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ARTICLE

Warming reduced flowering synchrony and extended community flowering season in an alpine meadow on the Tibetan Plateau

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Abstract

The timing of phenological events is highly sensitive to climate change, and may influence ecosystem structure and function. Although changes in flowering phenology among species under climate change have been reported widely, how species-specific shifts will affect phenological synchrony and community-level phenology patterns remains unclear. We conducted a manipulative experiment of warming and precipitation addition and reduction to explore how climate change affected flowering phenology at the species and community levels in an alpine meadow on the eastern Tibetan Plateau. We found that warming advanced the first and last flowering times differently and with no consistent shifts in flowering duration among species, resulting in the entire flowering period of species emerging earlier in the growing season. Early-flowering species were more sensitive to warming than mid- and late-flowering species, thereby reducing flowering synchrony among species and extending the community-level flowering season. However, precipitation and its interactions with warming had no significant effects on flowering phenology. Our results suggest that temperature regulates flowering phenology from the species to community levels in this alpine meadow community, yet how species shifted their flowering timing and duration in response to warming varied. This species-level divergence may reshape flowering phenology in this alpine plant community. Decreasing flowering synchrony among species and the extension of community-level flowering seasons under warming may alter future trophic interactions, with cascading consequences to community and ecosystem function.

KEYWORDS
alpine meadow, flowering phenology, functional group, precipitation changes, synchrony, warming

INTRODUCTION

Plant phenology, the seasonal timing of biological events, is one of the sensitive bio-indicators of climate change (Cleland et al., 2007; Peñuelas & Filella, 2001; Walther et al., 2002) and has extensive consequences for reproductive success, species interactions and coexistence (Godoy et al., 2014; Liu et al., 2011; Richardson et al., 2013). Temperature and precipitation are important drivers of phenology (Cleland et al., 2007; Ge et al., 2015), and flowering phenology is a crucial event in the life history of plants (Cleland et al., 2012; Fitter & Fitter, 2002). Recently, global climate observations suggested that high latitude and elevation regions are warming faster than other terrestrial habitats (IPCC, 2014; Rangwala & Miller, 2012), especially in the Tibetan Plateau (Qin et al., 2009). Meanwhile, changes in precipitation are variable with both increasing and decreasing trends observed in this region (Chen et al., 2013). However, the interactive effects of warming and changes in precipitation on flowering phenology remain unclear in alpine ecosystems.

Advanced flowering phenology influenced by warming has been observed globally (Barrett & Hollister, 2016; Bjorkman et al., 2015; Elzinga et al., 2007). However, the timing of flowering phenology (including the first and last flowering date) and flowering duration under warming, precipitation change, and their interaction are complex and less well understood (Jabis et al., 2020; Li et al., 2020). In alpine systems, warming may advance and extend the flowering period (Li, Jiang et al. 2016; Suonan et al., 2017), but may indirectly delay reproductive phenology and advance senescence by reducing soil moisture leading to water limitation (Oberbauer et al., 2013; Zhu et al., 2016) or breaking of dormancy (Yu et al., 2010). In some temperate regions, precipitation addition had little effect on flowering phenology (Cleland et al., 2006; Sherry et al., 2007), however, others have reported that spring phenology is affected by the interaction of warming and precipitation (Cleland et al., 2007; Shen et al., 2011). For example, in semiarid regions, variability in interannual precipitation controls the magnitude and direction (delay or advance) of flowering phenology in response to warming (Ganjurjav et al., 2020; Zelikova et al., 2015). Higher precipitation may compensate for the warming-induced reduction in soil moisture and thus advance phenology, while lower precipitation will further reduce soil moisture offsetting the positive effect of warming on phenology. Moreover, it is not clear whether first and last flowering time and flowering duration are uniformly sensitive to environmental conditions among different species. Indeed, recent studies have found either consistent (Jabis et al., 2020) or variable responses (CaraDonna et al., 2014; Li et al., 2020; Semenchuk et al., 2016) among different components of phenology, potentially impacting plant fitness and species interactions (Rafferty et al., 2016; Renner & Zohner, 2018). Therefore, understanding how flowering phenology of alpine species responds to warming and precipitation changes is crucial to predict the full impact of climate change on alpine plant communities.

