LONG-TERM TRENDS MASK VARIATION IN THE DIRECTION AND MAGNITUDE OF SHORT-TERM PHENOLOGICAL SHIFTS¹

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- **Premise of the study:** Plants are flowering earlier in response to climate change. However, substantial interannual variation in phenology may make it difficult to discern and compare long-term trends. In addition to providing insight on data requirements for discerning such trends, phenological shifts within subsets of long-term records will provide insight into the mechanisms driving changes in flowering over longer time scales.
- **Methods:** To examine variation in flowering shifts among temporal subsets of long-term records, we used two data sets of flowering phenology from snow-dominated habitats: subalpine meadow in Gothic, Colorado, USA (38 yr), and arctic tundra in Zackenberg, Greenland (16 yr). Shifts in flowering time were calculated as 10-yr moving averages for onset, peak, and end of flowering.
- **Key results:** Flowering advanced over the course of the entire time series at both sites. Flowering shifts at Gothic were variable, with some 10-yr time frames showing significant delays and others significant advancements. Early-flowering species were more responsive than later-flowering species, while the opposite was true at Zackenberg. Flowering shifts at Zackenberg were less variable, with advanced flowering across all 10-yr time frames. At both sites, long-term advancement seemed to be primarily driven by strong advancements in flowering in the 1990s and early 2000s.
- **Conclusions:** Analysis of long-term trends can mask substantial variation in phenological shifts through time. This variation in the direction and magnitude of phenological shifts has implications for the evolution of flowering time and for interspecific interactions with flowering plants and can provide more detailed insights into the dynamics of phenological responses to climate change.

Key words: arctic tundra; climate change; moving average; phenology; Rocky Mountain Biological Laboratory; snowmelt; subalpine; subsampling; variation; Zackenberg.

The timing of flowering is a critical aspect of plant life history (Rathcke and Lacey, 1985). Plant species in temperate and arctic communities are flowering earlier, and shifts in flowering time are consistent with altered temperature and precipitation regimes attributed to climate change (Abu-Asab et al., 2001; Fitter and Fitter 2002; Inouye et al., 2002; Miller-Rushing and Primack, 2008; Dunne et al., 2003; Høye et al., 2007b; Gordo and Sanz, 2010; Lambert et al., 2010; but see Zhang et al., 2007). Flowering phenology is tied to plant fitness because the timing of flowering determines the probability of exposure to harsh environmental conditions, available mates, interactions

with pollinators and floral antagonists, and competition with other plant species (Kochmer and Handel, 1986; Pilon, 2000; Inouye, 2008; Thomson, 2010). Plant species that advance their flowering time to track changing environmental conditions exhibit increased abundance and superior performance (e.g., growth and flower production) compared to less responsive species (Willis et al., 2008; Cleland et al., 2012); however, in some cases, plants that flower earlier are exposed to frost events for which they are not adapted, and they suffer substantial fitness declines (Inouye, 2008). Although taxon-specific differences among shifts in flowering onset and responses to climate change have been well studied (e.g., Fitter and Fitter, 2002; Miller-Rushing and Primack, 2008; Miller-Rushing and Inouye, 2009; Davis et al., 2010; Cook et al., 2012), very little is known about how variation in the direction and magnitude of phenological shifts among shorter timescales contributes to long-term patterns of changes in flowering phenology.

It is particularly important to understand variation in climate-driven shifts in flowering phenology because variability in climate is predicted to increase, with more extreme temperatures and greater fluctuations in precipitation expected over the next century (IPCC, 2007). Long-term flowering may advance as a result of sustained advancement through time with minimal variability among shorter timescales (Fig. 1A). Alternatively, long-term advancements may mask variation among shorter time intervals: temporal subsets of long-term data may contain substantial variability in both the magnitude and direction of

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Fig. 1. Conceptual figure demonstrating how long-term phenological trends may mask variation in temporal subsets of long-term data. Shifts in flowering time are shown as 10-yr moving averages, using hypothetical annual flowering dates. The long-term flowering trend, -0.45 d per year, is the same in panels (A) and (B). However, temporal subsets of long-term data may contain (A) relatively little variation among trends through time or (B) substantial variation in both the direction and magnitude of phenological shifts.

shifts in flowering phenology (Fig. 1B, in which the long-term flowering trend is identical to Fig. 1A). Variation in the direction and magnitude of such phenological shifts among shorter time frames has major implications for the evolution of flowering time, especially with regard to plasticity, and for interspecific interactions and ecosystem function (*sensu* Pau et al., 2011).

