrysopsis*) *villosa* (Pursh) Shinners	Asteraceae	6 August	7	−0.01	0.497	30

Notes: "Peak flowering date" is the average over all plots and years in which the species flowered. Plots in which the species flowered in at least 15 years were used for analysis of co-flowering communities; the number of such plots is reported. Mantel statistics are shown for correlations between snowmelt date and co-flowering communities (based on complete relative abundance data).

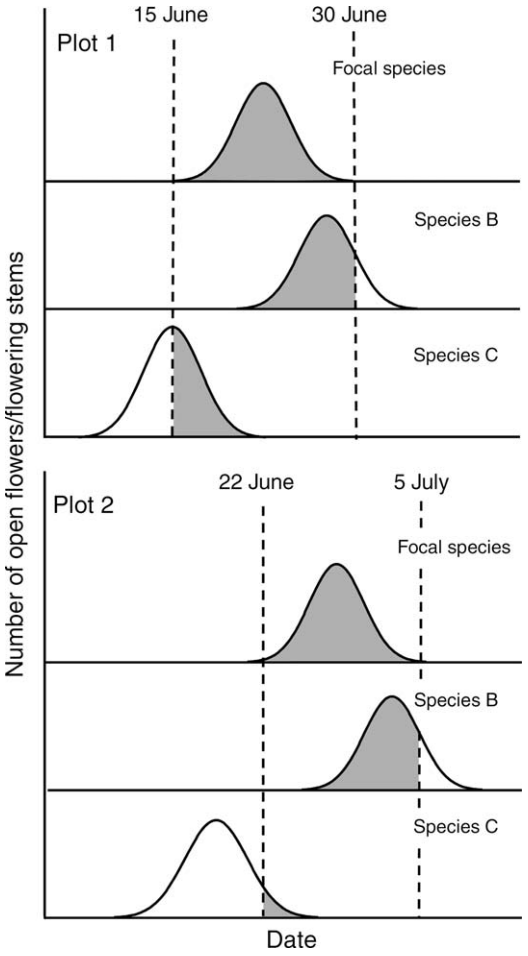


FIG. 2. Conceptual diagram illustrating the manner in which periods of flowering overlap were defined. The figure shows hypothetical flowering curves for three species occurring in two separate plots in one year. The period of flowering overlap for each plot is the time during which the focal species is in flower (the area between the dashed lines); this interval may differ across plots. The "co-flowering community" for the year is the summed floral abundances for all species flowering in all plots within the period of flowering overlap, including the focal species (i.e., the sum of the shaded areas).

1989); these large-bodied bees are likely the only effective pollinators of these plants (cf. Faegri and van der Pijl 1979). Because of the greater potential for pollinator-mediated interactions among these legumes, we conducted additional, more detailed analyses of patterns of overlap between pairs of these species.

Data analysis

Whole community overlap.—We took two approaches to quantifying flowering overlap for our focal species. In the first, we considered the entire assemblage of animal-pollinated plants that were in flower during the flowering period of each focal species to constitute a "co-flowering community" (Fig. 2). We then used multivariate statistics to ask whether the composition of this community in a given year (in terms of identity and relative abundances of co-flowering species) varied with the timing of snowmelt in that year.

We quantified the "abundances" of all species in the co-flowering community, including the focal species, by summing all flower (or inflorescence) counts for each species over the relevant time period. Missing individual data points (<1% of observations) were estimated by linear interpolation. In certain years (1976, 1977, 1992, and 1994), the beginning or end of the flowering season was missed, affecting our calculations of the co-flowering communities for certain species. These years were omitted entirely from analyses involving species' relative abundances, but were included in analyses that used only presence/absence data. Finally, 1976 was omitted from analyses of the *L. leucanthus* co-flowering community because the flowering period of that species was missed entirely in the mesic-meadow plots in that year.