Previous studies have emphasized that phenological responses to warming may differ based on life history traits such as flowering time (e.g., different flowering functional group: early-, mid-, and late-flowering species) (Fitter & Fitter, 2002). In many alpine and tundra ecosystems, mid- and late-flowering species are more sensitive to warming than early-flowering species (Meng et al., 2016; Prevéy et al., 2019; Suonan et al., 2017). Jabis et al. (2020) found that flowering timing and duration in early-flowering species were less sensitive to the direct effects of warming than were mid- and late-flowering species. However, differences in the sensitivity of different flowering functional groups to soil moisture may influence how warming affects phenology (Dorji et al., 2013). Divergent responses among different flowering species can affect phenological synchrony, the temporal overlap of phenological stages, and has potential impacts on ecological communities (Ims, 1990; Tiusanen et al., 2020).

Climate change has been increasingly shown to alter phenological synchrony within (Zohner et al., 2018) and among species (Hua et al., 2016, Ovaskainen et al., 2018). However, changes in synchrony are inconsistent (Parmesan, 2006; Yang & Rudolf, 2010), and may vary in degree (Ovaskainen et al., 2018) and across taxa (Hua et al., 2016; Zohner et al., 2018). Hence, we developed a conceptual model to predict flowering synchrony among early-, mid-, and late-flowering species (Figure 1). First, if early-, mid-, and late-flowering species responded in the same direction and magnitude to warming, then flowering synchrony would not change (Figure 1a). Otherwise, flowering synchrony could decrease (Figure 1b) or increase (Figure 1c). Shifts in flowering synchrony among species can affect the relationship between plants and their pollinators, and competition for pollination resources (Renner & Zohner, 2018; Tiusanen et al., 2020). Thus, a better understanding of how warming and precipitation changes affect flowering synchrony will help to determine how trophic interactions will respond to climate change in the future.

Changes in phenology among species can influence community-level phenological patterns (CaraDonna et al., 2014; Cleland et al., 2006; Crimmins et al., 2010; Diez et al., 2012). However, inconsistent responses of community-level flowering phenology to warming have been reported in alpine ecosystems. For example, species-specific responses of flowering to warming will determine the length of the community-level flowering season, which may be extended as summer temperatures