Despite the importance of understanding this variation in flowering shifts, few long-term studies exist—and even fewer can address variation in flowering time among shorter time intervals. Furthermore, almost all long-term studies of flowering phenology are limited to first flowering and are unable to consider variation in other aspects of flowering phenology (e.g., timing of peak floral abundance and end of flowering), which may respond to climate change at different rates than

first flowering (Miller-Rushing et al., 2008). Plant communities in which phenology is driven by both temperature and precipitation may be especially prone to variation among shorter timescales because flowering responses are a result of the integration of multiple abiotic cues. To determine whether long-term advancements are a result of sustained advancements through time or are instead composed of shorter time series in which shifts in flowering vary, we investigate variation in phenological shifts in two long-term records of flowering phenology in ecosystems in which onset of spring is largely driven by the timing of snowmelt: subalpine meadow and arctic tundra (Price and Waser, 1998; Dunne et al., 2003; Høye et al., 2007b).

MATERIALS AND METHODS

Study sites and data collection—We used two long-term flowering phenology data sets from snow-dominated ecosystems, the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO, USA ($38^{\circ}57.5'N$, $106^{\circ}59.3'W$, 2900 m a.s.l.) and Zackenberg, Northeast Greenland ($74^{\circ}28'N$, $20^{\circ}34'W$, 35–50 m a.s.l.). Data from both of these sites are sampled frequently enough to examine multiple aspects of flowering phenology: onset, peak, and end of flowering. The frequency of sampling, length of the time series, and richness of species make these two unique and valuable records of flowering phenology.

Gothic—The landscape around Gothic is a mosaic of mesic and wet meadows, dry rocky meadows, and mixed conifer forests and is characterized by a short growing season. Snowmelt typically occurs in May (38-yr mean = 20 May), and snowfall begins in late September to early October, with permanent winter snowpack beginning in early November (38-yr mean = 4 November). A series of 2×2 m plots was established in and around the RMBL in 1973 to monitor community flowering phenology (see Inouye, 2008 for a map of plots). The plots are generally located in two distinct habitats: relatively dry, rocky meadows (7 plots) and mesic or wet meadows (19 plots), which occur ca. 60 m lower in elevation than the dry meadows. The farthest distance between two plots is approximately 1 km (Miller-Rushing and Inouye, 2009). Depending on the species, either the number of flowers per stalk or number of flowering inflorescences (for species with numerous small flowers) were counted every other day throughout the growing season, for every species present in the plot (from 1974–2011, excluding 1978 and 1990).

Zackenberg—The growing season in this area is brief and spans June–August, limited by spring snowmelt and autumn frost. Snowmelt occurs in June, measured in permanent plots (16-yr mean = 16 June), and mean daily temperatures fall below $0^{\circ}C$ in August (14-yr mean = 27 August). The study area comprises four major plant communities: fen, grassland, willow snowbed, and heath (Elberling et al., 2008). Flowering phenology was measured for six common plant species that occur in 3–6 out of a total of 25 permanent plots within an area of approximately 2 km²: *Cassiope tetragona*, *Dryas octopetala*, *Papaver radicatum*, *Salix arctica*, *Saxifraga oppositifolia*, and *Silene acaulis* (Schmidt et al., 2012). Plots were established so that at least 200 inflorescences per species could be counted and therefore varied in size between 1 to 300 m². The phenological stage (bud, open flower, or senescent flower) of at least 200 inflorescences was recorded in each plot during weekly censuses throughout the growing season from 1996 to 2011.

Data analysis—We limited the analysis of the Gothic data for each species to years in which five or more flowers per plot were recorded in at least one census. The census started late in 5 years (1976, 1982, 1985, 1992, and 1994), and early-flowering species whose flowering onset was missed were excluded from analysis in these years. Floral abundance was summed across plots for each species, and we then determined the day of year when 10% (flowering onset), 50% (peak flowering), and 90% (end of flowering) of flowers were counted for each species. For example, the day on which 10% of flowers were counted was estimated using linear interpolation between the latest census in which <10% of flowers were counted and the earliest census in which >10% of flowers were counted (Høye et al., 2007a). Onset, peak, and end of flowering are strongly correlated with day of first flowering, day of maximum floral

Fig. 2. Across-species mean shift in flowering time in days per year, shown as 10-yr moving averages, for (A, D) onset, (B, E) peak, and (C, F) end of flowering. Significant 10-yr trends are indicated by ± 1 SE bars that do not overlap with zero.