Some plots have consistently earlier flowering (and snowmelt) than others. Considering the entire flowering period of a species across all plots would therefore inflate estimates of the number of co-flowering species and might obscure patterns related to interannual variation in climate. We instead considered the relevant set of co-flowering species to be those that overlapped with the focal species within each 2×2 m plot, although we recognize that pollinator-mediated interactions between plants are likely integrated over a larger scale than this. Thus we defined the flowering period of the focal species separately for each plot in each year; however, we summed floral abundances (within the relevant flowering periods) across all plots to construct the co-flowering community for each year (Fig. 2). We used only the plots in which the focal species was recorded as flowering in at least 15 of the 31 years.

We used a Mantel test to evaluate the relationship between date of first bare ground and co-flowering community composition across years. That is, we tested for a correlation between two matrices of distances between years: a matrix of differences in snowmelt dates and a matrix of Bray-Curtis distances between species compositions. Bray-Curtis dissimilarity is given by $\Sigma_j|y_{1j} - y_{2j}|/\Sigma_j (y_{1j} + y_{2j})$, where y_{1j} is the abundance of species j in year 1 (Quinn and Keough 2002). Bray-Curtis distances are more appropriate than Euclidean distances for species abundance data in which shared zeroes (joint species absences) are common but not necessarily informative (Quinn and Keough 2002). For calculating Bray-Curtis distance, we used relative abundances of all taxa for which we had complete data (i.e., number of flowers of each species or genus as a proportion of all flowers of all species in the plots in that year). We omitted from this analysis species for which we had only presence/absence data, rather than relative abundances, in certain years (*Salix* spp., *Paxistima myrsinites*, *Galium bifolium*). However, we checked the robustness of our results by repeating the analysis, first

with "common" species only (those that flowered in more than one year) and second using presence/absence data (common species only) instead of relative abundance. Significance of Mantel correlations was determined by randomization, with 1000 iterations.

To interpret better the Mantel correlation results for *L. leucanthus*, we used nonmetric multidimensional scaling (NMDS), based on Bray-Curtis distances, the same distance measure used in the Mantel tests, to plot co-flowering communities for each year in multidimensional space. The best NMDS solution was found by iteration (400×), and significance of each axis was assessed by Monte Carlo randomization. We then plotted the axis scores for each year against the corresponding date of first bare ground to determine whether any of the community axes was related to date of growing-season onset. Note that, unlike other ordination techniques such as canonical correspondence analysis (CCA), the approach we use does not force a relationship between the abiotic variable (snowmelt date) and community composition; rather, it simply allows us to summarize and visualize differences among communities and then independently assess whether these differences are related to variation in climate (Quinn and Keough 2002).

To help explain results obtained in the multivariate analyses, we investigated associations between snowmelt date and flowering variables for the 15 most abundant species in the *L. leucanthus* overlap community. For each species, we evaluated the effect of snowmelt date on peak flowering date, flowering intensity (the maximum number of flowers or inflorescences observed on one date), and flowering duration at the plot level. Flowering intensities were fourth-root transformed to achieve normality. We also tested for an effect of snowmelt date on the total number of species co-flowering with *L. leucanthus*. We verified that there was no detectable temporal autocorrelation in our variables by examining their autocorrelation functions; the absence of significant autocorrelation suggests that treating years as independent data points was justifiable. We conducted both the Mantel tests and NMDS in PC-ORD (McCune and Mefford 1999). All other analyses were done in R (R Development Core Team 2007).

Overlap between species pairs.—In the whole-community approach described here, each day within the flowering period of the focal species is given equal weight in terms of defining co-flowering community composition, regardless of the abundance of the focal species on that day. For the second approach, we focused on individual overlapping species and performed a more detailed analysis that took into account the proportion of the total flowering that occurred on each day within the flowering period. As our measure of the flowering overlap between two species, we used Schoener's index (SI) of niche overlap (Schoener 1970), $SI = 1 - (1/2)\,\Sigma_k\,|p_{ik} - p_{jk}|$, where p_{ik} is the proportion of flowering by species i occurring on day k. Schoener's index has values close to 0 when only the tails of the two species' flowering curves overlap and reaches a maximum of 1 when the flowering curves of the two species coincide perfectly. For each year, we calculated SI separately for each plot in which the two species occur; we then averaged the SI values across all plots for each year. Before calculating SI, we filled in values for flower counts on days without data by linear interpolation. We tested for a relationship between SI and snowmelt date using rank-based correlations instead of linear regression because of the large number of zero values. We conducted this analysis for two species pairs that could be expected to interact for pollinators: *Lathyrus leucanthus–Lupinus prunophilus* and *Lathyrus leucanthus–Vicia americana*. We applied a Bonferroni-corrected significance criterion of 0.025 because of the need to conduct the two pairwise tests separately.

