Journal of Ecology

Journal of Ecology 2011, **99**, 905–913 doi: 10.1111/j.1365-2745.2011.01826.x

Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change

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Summary

1. Shifts in the spatial and temporal patterns of flowering could affect the resources available to pollinators, and such shifts might become more common as climate change progresses.

2. As mid-summer temperatures have warmed, we found that a montane meadow ecosystem in the southern Rocky Mountains of the United States exhibits a trend toward a bimodal distribution of flower abundance, characterized by a mid-season reduction in total flower number, instead of a broad, unimodal flowering peak lasting most of the summer season.

3. We examined the shapes of community-level flowering curves in this system and found that the typical unimodal peak results from a pattern of complementary peaks in flowering among three distinct meadow types (dry, mesic and wet) within the larger ecosystem. However, high mid-summer temperatures were associated with divergent shifts in the flowering curves of these individual meadow types. Specifically, warmer summers appeared to cause increasing bimodality in mesic habitats, and a longer interval between early and late flowering peaks in wet and dry habitats.

4. Together, these habitat-specific shifts produced a longer mid-season valley in floral abundance across the larger ecosystem in warmer years. Because of these warming-induced changes in flowering patterns, and the significant increase in summer temperatures in our study area, there has been a trend toward non-normality of flowering curves over the period 1974–2009. This trend reflects increasing bimodality in total community-wide flowering.

5. The resulting longer periods of low flowering abundance in the middle of the summer season could negatively affect pollinators that are active throughout the season, and shifts in flowering peaks within habitats might create mismatches between floral resources and demand by pollinators with limited foraging ranges.

6. *Synthesis*. Early-season climate conditions are getting warmer and drier in the high altitudes of the southern Rocky Mountains. We present evidence that this climate change is disrupting flowering phenology within and among different moisture habitats in a sub-alpine meadow ecosystem, causing a mid-season decline in floral resources that might negatively affect mutualists, especially pollinators. Our findings suggest that climate change can have complex effects on phenology at small spatial scales, depending on patch-level habitat differences.

Key-words: climate change, cumulative flowering density, flower abundance, flowering phenology, plant–climate interactions, pollinators, resource availability, Rocky Mountain Biological Laboratory

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Introduction

Floral resources affect pollinators in complex ways at many spatiotemporal scales (Bronstein 1995; Potts *et al.* 2003; Kremen *et al.* 2007; Vázquez, Chacoff & Cagnolo (2009), but must be available throughout the life cycle of obligate flower visitors for successful reproduction. Some pollinators with short periods of activity may require only a single flower species, but pollinators active all season must have flowers available in sufficient numbers throughout the season. For example, bumblebees (*Bombus* spp.) – important pollinators in many temperate regions – require a pollen and nectar supply throughout the growing season to allow the queen to produce a colony and to produce reproductive castes at the end of the season (Heinrich 1979). Pollinators whose foraging range is limited by habitat or body size must have flowers available at the proper time in their locale. Changes in seasonal flower availability across large areas, or within individual habitats could have serious consequences for pollinator populations. Over the long-term, such changes could also have indirect negative effects on populations of animal-pollinated plants (Price & Waser 1998; Memmott *et al.* 2007).

Climate is a powerful driver of phenology (Gordo & Sanz 2010) and the effects of climate change on phenology have become a major focus of research (Sherry *et al.* 2007; Post & Forchhammer 2008; Both *et al.* 2009; Saino *et al.* 2009). Climate change might affect flowering phenology differently in different habitats, especially if the habitats are themselves largely characterized by differences in climate-related factors, such as temperature and moisture rather than by other factors such as fire, grazing or soil chemistry. Given that plant phenology is often driven primarily by temperature, precipitation and the timing of snowmelt (Inouye & Wielgolaski 2003; Wielgolaski & Inouye 2003), one might expect the response of flowering phenology to climate change to differ substantially between warm and cool sites, dry and wet sites, or sites with early and late snowmelt, particularly because we know that phenological responses to climate variability are nonlinear (Primack *et al.* 2009).

The montane meadows of the southern Rocky Mountains provide an example of flowering plant communities heavily influenced by snowfall and temperature (Inouye & McGuire 1991; Inouye, Morales & Dodge 2002; Dunne, Harte & Taylor 2003; Forrest, Inouye & Thomson 2010). We are conducting an ongoing study of flowering plant phenology in meadows in the Elk Mountains of Colorado begun in the mid-1970s. Recently, we have noted a mid-season decline in flowering totals for the system as a whole that could be an important change in the floral resources available to pollinators in these montane meadows. Here, we examine community-level flowering curves in this system and address the following questions: (i) is there a trend toward bimodality in the temporal distribution of flower abundance within the community?; (ii) how is the overall distribution of flower abundance affected by changes in flowering phenologies in different habitats? and (iii) what climate factors might be driving changes in the distribution of flower abundance in this community?