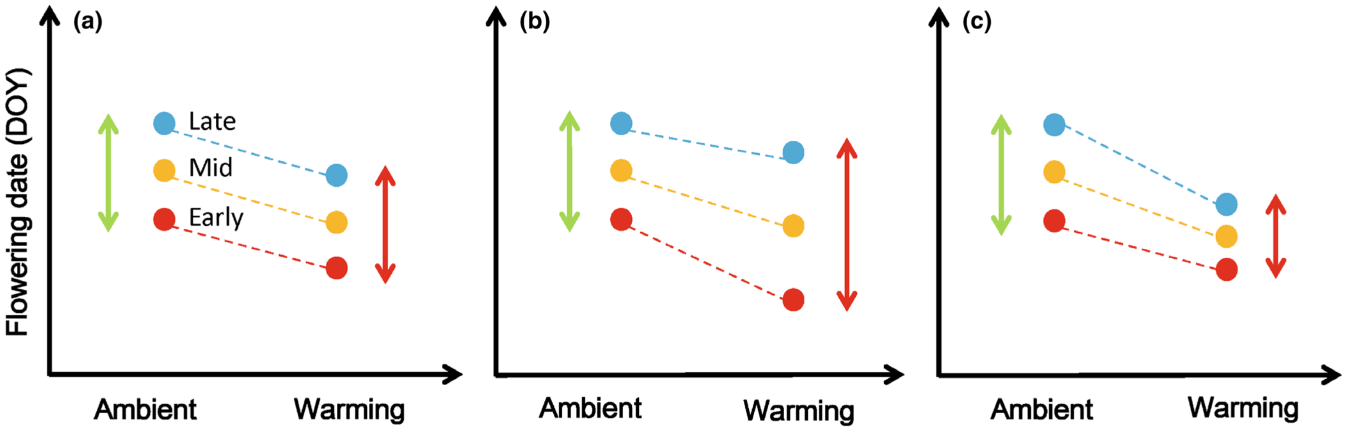

FIGURE 1 Schematic representation of flowering synchrony among early-, mid-, and late-flowering species and community-level flowering season length in response to warming. If early- (red dot), mid- (yellow dot), and late-flowering species (blue dot) responded similarly to warming, flowering synchrony and community-level flowering season would not change (a). Conversely, if early-species were more sensitive than mid- and late-flowering species, flowering synchrony would decrease and community-level flowering season would be extended (b), or if mid- and late-flowering species were more sensitive than early-flowering species, flowering synchrony would increase and community-level flowering season would shorten (c). Flowering variation among species or community-level flowering season length under ambient or warming are illustrated by the solid green and red arrows, respectively.

increase (CaraDonna et al., 2014; Diez et al., 2012). Both shorter and unchanged flowering season have been reported (Jabis et al., 2020; Prevéy et al., 2019). Changes in the length of the community-level flowering season will be governed by the responses of early-, mid-, and late-flowering species. Based on our conceptual model, if early- and late-flowering species respond similarity to warming, the community-level flowering season could be unchanged (Figure 1a). However, if early- and late-flowering species respond differently to warming, the community-level flowering season could be extended (Figure 1b) or shortened (Figure 1c). Furthermore, precipitation may be an important covariate in addition to temperature in shaping flowering phenology (Crimmins et al., 2010; Ganjurjav et al., 2020). Therefore, warming and precipitation changes may reshape flowering phenology, although it is not clear how differences among species in their flowering responses scale up to influence community-level flowering phenology patterns in alpine ecosystems.

To explore the effects of warming and precipitation changes on flowering phenology from the species to the community levels, we conducted a warming and precipitation addition and reduction experiment in an alpine meadow on the Qinghai-Tibet Plateau. From 2019 to 2020, we recorded the first and last flowering date, and flowering duration for 10 common species from three flowering functional groups (Table 1). Based on previous research, we tested three hypotheses: (1) warming, precipitation changes, and their interaction would impact the flowering phenology of alpine meadow plants. We predicted that warming would advance and extend flowering periods, and precipitation addition would accelerate the advancement and extension of flowering under warming, while precipitation reduction would offset it through decreased soil moisture. (2) Phenological variation in different flowering functional groups would affect interspecific flowering synchrony. We predicted that late-flowering species would be more sensitive to warming than early-flowering species, which would increase flowering synchrony in this alpine meadow community. (3) Species-specific responses of plants to climate change would collectively reshape the community-level phenological pattern. We predicted that warming would shorten the community-level flowering season by advancing late-flowering species more than early-flowering species.

METHODS

Study site

We conducted our experiment in the eastern Tibetan Plateau, Gannan Grassland Ecosystem National Observation and Research Station (33°40′ N, 101°52′ E, altitude 3540 m above sea level [asl]) in Maqu County, Gannan Tibetan Autonomous Prefecture, Gansu Province, China. The experimental site is characterized as a cold alpine meadow, with a short growing season. Mean annual temperature is 1.2°C and mean annual precipitation is 620–780 mm, mainly occurring during the growing season from June to September (Niu et al., 2014). The soil type is alpine meadow soil. Common plant species at the experimental site were *Kobresia graminifolia*, *Koeleria cristata*,

TABLE 1 The 10 species monitored in this study from three flowering functional groups and three life forms.

Species	Abbreviation	FFG	Biomass (%)	Cover (%)	Abundance (%)
Kobresia graminifolia	Kg	Early	34.5	18.0	9.8
Elymus nutans	En	Mid	15.8	9.6	6.1
Koeleria cristata	Kc	Mid	6.4	4.3	2.8
Anemone rivularis	Ar	Mid	5.5	5.6	4.0
Poa pachyantha	Pp	Mid	5.4	5.9	5.7
Pleurospermum camtschaticum	Pc	Mid	3.1	7.3	6.5
Anemone obtusiloba	Ao	Early	2.2	6.1	6.3
Euphorbia esula	Ee	Early	1.7	4.5	3.6
Potentilla fragarioides	Pf	Mid	1.1	6.0	6.8
Delphinium kamaonense	Dk	Late	0.7	2.3	1.5

Note: These species accounted for 76.4% of the total aboveground biomass. Relative biomass (%), cover (%) and abundance (%) for each species monitored in the community. Species flowering before the start of June, between June and July, and after August are defined as early-, mid-, and late-flowering species, respectively.