Results

Temporal autocorrelation

We detected no significant temporal autocorrelation in snowmelt date, peak flowering dates of focal species, or the intensity or duration of flowering of *L. leucanthus* ($P > 0.05$), suggesting that individual years may reasonably be treated as independent data points. However, it should be noted that the length of the time series and the two missing years give limited power to detect autocorrelation.

Whole community overlap

There is a significant Mantel correlation between date of first bare ground and composition of the co-flowering community for two of the four species considered, *L. leucanthus* and *H. hoopesii* (Table 1). Obtaining the observed P values (three of which fall below 0.11) in a set of four independent tests would be highly unlikely in the absence of any real effect (Fisher's method for combining P values, $\chi^2 = 23.4$, $df = 8$, overall $P = 0.0029$; Quinn and Keough 2002). These results are largely unchanged if we remove from the analysis species that flowered in only one year, but doing so strengthens the pattern observed in *M. fusiformis* (new Mantel $r = 0.18$, $N = 27$ years, $P = 0.055$; the original P value was 0.109). We also repeated the analyses using presence/absence data (coding any species that overlapped with the focal species as "present" and any that did not as "absent") instead of relative abundances. Doing this rendered the pattern for *M. fusiformis* significant (Mantel $r = 0.15$, $N = 31$, $P = 0.031$), because of the increased power afforded by including four additional years in which relative abundance data were unreliable, but did not qualitatively change results for the other species.

Nonmetric multidimensional scaling of *L. leucanthus* co-flowering communities for all years produced three significant axes, explaining 34.8%, 34.3%, and 15.2% of the variation, respectively. Scores on the first axis were significantly associated with date of first bare ground (Fig. 3), suggesting that one major axis of variation in

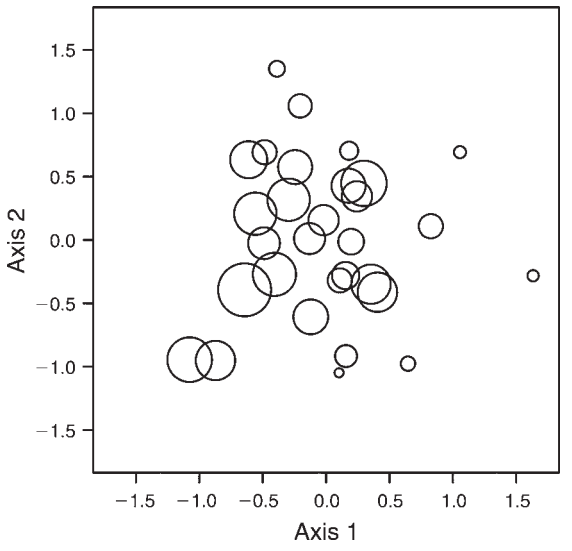


FIG. 3. Nonmetric multidimensional scaling of *Lathyrus leucanthus* co-flowering communities (two of three significant axes shown, representing 69% of the variation in community composition). Points in the scaling are individual years; point size is proportional to snowmelt date in that year (larger points indicate later date). There is a negative association between axis-1 scores and snowmelt date ($R^2 = 0.32$, $P = 0.0006$).

community composition is related to snowmelt date. Species with low scores on axis 1 had later peak flowering dates (means across all plots and years; Pearson's $r = -0.66$, df = 13, $P = 0.0080$), indicating that, in years with low scores on this axis (late years), *L. leucanthus* overlapped to a greater extent with later-season species. We detected no significant temporal autocorrelation in axis 1 scores ($P > 0.05$). However, the axis 3 autocorrelation function shows a consistent decrease in the partial autocorrelation coefficient as the lag interval increases, indicating greater dissimilarity among communities separated by larger time intervals; this axis may therefore reflect changes in species abundance over time.