Materials and methods

STUDY SITE AND SAMPLING

In this study, we analyse data from long-term records of flowering plant phenology in montane meadows at *c.* 2900 m a.s.l in Gunnison County, Colorada, USA. The study area includes plots in a variety of habitats ranging from dry, rocky slopes to wet, low areas. These plots were originally chosen to capture the full range of meadow communities in this system and represent all non-forest, open-meadow habitats in the study area where flowers and pollinators are common. Data were collected from thirty 2 × 2 m plots, the first of which were established in 1973 at the Rocky Mountain Biological Laboratory (RMBL) (see Inouye 2008 for detailed description of site location). There are 6–15 plots in each of three habitat types within the montane meadow ecosystem of RMBL: dry, rocky sites (*dry*) typically occur on slopes and outcrops with shallow soil, wet sites (*wet*) occur either on lower level ground or immediately adjacent to seasonal or permanent streams and intermediate sites (*mesic*) are dryer than the wet sites, but level and with more developed soil than the dry sites. Replicate plots within these habitats are located in discrete spatial areas (see Inouye 2008 for map), although the three habitats occur in a mosaic throughout RMBL.

This study is ongoing, and plots have been surveyed every year 1973–2009, except 1978 and 1990, for most or all of the flowering season. Every 2 or 3 days, all flowers on all species are counted in each plot. Some species with very large numbers of very small flowers are counted as flowering stalks or ramets, and inflorescences of the Asteraceae are counted as single ‘flowers’ (capitulate). Metadata for the project are available at Websites of the RMBL and the Digital Repository at the University of Maryland.

Data on snowmelt date (melt) have been collected by one of us (Barr) since 1975; data on temperature and precipitation for summer months are missing prior to 2000 from this source. We used data from a NOAA weather station in Crested Butte, Colorado – *c.* 13 km south of and 210 m lower than RMBL – for precipitation and temperature in all years, although July temperature data for 1980 and 2009 were unavailable. Snowmelt date was recorded at a single location in RMBL that melts out later than some of our plots, resulting in some flowering records in our plots appearing before snow has melted. We have recently added data loggers in all plots that will provide plot-specific snowmelt dates for future analyses.

FLOWERING CURVES

We restricted our analyses to those species counted as ‘flowers’, not stalks or ramets, which resulted in the exclusion of 18 zoophilous species that have small flowers in relatively dense inflorescences. However, these species make little contribution to the flowering counts: of the 18, only one – *Eriogonum umbellatum* – departed from the phenology typical of the species we included in the analysis. *Eriogonum umbellatum* occurred in the dry habitat and reached its peak flowering during the mid-season period of low flower abundance typical of that habitat. Sometimes as many as 150 inflorescences of *E. umbellatum* were open on a single day. However, the flowers are small and rarely, if ever, visited by hummingbirds and large-bodied bees. We also excluded graminoids and other wind-pollinated species from our analysis, although we acknowledge that these species may be an occasional pollen source for some insects. Flowering curves were constructed by summing flower counts across plots within each habitat. The census period was severely truncated in 5 years (1976, 1982–85 and 1992–94), usually beginning well after the onset of flowering, which resulted in artificially skewed flowering curves. Those years were excluded from the analysis, leaving 29 years of data from 1974 to 2009.

CUMULATIVE FLOWERING DENSITY

We used cumulative flowering density curves (CFD) to analyse the shapes of flowering curves by habitat and year. Such curves have several advantages over 'raw' curves of total flower numbers: (i) CFD is a smoother curve with much less noise; (ii) the moments of CFD provide reliable indications of their shape – given a regular sampling interval – and can be compared with expected values from a normal or uniform distribution and (iii) the y-axis is standard (0…1) among all CFDs, regardless of variation in the magnitude of the raw flowering curves. To illustrate the second point, we present data from 1976 – a year we excluded from other analyses because of truncated sampling (Fig. 1). A uniform CFD will be linear (Fig. 1a, filled circles) and have a mean of 0.5. A skewed flowering curve will produce a CFD that is either concave or convex depending on the direction of the skew, and the mean of which will depart from 0.5 with increasing skew as points are more concentrated at one end or the other. A right-skewed flowering curve – one with an early peak – will produce a CFD that accelerates rapidly, then flattens, resulting in a mean > 0.5, while CFDs of a left-skewed flowering curve – one with a late peak – will accelerate more slowly and then rise rapidly, resulting in a mean < 0.5. A bimodal flowering curve (Fig. 1a, triangles) will produce a CFD with a horizontal 'kink' representing the downturn between peaks. Because of this relatively flat section, the variance of the bimodal CFD will be lower than that of the linear CFD as more points are located near the mean of the CFD (Fig. 1a, open circles).

The standard y-axis of all CFDs allows us to use the x-axis (sampling days) to compare the shapes of different CFDs. We can choose points on the y-axis that are necessarily the same for all CFDs and look for differences among their corresponding locations on the x-axis (hereafter, we refer to these x-axis locations as 'D05', 'D25', etc. meaning the day on which the CFD equalled 5%, 25%, etc.). We can quantify the symmetry of a flowering curve by comparing the time between pairs of 'D' values. For example, in an early peaking flowering curve, D95-D50 will be much larger than D50-D05, as it takes much less time to accumulate the first 45% of flowering density than it takes to accumulate the next 45%. The CFD for a bimodal flowering curve will have smaller intervals between pairs of early and pairs of late 'D' values, while the interval in the middle will be much larger (Fig. 1b – compare D95-D75 to D75-D50).