Abbreviation: FFG, flowering functional group.

Elymus nutans, *Poa pachyantha*, *Stipa capillata*, *Anemone rivularis*, *Delphinium kamaonense*, *Euphorbia esula*, *Anemone obtusiloba, Pleurospermum camtschaticum* and *Potentilla fragarioides* (An et al., 2020; Ma et al., 2018).

Experimental design

A multifactor experimental platform of warming combined with either precipitation addition or reduction was established in May 2017 in a randomized block design. The experiment includes two temperature treatments (ambient and warming) and three levels of precipitation treatment (ambient, 40% reduction and 40% addition). Thus, there was a total of six treatment combinations, (1) control (ambient), (2) drought (40% reduction in precipitation), (3) wet (40% addition in precipitation), (4) warming, (5) warming plus drought (warming plus 40% reduction in precipitation), and (6) warming plus wet (warming plus 40% addition in precipitation). There were five replicates per treatment, and each plot was 3 m × 3 m located at least 2 m apart from each other, for a total of 30 plots (Appendix S1: Figure S1).

We used an open-top chamber (OTC) for the warming treatment (Hollister & Weber, 2000), which is a hexagonal chamber built of methacrylate plates with a height of 0.45 m, base length of 0.65 m and top length of 0.51 m (see in Appendix S1: Figure S1). OTCs were open on their top to allow precipitation and airflow and placed in the middle of the warming treatment plots throughout the year. Precipitation addition and reduction was conducted from late April to late October to manipulate growing season precipitation changes (Gherardi et al., 2015; Ma et al., 2017). Precipitation was manipulated using a rainout shelter (Yahdjian & Sala, 2002) with evenly distributed six V-shaped clear polycarbonate slats placed at a 15° angle to reduce rainfall by 40% relative to ambient. Excluded precipitation drained into a storage tank and water was manually transferred to the wet treatments after each rain event to increase the precipitation by 40% (Appendix S1: Figure S1). The number and timing of rainfall events were similar to those of natural conditions and constant across treatments. Additionally, to reduce surface runoff, we inserted stainless steel sheets into the soil around the edge of each plot.

Temperature and moisture measurements

Daily average air temperature, soil temperature, and soil moisture from May to October periods were monitored in experimental plots every year. HOBO U23 Pro v.2 Temp/RH probes (Onset Corporation, Bourne, MA, USA) were installed 15 cm above the soil surface to measure air temperature (Sherry et al., 2007). Soil temperature and moisture at a 5-cm depth (the primary rooting zone) were measured using the EM 50 Data Collection System (Decagon Devices, Inc., NE, USA) automatically every 15 min during the experiment in each year (from May to October) (Ganjurjav et al., 2020).

Phenology monitoring

Dominance and flowering patterns of common plants were used to select species for phenological monitoring (Ganjurjav et al., 2020; Suonan et al., 2017). Using these criteria, we selected 10 species that maximally represented plant community composition based on their relative aboveground biomass, cover and flowering rate (Table 1; Appendix S1: Table S1 for more details). The selected species accounted for 70%–80% of total aboveground biomass and 60%–70% of plant cover. To estimate the aboveground biomass, cover and abundance of individual species, one 0.5 m × 0.5 m quadrat was randomly located within each plot and vegetation was clipped at ground level in late August during peak biomass each year, and sorted by species. The percentage of each parameter was determined as the average across all replicates of each treatment (Ma et al., 2020; Niu et al., 2014). Nevertheless, due to naturally short and cold growing seasons on the Tibetan Plateau, the flowering rate of many common flowering plants is relatively low, and most species also reproduce clonally, such that flowering phenology was not always observable in all experimental plots.

Based on species life history traits, and following criteria used in other studies in alpine ecosystems (e.g., Jabis et al., 2020; Suonan et al., 2017; Wang, Meng, et al., 2014) we binned the 10 selected species into three early-season (flower between May and June), six mid-season (flower after July) and one late-season (flower after August) flowering species. Because late-flowering species are extremely rare in this alpine meadow community (three species in total), we selected only one species (*Delphinium kamaonense*) to represent the late-flowering group. This species had higher biomass, cover, relative abundance, and flowering rate than the other two species (Appendix S1: Table S1).