This result suggests that *L. leucanthus* may shift its flowering period disproportionately earlier, compared to other members of the community, in early snowmelt years. *Lathyrus leucanthus* does have a relatively strong response to variation in snowmelt, particularly compared to later-flowering species (see Appendix). However, individual species have largely homogeneous responses to variation in snowmelt (Fig. 4). Although the slopes of the relationship between peak flowering date and snowmelt date differ slightly among species (ANCOVA, snowmelt date × species $P = 0.089$), this effect is due to a single annual species, *Collomia linearis*, that is relatively unresponsive to variation in snowmelt (Fig. 4; Appendix). The effect of snowmelt date on the *L. leucanthus* overlap community is not influenced by inclusion of this species (Mantel test with *C. linearis* omitted, $r = 0.23$, $P = 0.004$). Thus, a simple examination of shifts in peak flowering across years would not, by itself, point to a relationship between co-flowering patterns and snowmelt date.

The peak number of *L. leucanthus* flowers (summed across plots, fourth-root transformed) was greater in years with later snowmelt (linear regression, $R^2 = 0.16$, $N = 31$, $P = 0.016$). However, mean flowering duration of *L. leucanthus*, although strongly correlated with flowering intensity (Pearson $r = 0.57$, $P = 0.0006$), was not significantly influenced by snowmelt date (linear regression, $R^2 = 0.053$, $N = 31$, $P = 0.11$). In fact, flowering durations of most of the species in this data set were not strongly affected by variation in snowmelt date (Appendix).

Three of the species that showed the strongest positive association between flowering intensity and snowmelt date are relatively late-flowering species (*Delphinium barbeyi*, *Lupinus prunophilus*, and *Mertensia ciliata*; Appendix). Greater numbers of flowers of these species in years of late snowmelt might contribute to greater overlap between *Lathyrus leucanthus* and later-flowering species in these years. However, because Mantel test results were essentially unchanged when we used presence/absence rather than relative abundance data, it is unlikely that variation in flowering intensity is the sole driver of the patterns we observe. Indeed, variation in snowmelt date also influenced the number of species with which *L. leucanthus* overlapped. There was a positive relationship between snowmelt date and species richness of the co-flowering community (range = 13–34 species; linear regression, $R^2 = 0.12$, $N = 30$, $P = 0.032$), and this relationship remained significant even if only species with more than 10 open flowers or inflorescences

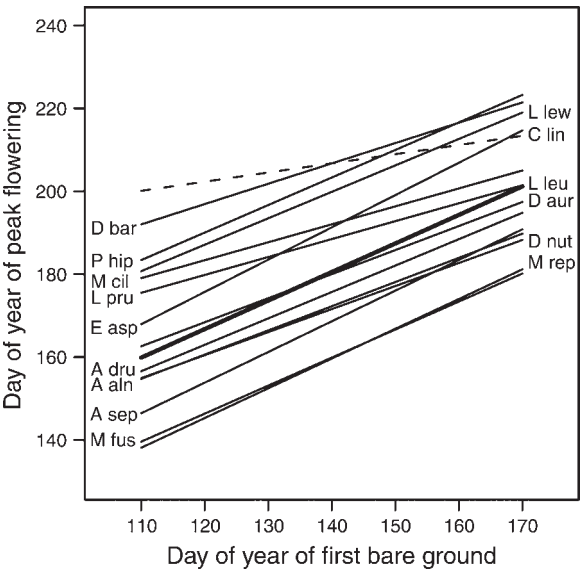


FIG. 4. Regression lines for peak flowering date vs. snowmelt date for the 15 most abundant species in the *Lathyrus leucanthus* co-flowering community. Complete species names are provided in the Appendix. The dashed line represents the annual species *Collomia linearis*; the thicker solid line represents *L. leucanthus*. Individual data points are omitted for clarity.

per year (over all plots, during the *L. leucanthus* flowering period) were considered.

Despite a trend for earlier melting over the period 1975–2007 (Kendall's $\tau = -0.28$, $P = 0.026$) and a similar trend for earlier peak flowering in *L. leucanthus* over the same time period (Kendall's $\tau = -0.25$, $P = 0.049$), there is no temporal trend in NMDS axis scores ($|\tau| < 0.2$, $P > 0.3$).