This method of CFD analysis is not intended as a statistical test of departure from a null model curve. The purpose is not to determine whether a given distribution is significantly skewed or bimodal, it is to provide an indication of the degree to which a curve is skewed or bimodal that can in turn be analysed as a response variable. In the former case, skewness – the third moment – of raw flowering curves can be directly calculated and there are tests for significance (e.g. D'Agostino 1970). We assessed our method by comparing the 5 years in our data set that ranked as most (or least) skewed by third moment to the five that had the highest (or lowest) mean CFD – recall that mean CFD = 0.5 in a non-skewed distribution. Raw flowering curves and CFD were similar for the two matched sets of years (Fig. 2). However, the skewness of the curve for the high-skewness years was twice as large as for the high-mean CFD years (0.78 vs. 0.39), while mean CFD for the two groups were essentially identical (0.615 vs. 0.616). Similarly, the 5 years that were least skewed according to each metric showed similar mean CFD (0.513 vs. 0.526), but quite different skewness values (−1.36 vs. −0.52). Thus, similarly shaped raw flowering curves are called similar by our mean CFD method, but different according to calculations of skewness. Indications of skewness vs. mean CFD were not entirely different, however, Of the 10 years with highest mean CFD, six also had significant skewness according to D'Agostino tests.

Unlike skewness, bimodality is not a moment of a distribution and cannot be calculated directly. Bimodality is a qualitative characteristic of a distribution and can be assessed only relative to some deterministic null model of curve construction; in the case of flowering curves, it is not clear what that null model should be (see Hartigan & Hartigan 1985). We decided not to use Hartigan's Dip test of

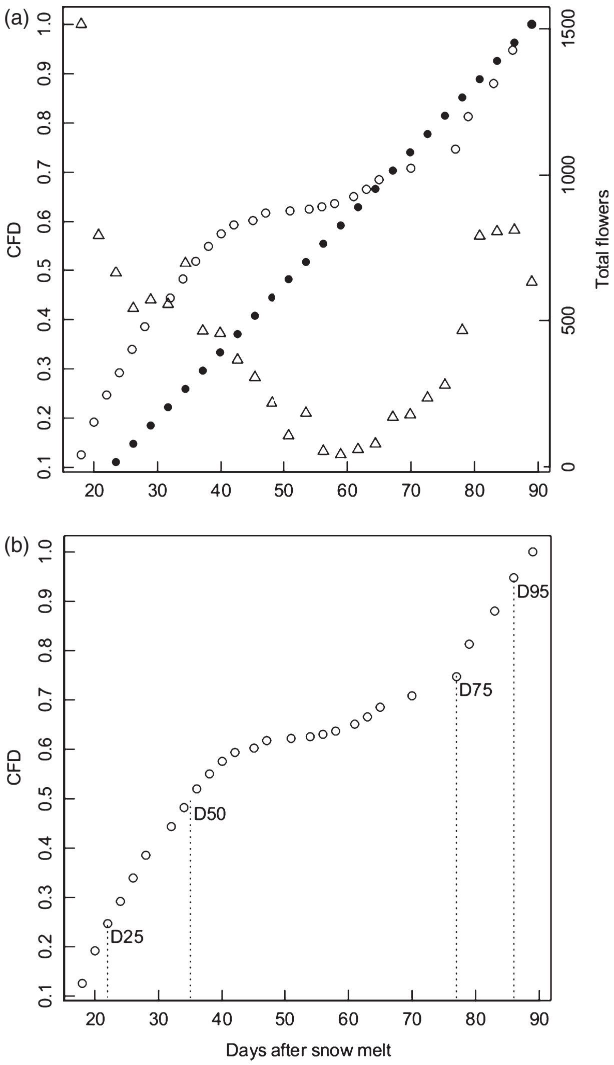

Fig. 1. Cumulative flowering density (CFD; points) and flowering curve (triangles) for the year 1976 from a montane meadow ecosystem in Colorado, USA. Panel a: triangles are the total number of flowers in all plots; open circles are the observed CFD; filled circles are a uniform CFD for the same number of sampling dates. Note that the observed CFD has a preponderance of points around 0.6 compared to the uniform CFD and thus a higher mean and lower variance (means: 0.577 vs. 0.500; variances: 0.047 vs. 0.093, respectively). Panel b: open circles are the observed CFD; dotted lines show the sampling days that correspond to CFD equal to 0.25 (D25), 0.5 (D50), 0.75 (D75) and 0.95 (D95). Because sampling missed the beginning of the flowering season, CFD was > 0.05 on the first sampling date, hence D05 is not represented on the x-axis.