TABLE 1. Summary of tests for differences in phenological shifts of flowering responses (onset, peak, end) from zero. Shown here are mean shifts (d/yr), averaged across all 10-yr time segments (29 for Gothic; 7 for Zackenberg), and the percentage of comparisons that were significantly different from zero at $P < 0.05$. See Appendix S3 for results of all tests.

Site	Response	Mean shift (d/yr $\pm$ 1 SE)	Significantly different shifts (%)
Gothic	Onset	-0.31 ± 0.24	93
	Peak	-0.27 ± 0.24	93
	End	-0.20 ± 0.22	93
Zackenberg	Onset	-0.93 ± 0.20	100
	Peak	-0.91 ± 0.12	86
	End	-0.92 ± 0.16	71

abundance, and last day of flowering at Gothic (data not shown), and are likely to be more comparable across years and sites with different floral abundance and sampling intensity. Similarly, for the Zackenberg data, we used linear interpolation between weekly censuses to define onset of flowering as the day on which 50% of buds had opened, end of flowering as the day on which 50% of the flowers had senesced and peak flowering as the midpoint between onset and end of flowering (Høye et al., 2007a). Appendix S1 in the Supplemental Data in the online version of this article contains the data set used for our analyses. Analyses were performed separately for each site. For Gothic, the slope of a line representing time of flowering by year was calculated over 10-yr time intervals for each species for each flowering response (29 10-yr time segments, each for onset, peak, and end of flowering; see figure in Appendix S2 online). For Zackenberg, the slope of a line representing time of flowering by year was calculated over 10-yr intervals first for each plot (each species was present in 3–4 plots), and then the mean slope was calculated for each species for each flowering response (seven 10-yr segments). Only species present for more than 5 yr were included for analysis in each 10-yr time frame (mean $N = 56$ species for Gothic; $N = 6$ species for Zackenberg). Next, we calculated the mean of the slope across all species for each 10-yr segment as a moving average. (Other time intervals, e.g., 5, 8, and 15 yr, exhibited similar trends [D. W. Inouye, unpublished data].) This calculation provided an across-species mean slope of phenological change over 10 yr, in days per year. For example, a value of 0.43 (onset of flowering

from 1974 to 1983 at Gothic) means that the flowering community delayed its onset of flowering by 4.3 d over 10 yrs. We tested whether each 10-yr phenological trend differed from zero using t tests. If phenological trends differ from zero, this indicates significant changes in flowering time over a particular 10-yr time segment. Simple linear regression was used to examine the relationship between the slope of shifts in snowmelt over 10-yr time intervals and shifts in flowering.

We also tested for differences in phenological trends between early- and late-flowering species. Earlier-flowering species tend to advance their first flowering dates at a faster rate than later-flowering species (Fitter and Fitter, 2002; Menzel et al., 2006; A. M. Iler, et al., unpublished data), and we test whether this trend holds for peak and end flowering as well. The across-species mean of average flowering dates in Gothic was 12 July, and this midpoint date was used to assign species to early (mean flowering < 12 July) and late categories (mean flowering > 12 July). At Gothic in most years, there is a spring and summer peak in community-level floral abundance (Aldridge et al., 2011); 12 July occurs in the middle of these two peaks in floral abundance, thereby categorizing early- and late-flowering species in a biologically meaningful way. For Zackenberg, we grouped the three species with the earliest mean peak flowering dates as early-flowering species (*D. octopetala*, *S. oppositifolia*, and *S. acaulis*) and the other three species (*C. tetragona*, *P. radiculatum*, and *S. arctica*) as late-flowering species. F -tests were used to compare shifts between early- and late-flowering species for each phenological response and each 10-yr time segment. Because our sample size for these comparisons was limited by the number of species at Zackenberg ($N = 3$ early-flowering and 3 late-flowering species), we also used simple linear regression to assess the relationship between the difference in flowering shifts between early- and late-flowering species (response) and the overall mean shift in flowering within each 10-yr time segment (predictor). A positive relationship between these two variables indicates that early-flowering species shift more rapidly than late-flowering species, i.e., are more responsive. All analyses were performed in SAS version 9.3 (SAS Institute, 2012).