Species pairs

Overlap between *Lathyrus leucanthus* and the later-flowering *Lupinus prunophilus* is significantly lower in years of early snowmelt (Spearman correlation between SI and snowmelt date, $\rho = 0.66$, $\alpha = 0.025$, $P < 0.0001$; Fig. 5a). In fact, in early years (date of first bare ground < 139), there typically has been no temporal overlap (SI $= 0$) between the two species at the scale of individual plots, while in later years, overlap values mostly fall between 0.25 and 0.65. Overlap has tended to be less in recent years, but this trend is marginally nonsignificant (Kendall's $\tau = -0.26$, $P = 0.052$; Fig. 5a). There is no relationship between snowmelt date and overlap between *Lathyrus leucanthus* and *Vicia*, the last species of the three to flower (Spearman $\rho = -0.07$, $\alpha = 0.025$, $P = 0.72$; Fig. 5b).

Discussion

For at least two of the four focal species we examined, among-year differences in flowering overlap were partially explained by variation in snowmelt date. In years of early snowmelt, these species flowered together with, and likely shared pollinating animals with, a different suite of other plants than they did in late-snowmelt years. In a third species (*Mertensia fusiformis*), co-flowering patterns may also have been influenced by snowmelt date, but the significance of the effect depended on how we treated the data. Only for *Heterotheca villosa*, one of the latest- and longest-flowering species in these meadow communities, was there no indication of a trend related to snowmelt date. Previous work, both at the RMBL and elsewhere, has shown that flowering times of earlier-flowering species tend to be more responsive to variation in the timing of the start of the growing season (Fitter and Fitter 2002, Dunne et al. 2003, Miller-Rushing et al. 2007); our results are consistent with the idea that effects of phenological variation can be muted for later-flowering species.

For *Lathyrus leucanthus*, the species we examined in most detail, interannual differences in the assemblage of co-flowering species appeared to be related to a tendency for the species to overlap with more species overall, and to a greater extent with later-flowering species, in years of relatively late snowmelt. In particular, temporal overlap with the later-flowering *Lupinus prunophilus* was greatly reduced in early-snowmelt years. These patterns may be partly due to slight (nonsignificant) differences among species in the extent to which the date

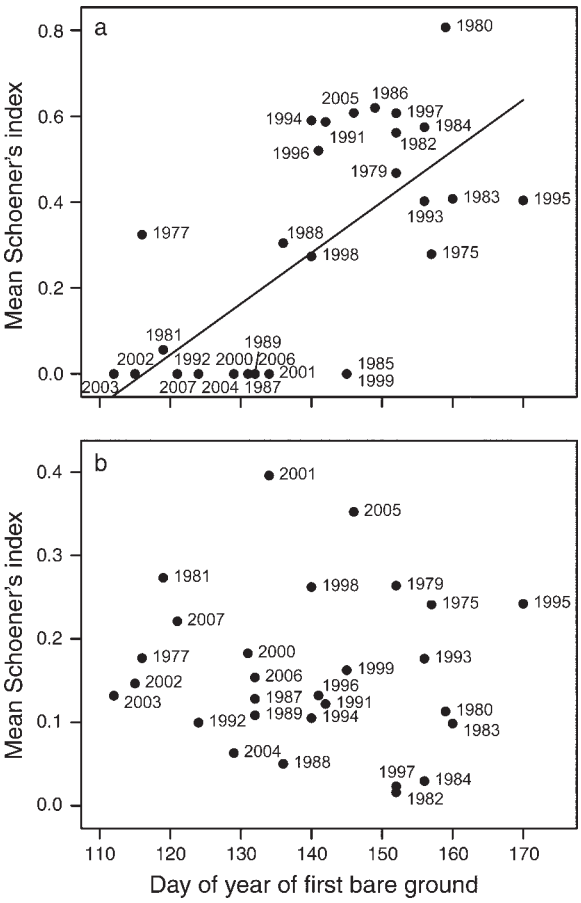


FIG. 5. Temporal overlap (Schoener's index) between *Lathyrus leucanthus* and (a) *Lupinus prunophilus* and (b) *Vicia americana* as a function of snowmelt date ($N = 30$ years). The regression line in panel (a) is $y = 0.012x - 1.38$ ($R^2 = 0.42$).