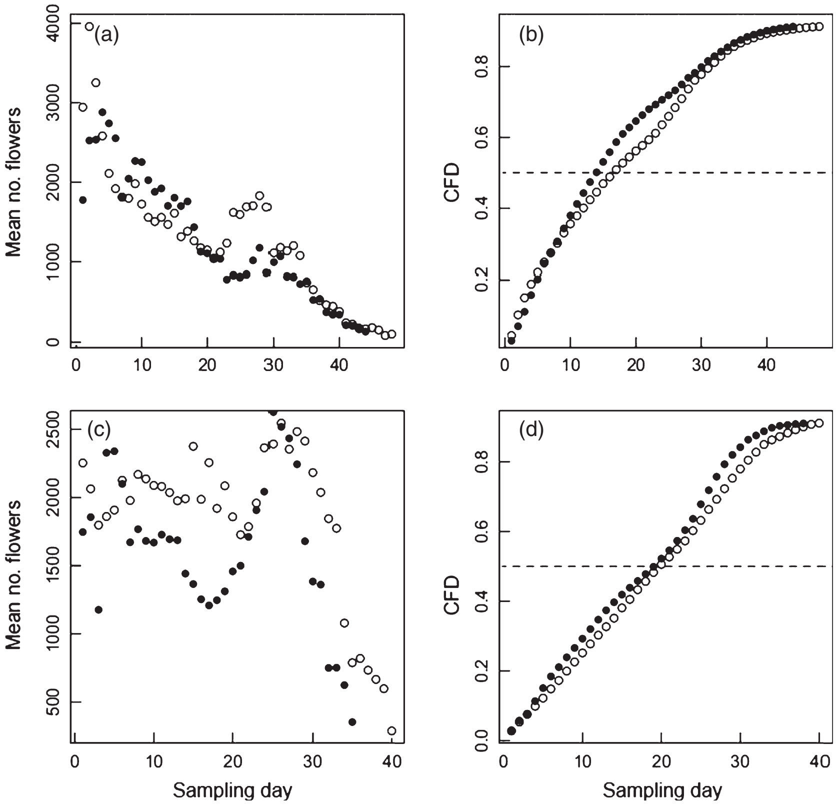

Fig. 2. Raw flowering curves (a,c) and cumulative flowering density (CFD; b, d) for 10 years of flowering in montane meadows in the Rocky Mountains, Colorado, USA. Open circles represent means from 5 years with highest (a, b) or lowest (c, d) skewness; filled circles represent means from 5 years with highest mean CFD (a, b) or mean CFD closest to 0.5 (c, d).

unimodality because, again, we were not primarily interested in assessing statistical significance of departures from unimodality. Furthermore, when we tested our *total* flowering curves with Hartigan's Dip, all were significantly non-unimodal because of the magnitude of the *y*-axis and the noisiness of the data. We therefore developed a more conservative method, specifically for quantifying bimodality, based on the cumulative flowering distribution. We used the difference between the variance of the observed CFD and that of a uniform distribution of the same length as a quantification of the *amount of bimodality* in a distribution; we call this difference a 'standard variance deviate' (SVD). Cumulative flowering density variances that are small relative to those of the corresponding uniform distributions give negative values of SVD and reflect more pronounced bimodality in the observed flowering curve (Fig. 3).

We wish to emphasize that these analyses of CFD are possible only when the sampling interval is regular among all curves being compared, and reiterate that these analyses quantify trends in curve shape and are not useful for assigning statistical significance to departure of any given curve from a null expectation.

We calculated raw flowering curves and CFD for each habitat and for the total of all habitats in each year. We analysed only the middle 90% of each CFD, to control for variation in early and late-season tails that might result from inconsistencies in sampling rather than biologically important effects. Flatness of the middle 50% of CFD was calculated as (D75-D50)/(D75-D25). An increase in flatness means a slowing of the accumulation of flowering density between 50% and 75% compared with the same between 25% and 50%, which reflects a mid-season downturn in the raw flowering curve.

We used linear regressions of mean, SVD and flatness of CFD over July–August mean temperature to test for effects of increases in mid-summer temperature on the shapes of flowering curves. We focused on July–August mean temperature because exploratory analysis of climate trends in our study area showed that this variable has increased by 1.4 °C since 1974 (Fig. 4); other climate variables have shown no significant trend over this period. Finally, we tested raw flowering curves (middle 90%) for normality using the Shapiro–Wilk W statistic, and logistic regression of the frequency of non-normality of W ($\alpha = 0.05$) over time to compare our CFD method to a traditional statistical test for temporal changes in the shapes of flowering curves. All analyses were performed in R (R Development Core Team 2009).

Results

Flowering patterns differed among the three habitats (Fig. 5). The *dry* habitat was consistently right-skewed, with a high early season peak and a lower late-season peak (Fig. 5a, open circles), resulting in a convex CFD with a small 'kink' reflecting the mid-season valley (Fig. 5a, line). The *mesic* habitat had a single somewhat narrow peak that occurred between the peaks in *dry* (Fig. 5b. open circles), resulting in a steep, linear CFD (Fig. 5b, line). *Wet* habitats showed the same bimodal pattern as *dry*, except the relative heights of the peaks were reversed (Fig. 5c, open circles). These three curves combined produced a *total* flowering curve with a broad peak lasting from *c.* −25 to 90 days after snow melt (Fig. 5d, open circles), and a linear CFD similar to that in *mesic*, but with a shallower slope (Fig. 5d, line). The pattern of early and late peaks in *dry* and *wet* straddling the single peak in *mesic* results in the mid-season flower abundance being especially sensitive to the timing of the *mesic* peak.