RESULTS

Gothic—There was substantial variation in the direction and magnitude of 10-yr trends (spanning 1974–2011) for each flowering response, with some time segments showing delayed flowering and some earlier flowering (Fig. 2A–C). A total of

Fig. 3. Rate of change in timing of snowmelt in days per year, shown as overlapping 10-yr time intervals in (A) Gothic and (B) Zackenberg. Error bars are ± 1 SE.

TABLE 2. Summary of tests for differences in phenological shifts between early- and late-flowering species. A t test was performed to compare shifts between early- and late-flowering species for each flowering response (onset, peak, and end) and each 10-yr time segment (see Appendix S4 for results of all comparisons). Shown here are mean shifts (d/yr), averaged across all 10-yr time segments (29 for Gothic; 7 for Zackenberg), and the percentage of comparisons that were significantly different at $P < 0.05$.

Site	Response	Mean early (d/yr $\pm$ 1 SE)	Mean late (d/yr $\pm$ 1 SE)	Significantly different shifts (%)
Gothic	Onset	-0.41 ± 0.28	-0.17 ± 0.21	55
	Peak	-0.35 ± 0.28	-0.16 ± 0.19	55
	End	-0.31 ± 0.27	-0.056 ± 0.18	62
Zackenberg	Onset	-0.85 ± 0.051	-0.89 ± 0.23	14
	Peak	-0.87 ± 0.075	-0.89 ± 0.29	0
	End	-0.90 ± 0.10	-0.88 ± 0.35	0

93% of these shifts were significantly different from zero for onset, peak, and end of flowering (27 of 29 10-yr time segments; Fig. 2A–C; Table 1; see online Appendix S3 for tests for each 10-yr interval and flowering response). Trends for individual species mirror community-level shifts (for an example, see figure in Appendix S2). There was a trend toward earlier flowering for each phenological response over the entire 38 yr of the data set, owing to larger advancements in flowering relative to delays, particularly from the early 1990s to early 2000s (e.g., a 26.9 ± 1.2 d advancement in peak flowering from 1995–2004). Across all 38 yr, onset of flowering advanced by an average of 3.1 ± 2.4 d per decade, peak flowering by 2.7 ± 2.4 d per decade, and end of flowering by 2.0 ± 2.2 d per decade. Snowmelt date was a strong predictor of mean timing of flowering at Gothic (onset: $R^2 = 0.74$, $F_{1,33} = 94.5$, $P < 0.0001$; peak: $R^2 = 0.74$, $F_{1,33} = 95.9$, $P < 0.0001$; end: $R^2 = 0.75$; $F_{1,33} = 99.0$, $P < 0.0001$; see Fig. 3A for shifts in snowmelt over 10-yr time intervals).

Early-flowering species exhibit stronger advancements and delays in flowering compared to later-flowering species in the majority of 10-yr time segments (Table 2; Appendix S4). When the 10-yr trend is to flower earlier, the difference in the magnitude of change between early- and late-flowering species is negative, indicating that early species advance at a faster rate than late species, and vice versa for delayed flowering (Fig. 4A–C). Early species are more responsive in terms of flowering onset, peak flowering, and end of flowering (onset: $R^2 = 0.58$, $F_{1,27} = 37.0$, $P < 0.0001$; peak: $R^2 = 0.52$, $F_{1,27} = 29.4$, $P < 0.0001$; end: $R^2 = 0.48$, $F_{1,27} = 25.3$, $P < 0.0001$; Fig. 4A–C, respectively).

Zackenberg—For each flowering response, all 10-yr trends ranging from 1996–2011 advanced, with larger advances in the first half of the long-term data set (Fig. 2D–F). All of these shifts were significantly different from zero for onset of flowering (Fig. 2D), 86% (6 of 7) of shifts were significant for peak flowering (Fig. 2E), and 71% (5 of 7) of shifts in end of flowering advanced significantly (Fig. 2F). There was a trend toward earlier flowering for each phenological response over the entire 16 yr of the data set. Across all 16 yr, onset of flowering advanced by an average of 8.7 ± 1.3 d per decade, peak flowering by 8.8 ± 1.7 d per decade, and end of flowering by 8.9 ± 2.2 d per decade. Snowmelt date was a strong predictor of mean timing of flowering at Zackenberg (onset: $R^2 = 0.72$, $F_{1,14} = 36.5$,

$P < 0.0001$; peak: $R^2 = 0.70$, $F_{1,14} = 32.4$, $P < 0.0001$; end: $R^2 = 0.65$, $F_{1,14} = 25.58$, $P = 0.0002$; see Fig. 3B for shifts in snowmelt over 10-yr time intervals).