of peak flowering responds to snowmelt timing. At least as important are interspecific differences in the relationship between snowmelt timing and intensity of flowering. As has previously been noted (Inouye et al. 2002, Miller-Rushing and Inouye 2009), certain midsummer species, notably *Mertensia ciliata* and *Delphinium barbeyi*, flower more abundantly in years with greater snowpack or later snowmelt. For some species at our study site (*Helianthella quinquenervis*, *Erigeron speciosus*), early snowmelt is accompanied by a high risk of frost damage to buds and a severe reduction in flowering. For these species, there appears to be a threshold snowmelt date, around 19 May, before which frost damage to flower buds is very likely (Inouye 2008). Buds of *L. prunophilus* are also frost-sensitive, and flowering can be severely depressed in these early-snowmelt years (Inouye 2008; also J. Forrest, D. W. Inouye, and J. D. Thomson, *personal observations*); this helps explain the 19 May threshold we observe in the pairwise overlap with *Lathyrus leucanthus* (Fig. 5a), particularly if the earliest buds are those most likely to be affected by killing frosts. A threshold effect is

not apparent, however, in the community-level analysis (Fig. 3).

Idiosyncratic effects of snowmelt timing on flowering duration, with some species flowering for longer periods in late years and some flowering longer in early years, may also explain part of the community-level pattern. Effects on flowering duration were significant for only two of 15 species considered, however: duration was increased in early years for the relatively early species *Mahonia repens*, but was decreased in early years in the later-flowering, but frost-sensitive *D. barbeyi*. In contrast to some previous work (spatial gradient study in Price and Waser 1998, Dunne et al. 2003), we did not find a general positive effect of early snowmelt on flowering duration for early-flowering species. This is most likely because we considered the flowering period at the plot level, rather than at the level of individual plants, and any individual-level increases in flowering duration could have been compensated for by decreases in abundance of flowering in early-snowmelt years (e.g., in *D. nuttallianum*). In any case, it is clear that the community-level patterns we document here could not be easily predicted from considering species-specific changes in peak flowering dates or flowering intensities alone; instead, they reflect the integrated changes in flowering patterns of multiple species across years and highlight the value of a multivariate approach for understanding community change.

We did not detect strong temporal trends in co-flowering patterns, despite a measurable advance in snowmelt date over this time period. This is partly owing to the great interannual variability in climate, but also to the large amount of variation in flowering patterns that could not be explained by variation in snowmelt timing. Including air temperature data in the matrix of climate variables did not improve correlations between climate and patterns of flowering overlap; but it is possible that other unmeasured or finer-scale climate variables (e.g., snowmelt dates for individual plots) might be important. Gradual demographic changes such as plant growth, death, and recruitment within plots must also contribute to among-year variation in flowering, independent of year-to-year changes in snowmelt date. However, most plants in these communities are long-lived perennials, and there have not been any large-scale changes in species composition during the study period. Losses of flowers to herbivores (e.g., deer) and local frost events may explain some of the remaining variance, but at least the focal species do not appear to be much affected by specialist herbivores. Clearly, predicting future co-flowering patterns would not be straightforward, even if we had reliable local climate forecasts. In addition to the effects of climate on flowering patterns that we have shown here, there is likely to be a longer-term effect of climate change on the relative abundances of species in these communities (de Valpine and Harte 2001, Saavedra et al. 2003). Understanding how the phenological and demographic effects of climate change will interact remains a challenge.

We know of no other long-term data sets that would permit an analysis of the type conducted here. A single-season experiment in grassland plots (Sherry et al. 2007) also showed a change in relative flowering times caused by severe (4–5°C) experimental warming, leading to a midsummer gap in flowering. However, as many species in that system were wind-pollinated grasses, the potential for pollinator-mediated interactions among plants was limited. Spatial variation in patterns of flowering overlap (e.g., across elevational gradients) may be similar to the temporal variation we have dealt with. Among-site comparisons of co-flowering patterns, and their fitness consequences for focal plant species, would be a useful complement to our data.