Mean of CFD in *dry* decreased with increasing July–August mean temperature (linear regression: $\beta = -0.03$, d.f. = 26,

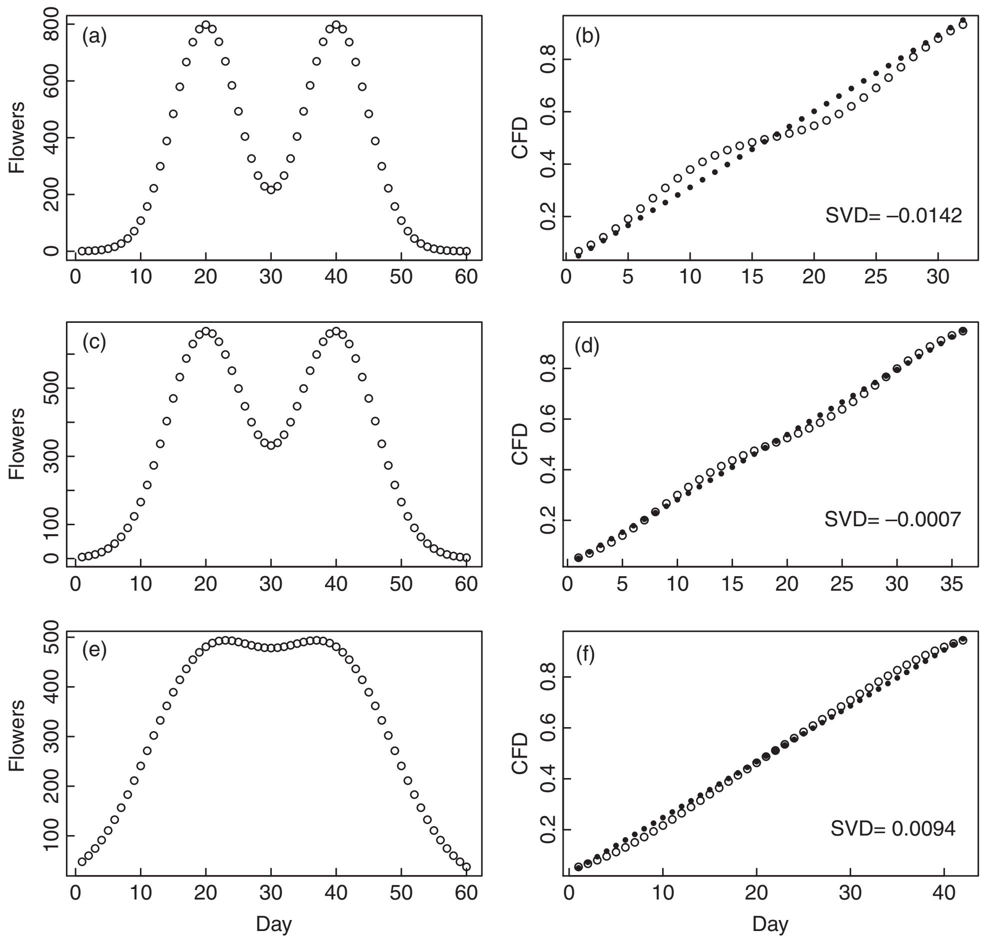

Fig. 3. Simulated flowering curves with varying degrees of bimodality (a, c, e) and middle 90% of cumulative density of those curves (b, d, f). Cumulative flowering density curves (CFD, open circles) are shown relative to uniform densities of equal length (filled circles). Numbers are var(CFD)-var(uniform). Note that sign changes while curve still shows slight bimodality (e, f).

P = 0.039), reflecting a delay in the second flowering peak and more pronounced mid-season valleys in flowering with warmer temperatures. SVD (standardized variance deviate of CFD) in *wet* also decreased with increasing Jul-Aug mean temperature (β = –0.05, d.f. = 26, P = 0.043), due to reductions in the second flowering peak and longer mid-season valleys, which resulted in less left-skewed and more bimodal flowering curves. Increasing July–August mean temperature increased flatness in *mesic* CFD (β = 0.05, d.f. = 26, P = 0.031), reflecting an increase in the number of days between 50% and 75% of cumulative flowering density in warmer summers.