In contrast to Gothic, later-flowering species tended to exhibit stronger phenological trends than earlier-flowering ones; this difference was only significant in one 10-yr time segment for onset of flowering (Table 2; Fig. 4D–F). However, the stronger the 10-yr trend toward earlier flowering, the more positive is the difference in flowering advancements between early- and late-flowering species, indicating that late-flowering species advance at a faster rate than early-flowering species (onset: $R^2 = 0.85$, $F_{1,5} = 27.9$, $P = 0.0032$; peak: $R^2 = 0.84$, $F_{1,5} = 26.7$, $P = 0.0036$; end: $R^2 = 0.84$, $F_{1,5} = 26.7$, $P = 0.0036$; Fig. 4D–F, respectively).

DISCUSSION

Traditional analysis of long-term data can mask substantial variation in phenological shifts through time. In a 38-yr record of flowering phenology for a subalpine meadow plant community (Gothic), overlapping 10-yr time intervals reveal considerable variation in the direction and magnitude of flowering shifts. Despite an overall trend of earlier flowering by approximately 3 d per decade, examination of shorter time intervals uncovers significant delays in flowering. Yet, in a 16-yr record of flowering phenology for a tundra plant community (Zackenberg), sustained advancements in flowering among shorter time intervals drive long-term trends toward earlier flowering by approximately 9 d per decade. In contrast to the Gothic time series, we find no delays in flowering across any time scales in the Zackenberg time series. This lack of variation in the direction of flowering responses may be characteristic of tundra plant communities, especially given that rapid change is expected in arctic ecosystems because temperatures are warming at a rate almost double the mean global rate of warming (Kattsov et al., 2005). Consistent with this interpretation, the timing of snowmelt, a strong predictor of change in flowering phenology in both plant communities, is less variable at Zackenberg compared to Gothic (CV = 0.10 vs. 0.067, respectively). These differences may be in part a consequence of the large differences in latitude between the sites. Alternatively, the less variable flowering and snowmelt responses may simply reflect the shorter time series of the Zackenberg data set. As illustrated when comparing these two long-term records, variation in the direction of phenological change over shorter timeframes may explain why some ecosystems seem to respond more strongly to climate change than others over the long-term.

We observe site-specific differences in the rate at which early- and late-flowering species shift their flowering times. In Gothic, early species are generally more responsive, in terms of both advancements and delays in flowering. This trend is consistent across all flowering responses: onset, peak, and end of flowering changed at faster rates in early species, building on previous research showing that spring-flowering species advance their first flowering dates at a faster rate than summer-flowering species (Fitter and Fitter, 2002). Indeed, species active during rapid environmental transitions, such as spring snowmelt, are predicted to be the most responsive to climate change, especially in areas with short growing seasons (Pau et al., 2011). While early-flowering species seem to be more responsive in Gothic, some of these early species also appear to be approaching their limits of phenological advancement, as

Fig. 4. Comparison of flowering shifts between early- and late-flowering species for (A, D) onset of flowering, (B, E) peak flowering, and (C, F) end of flowering for (A–C) Gothic and (D–F) Zackenberg. Difference between early- and late-flowering species is shown as a function of the mean shift in flowering time. Each dot represents one 10-yr time interval. Line of fit is from simple linear regression and is significant at $P < 0.05$ in all panels. A positive slope indicates that early-flowering species shift more rapidly and a negative slope that late-flowering species shift more rapidly.

shown by earlier flowering until a threshold snowmelt date, beyond which flowering ceases to advance in the earliest snowmelt years (A. M. Iler et al., in press; sensu Inouye, 2008; Steltzer et al., 2009). We detect the opposite pattern in Zackenberg; later-flowering species advance their flowering at a faster rate than early-flowering species. Differences between sites in patterns and rates of snowmelt may be driving this discrepancy. In Zackenberg, late-flowering species are more likely to occur in snow banks where the timing of snowmelt is more variable across years (Høye et al., 2007a). Although there are some areas with late-lying snowbanks in Gothic, they represent a tiny percentage of the overall landscape and are not represented in the long-term phenology plots.