Presumably, changes in the identities of co-flowering species could influence both the behavior and population dynamics of flower-visiting insects, leading to altered selective environments for plants (cf. Kudo 2006). However, there are few long-term data sets on North American insects (Williams et al. 2001) and none of which we know with a resolution comparable to the plant data set we have used here; we therefore lack information on temporal variation (both within and among years) in the populations of what we presume are important selective agents. In the absence of hard data on pollinators, we may imagine some possible consequences of the climate-mediated changes in co-flowering patterns we observe: reductions in the abundance and overlap of flowers that share pollinators (e.g., *Lathyrus leucanthus* and *Lupinus prunophilus*) could reduce interspecific competition among plants for those pollinators. Alternatively, it could lead to a failure to attract and maintain local populations of generalist pollinators. For example, the presence of flowering individuals of one species can increase pollinator visitation and seed set in a second species (Laverty 1992, Moeller and Geber 2005). This effect is possible if the first species is more attractive to pollinators (a "magnet species"; Thomson 1978) or if both species are equally attractive but pollinator visitation is an accelerating function of density (Feldman et al. 2004) and the cost of receiving heterospecific pollen is low (e.g., Schemske 1981). Changes in the assemblages of species flowering together at the local patch scale may therefore alter the patch selection decisions of pollinators. Over a longer term and larger scale, pronounced reductions in flowering overlap within guilds of pollinator-sharing plants could mean that those pollinators face resource shortages during particular periods of the flowering season, with unknown consequences for pollinator populations. Long-term studies of plant–insect interactions in a community context, and their consequences for plant populations, would help to answer some of these questions.

A further complication is that climate variation also has a direct impact on pollinator phenology. In a recent

synthesis of the evidence that climate change may disrupt plant–pollinator relationships, Hegland et al. (2009) point out that, in many cases, both plant and insect phenology appear to be governed by temperature, perhaps making changes in interactions unlikely. However, some studies suggest that plants and pollinators may not respond in parallel to climate change (Kudo et al. 2004, Gordo and Sanz 2005); and, as our results show, even when members of a community are similarly responsive to environmental cues, shifts in temporal co-occurrence patterns are possible. Population-level consequences of asynchronies between plants and pollinators remain largely untested (Hegland et al. 2009).

In conclusion, we have shown that year-to-year variation in snowmelt timing has affected co-flowering patterns in subalpine meadows over the last three decades, influencing the identity and relative abundances of potentially competing plants, despite broad similarities in individual species' responses to snowmelt date. For *Lathyrus leucanthus*, this has meant flowering concurrently with fewer species overall and overlapping less with other pollinator-sharing legumes in early-snowmelt years. We detected no strong temporal trends in community patterns using this data set, but an increasing frequency of early-snowmelt years with climate warming seems likely to cause long-term change in co-flowering patterns in subalpine communities.

Acknowledgments

We are grateful to the Rocky Mountain Biological Laboratory for providing research facilities and access to study sites, to billy barr for collecting snowpack data, and to the many people who helped count flowers in the phenology plots. The programming wizardry of Josie Hughes made data compilation less painful, and careful editing by Abe Miller-Rushing removed numerous idiosyncrasies from the data set. Abe Miller-Rushing, Nickolas Waser, and Ørjan Totland provided constructive comments on the manuscript. Funding and research assistance for collection of phenology data were provided by the National Science Foundation (dissertation improvement grant, grants DEB 75-15422, DEB 78-07784, BSR 81-08387, DEB 94-08382, IBN-98-14509, and DEB-0238331), Sigma Xi, an NDEA Title IV predoctoral fellowship, research grants from the University of Maryland's General Research Board, and assistance from Earthwatch and its Research Corps (all to D. W. Inouye). J. Forrest was supported by postgraduate scholarships from the Natural Sciences and Engineering Research Council of Canada and the Fonds Québécois de la Recherche sur la Nature et les Technologies.

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APPENDIX

Mean peak flowering dates and regression slopes for the 15 most common species with flowering periods overlapping that of *Lathyrus* (*Ecological Archives* E091-032-A1).