Comparing the first and forth quartile of July–August mean temperatures illustrated the effects of warmer summers on the flowering phenology in our system. The second peak in *dry* was lower and ca.25 days later in the 7 years with the highest July–August temperatures (warm) vs. the 7 years with the lowest July–August temperatures (cool; Fig. 6a). In *mesic*, warmer years produced a more bimodal curve with a valley where the peak was in cool years (Fig. 6b). The time between peaks in the *wet* habitat increased by ca.20 days and the second peak was lower in warm years (Fig. 6c). The overall effect of these

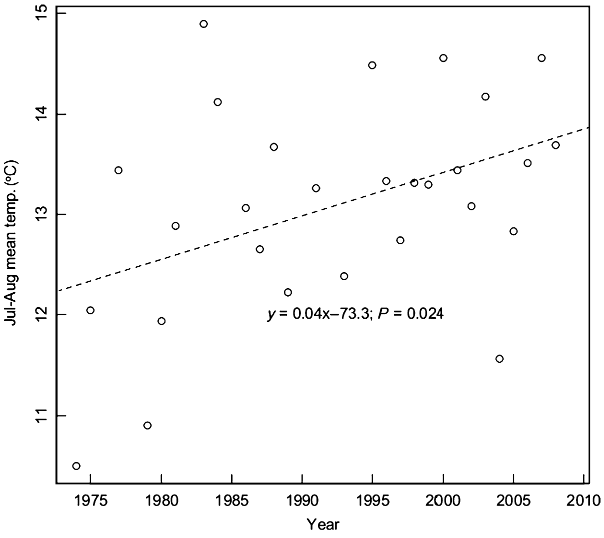

Fig. 4. July–August mean temperature in Crested Butte, Colorado, USA, 1974–2008 (2009 unavailable). Data are from NOAA weather station in Crested Butte, *c.* 13 km south of the Rocky Mountain Biological Laboratory in Gunnison County. The equation and P-value of the linear regression are shown.

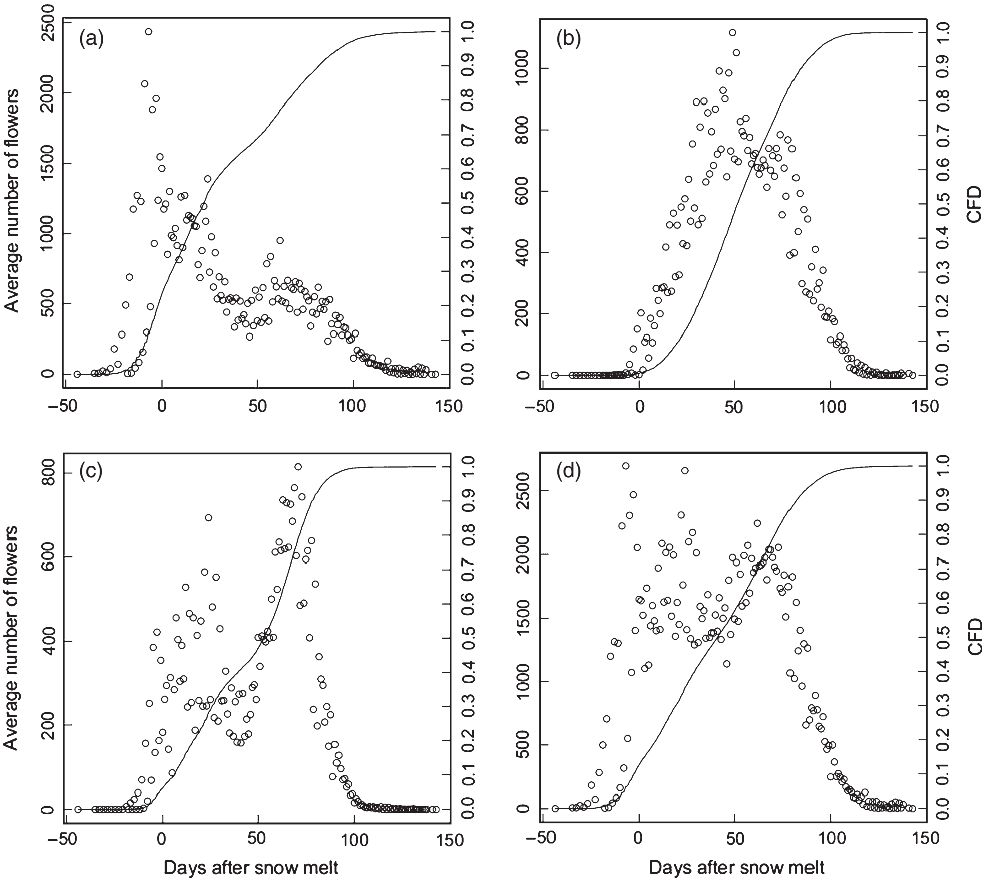

Fig. 5. Flowering curves (points) and cumulative flowering densities (CFD) (lines) for three types of montane meadows in the Rocky Mountains of Colorado, USA, averaged over the years 1974–2009. Average flower numbers are for all species flowering in replicate 2 × 2 m plots in dry (a), mesic (b) and wet (c) habitats and the total of all three (d) at the Rocky Mountain Biological Laboratory, Gunnison County, Colorado. Note changes of scale on primary *y*-axes.

shifts was a longer mid-season valley in the *total* flowering curve and a later second peak (Fig. 6d).