Moving averages can reveal variation among phenological shifts over temporal subsets of long-term data. A 10-yr time frame is arbitrary, given that biological processes operate at various temporal scales, but reports of phenological shifts are commonly reported in days per decade (Root et al., 2003; Parmesan, 2007; Thackeray et al., 2010), and we have found that often 8–10 yr of data are needed to find statistically significant trends in phenological data from Gothic, given the large interannual variation in flowering times (D. W. Inouye, unpublished data). Our goal was to focus on shorter time frames within long-term data to detect and describe any variation in trends through time. Indeed, temporal variation in phenology can make it difficult to discern long-term trends, highlighting the importance of long-term data sets and historical records (Vellend et al. 2013, in this issue). In Gothic, flowering was delayed for 13 and 14 yr in the mid 1970s–1980s and the mid 1980s–1990s, respectively, but flowering advanced from 1974 to 2011. At both sites, strong advancements in the 10-yr time segments spanning the 1990s to early 2000s seem to largely drive the long-term trend toward advanced flowering, a pattern particularly striking in the Gothic data set (Fig. 2). One may therefore come to different conclusions about directional shifts in flowering depending on the timeframe examined. Failing to control for the length and time frame of long-term data could severely bias comparisons of rates of phenological change across data sets. Even studies that standardize for the length of data sets could arrive at different conclusions based on the time frame examined (e.g., Thackeray et al., 2010), probably because of differences in rates of climatic change among decades. For example, the trend in Gothic from 1974 to 2003 is toward advanced flowering and from 1982 to 2011 is toward delayed flowering (data not shown), showing that the inclusion of just 10 different years of data in a 30-yr record can alter the direction of phenological change detected.

The variation in phenological shifts that we observe in this study likely has major implications for the evolution of flowering time and for ecological interactions with flowering plants. At Gothic, we expect directional selection for earlier flowering, while at the same time, given high interannual variation in abiotic conditions, we also expect strong selection for plasticity in flowering time. At Zackenberg, stronger directional selection for earlier flowering may occur in light of less variable abiotic conditions (e.g., snowmelt), but our predictions are limited by the length of the data set. Genetic variation in flowering time is prevalent within and among plant populations (reviewed by Mazer and Lebuhn, 1999; Bennington et al., 2012), providing opportunities for both directional selection and selection for plasticity in flowering time. Although there is widespread evidence of strong directional selection for earlier flowering in response to climate change, very little is known about the relative contribu-

tions of adaptive evolution and phenotypic plasticity to responses of flowering time to climate change (Etterson and Shaw, 2001; Franks et al., 2007; Hoffmann and Sgro, 2011; Munguia-Rosas et al., 2011; Anderson et al., 2012). Highly variable systems provide a framework for examining relative contributions of plasticity and adaptive responses to observed changes in flowering phenology. For example, Anderson et al. (2012) found evidence that natural selection accounts for up to 20% of the long-term change in flowering time in a short-lived perennial (*Boechera stricta*) in Gothic, suggesting that the majority of phenological change is a result of plasticity. While directional selection may deplete genetic variation for flowering time and limit the degree to which species can respond to a changing environment (Anderson et al., 2012), the variation in the magnitude of flowering responses we observe in this study may impose a constraint on the strength of selection for earlier flowering.

The differences between sites in the responsiveness of early- and late-flowering species have implications for changes in the duration of flowering at the community-level. In Gothic, stronger advancements in early-flowering species should extend the start of the flowering season, resulting in a longer duration of community-level flowering (A. M. Iler et al., unpublished data). Consistent with this trend, earlier-flowering families, in addition to earlier-flowering species, are more responsive to temperature (Mazer et al., 2013, in this issue). Additionally, Wolkovich et al. (2013) report in this issue that invasive plant species may be responsible for extended flowering seasons under climate change in many temperate plant communities; only one nonnative species is present in our data set, and it flowers midseason (*Taraxacum officinale* at Gothic). On the other hand, in Zackenberg, stronger advancements in later-flowering species should constrict the end of the flowering season, resulting in a shorter duration of community-level flowering (Høye et al., in press). Such changes in the duration of flowering may affect the composition of the floral community and the temporal window of opportunity for interspecific interactions. Similarly, alternating delays and advancements in flowering through time may affect the temporal synchrony of interactions with mutualists or floral antagonists, especially if they do not respond to the same cues or respond to the same cues at different rates (Hegland et al., 2009). Given that preclimate change phenological baselines are largely unknown, it is difficult to predict the ecological consequences of variability in phenological shifts for species interactions (Miller-Rushing et al., 2010; Singer and Parmesan, 2010). Ultimately, variation in phenological shifts among relatively short timescales nested within long-term trends may have demographic consequences and scale up to impact ecosystem function.

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