Despite the significant increase in July–August temperatures since 1974 in our study area, and the relationship between summer temperatures and flowering curve attributes, the temporal trend in frequency of non-normal *total* flowering curves was marginally non-significant (logistic regression: d.f. = 28; $P = 0.054$; Fig. 7).

Discussion

Our results indicate that increasing July and August (mid-summer) mean temperatures might be causing a disruption in the timing of flowering peaks among habitats differing in soil moisture in our montane meadow ecosystem. These changes result in an increased tendency toward a bimodal flowering curve in all habitats, and a shift toward a later second flowering peak. Warmer mid-summer temperatures caused a broadening of the valley in the already bimodal *dry* and *wet* habitats, and the emergence of bimodality in the *mesic* habitat. Given the importance of the *mesic* flowering peak in ‘filling’ the relatively flower-poor period between peaks in *dry* and *wet*, the emergence of a mid-season valley in flowering in *mesic*, along with the late-shift of the second peak in *dry* and *wet* could pose a resource problem for pollinators.

Climate change models predict a trend toward warmer weather with lower snowfall for the southern Rockies in the next century (Mote *et al.* 2005; Knowles, Dettinger & Cayan 2006). Although we found no significant trend in total snow water equivalent (SWE) over time in our data, flatness in *total* CFD did increase with decreasing SWE (linear regression: $\beta = 0.003$, d.f. = 27, $P = 0.029$). Recall that increased flatness is associated with increased bimodality of raw flowering curves, so less water from winter snow in the future might further exacerbate the trends we have found from increasing summer temperatures.

The increased frequency of bimodal *total* flowering curves as mid-summer temperatures rise might have important consequences for pollinators in this system. Mid-season reductions in flowering, or an increased tendency to early decline in flowering, could deprive pollinators of vital food resources. We found that the mid-season valley in flower abundance is getting longer in all three habitats. Thus, not only might pollinators that forage in all habitats find food to be relatively scarce in the mid-season, but those restricted to single habitats might also be experiencing disruption of their normal resource

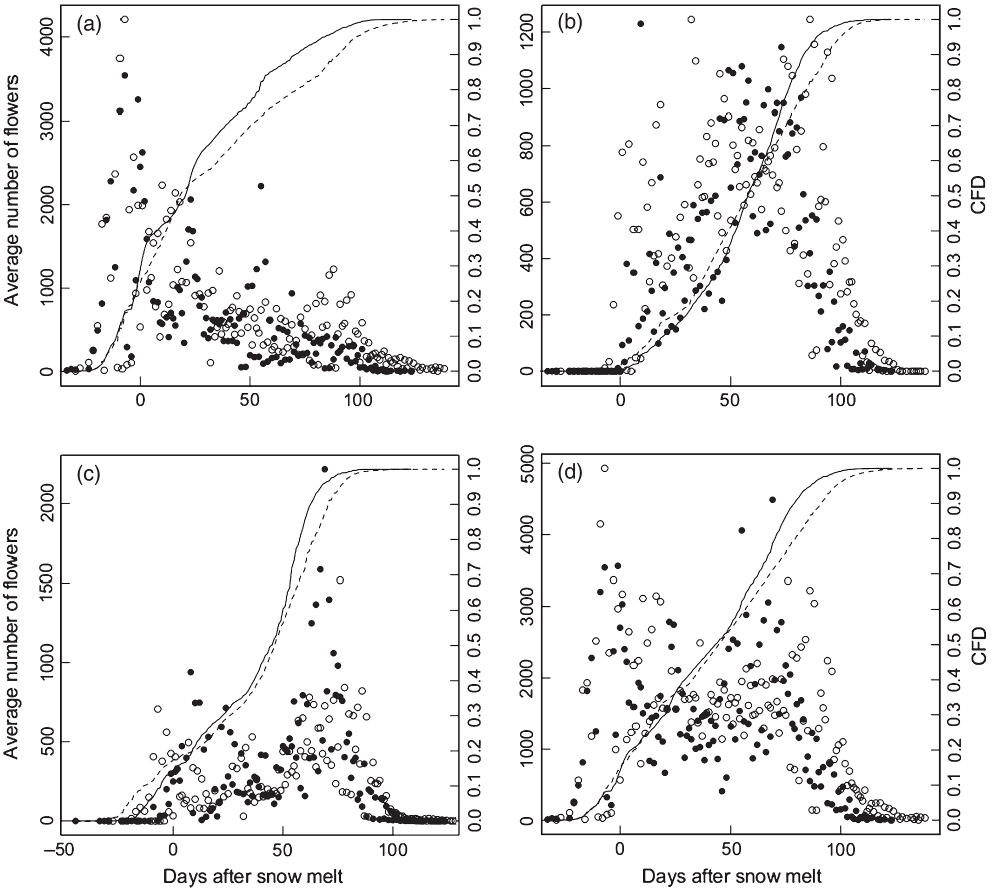

Fig. 6. Flowering curves (circles) and cumulative flowering density curves (CFD) (lines) for a montane meadow ecosystem in warm (open circles and dashed lines) and cool (filled circles and solid lines) summers. Panels show data for dry (a), mesic (b) and wet (c) habitats and the total for all three habitats (d).

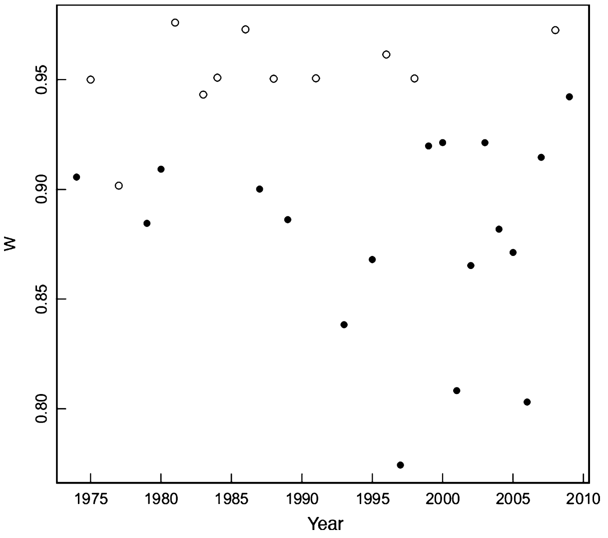

Fig. 7. Shapiro–Wilk *W* values for flowering curves in a montane meadow ecosystem in Colorado, USA. Filled circles indicate significantly non-normal distributions.

availability. As mentioned earlier, these three habitat types occur in a mosaic throughout the study area, and grade into one another, so it is likely that pollinators use and depend on resources in more than one habitat over the course of the season. Workers of the bumblebee *Bombus terrestris* have been found to forage at least 1.5 km from the colony (Osborne *et al.* 2008), a distance that easily encompasses our study area, but smaller bees may have a foraging range less than a few hundred metres (Zurbuchen *et al.* 2010).

Pollinators in this system are predominantly generalists and include 13 species of bumblebees (*Bombus* spp.) (Inouye 1980; Pleasants 1980; Pyke 1982) and a resident hummingbird (*Selasphorus platycercus*; broad-tailed hummingbird) (Miller & Inouye 1983) that have high energy demands for the entire summer season. Nesting activity and reproductive success of *S. platycercus* are closely synchronized with the phenology of its four principal food plants at RMBL (Waser 1976) and it has already been shown that flower abundance can influence use of artificial feeders by these hummingbirds (Inouye, Calder & Waser 1991). Additional migratory hummingbirds (primarily *S. rufus*; Rufous hummingbird) and a variety of butterfly, moth, fly and solitary bee species are also important pollinators in these meadows. Many of these species have foraging periods that last longer than the flowering period of individual plant species and are therefore dependent upon the community of plant species for successful reproduction.

We have confined our analyses here to whole-community-level flowering curves for these three habitat types, although our data extend to the species level. Further analysis will determine whether the patterns we report here are due to different species assemblages in the different habitats or to the same species responding differently, and whether these changes are due to whole-community responses or to certain key species. We have also restricted our analysis to flowers, whereas a more relevant resource measurement for pollinators might be pollen and nectar production. In general, we suspect that there is a strong correlation between flower production and availability of these resources, although in some cases drought may not severely reduce flower number but could significantly reduce nectar production (Carroll, Pallardy & Galen 2001; Bissuel-Belaygue *et al.* 2002).

We have recently extended our research in this system beyond observations of flowering phenology. Work now under way will quantify pollinator communities and flower visitation by individual species and guilds of pollinators, lifetime female fitness estimates for focal plant species, and experimental manipulation of warming, snowmelt and water availability. We suspect (unpublished observations) that drought, resulting from a combination of hotter summer temperatures and earlier snow melt, might be responsible for mid-summer declines in flowering. Watering experiments are being conducted to test this possibility.

In conclusion, it appears that flowering phenology in this montane meadow ecosystem is becoming more prone to disruption of the mid-season peak in floral resources, due to an interaction of changes in different moisture habitats that result in a bimodal curve of total flower numbers. This trend appears to be the result of long-term changes in climate, specifically high temperatures in July and August. Higher mid-summer temperatures appear to affect floral resources by shifting the second peak in the *dry* and *wet* habitats to a later time lowering that same peak, and causing a trend toward bimodality and later peak flowering in *mesic* habitats. Some of the same environmental changes have recently been documented (Ozgul *et al.* 2010) to have significant effects on a herbivore (yellow-bellied marmot), and we suspect that there may also be ongoing consequences for pollinators and pollination. This reduction in the mid-season abundance of total floral resources could have negative consequences for pollinators in this system, especially those that require resources throughout the summer season, such as hummingbirds and bumblebee colonies.

Acknowledgements

We thank Nick Waser and an anonymous reviewer for providing valuable comments on this manuscript. Funding and research assistance for this project 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, DEB-0238331 and DEB 0922080), 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 [DWI]. Research facilities and access to study sites were provided by RMBL and John Tuttle.

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Received 27 August 2010; accepted 11 February 2011
Handling Editor: Jonathan Newman