Up to five individuals or stems for each species were randomly labeled in each plot for phenological monitoring, which was measured weekly from April to October in 2019 and 2020 (Li, Jiang, et al. 2016; Sherry et al., 2007). Once buds were noticed on any individual of each species, the collection of phenological data of flowering began for that species. For each of the labeled individuals, the first date that a flower or pollen was observed was defined as the first flowering day (Jabis et al., 2020). The last flowering date was defined as the date when anthers withered or the last petal fell off and, flowering duration was calculated as the period between first and last flower date. The first and last flowering day, and flowering duration were averaged for the five individuals of each species within each plot.

Calculations of flowering synchrony and community-level flowering season

To examine the flowering synchrony among species, we used the standard deviation of the first flowering dates (Zohner et al., 2018). High standard deviation for first flowering date indicates low flowering synchrony. For each year within each plot, the standard deviation was calculated for the average of the first flowering dates of all species. Based on previous research, three aspects of community-level phenological dynamics can be measured by calculating (1) the mean of the first, last flowering date and flowering duration for all observed species in the plant community (Ganjurjav et al., 2020; Jabis et al., 2020; Suonan et al., 2017), (2) changes in community-level peak flowering date, flowering abundance and the distribution of first flowering date in the time series among species over the flowering season (CaraDonna et al., 2014; Diez et al., 2012), and (3) the number of days between the average first flowering dates of the earliest-flowering species and the average last flowering dates of the latest-flowering species to quantify community-level flowering season length (Diez et al., 2012; Prevéy et al., 2019). We chose the third approach because flower abundance or peak flowering dates was not monitored for all plant species in our study. This approach has been used to examine how species-specific shifts will affect community-level phenological patterns (length or duration of the flowering season) in different ecological communities that may harbor diverse species with distinct responses to experimental treatments and climate change (Diez et al., 2012; Prevéy et al., 2019). Although changes in the first and last flowering dates for these 10 species do not always represent community-level changes over the entire flowering season (Miller-Rushing et al., 2008), our approach based on that proposed by Diez et al. (2012) and Prevéy et al. (2019) can provide an estimate of how the length of the flowering season may change with future climate change.

Statistical analysis

We used linear mixed-effects models (restricted maximum likelihood [REML] estimation) to test the separate and interactive effects of year, warming, and precipitation changes on air temperature and soil moisture. We set time, warming and precipitation treatments as fixed effects, and plots as a random effect in the model to account for variation among repeated measurements of temperature or moisture.

Linear mixed-effects models were used to test the separate and interactive effects of year, warming, precipitation changes and species on the first and last flowering day, and flowering duration. We set time, warming, precipitation treatments, and species as fixed effects and plots as a random effect in the model. Tukey's tests were used to conduct pairwise comparisons of differences of first and last flowering days, and flowering duration among treatments. Similarly, to assess the responses of different functional groups (early-, mid-, or late-flowering species), we set year, warming, precipitation treatments, and functional groups as fixed effects, and species nested within plot as a random effect. Then, we used Tukey's tests to compare the differences in phenology among early-, mid-, and late-flowering functional groups within treatments.

Finally, we used a linear mixed-effects model to assess the effects of warming and precipitation changes on flowering synchrony and community-level flowering season length. For this model, we set the year, warming, and precipitation change as fixed effects and plots as random effects, and Tukey's test was used to conduct pairwise comparisons of differences in flowering synchrony and community-level flowering season between all treatments.

We used the R 4.0.3 statistical software (R Core Team, 2020) for all analysis. All linear mixed-effects models were built using the *lme* function from the *nlme* package (Pinheiro et al., 2007), and we reported the ANOVA results of all linear mixed-effects models when differences were significant at $p < 0.05$. All Tukey's tests for pairwise comparisons of differences use the *TukeyHSD* function in the *multcomp* package (Bretz et al., 2010). All graphics were drawn using the *ggplot2* package (Wickham, 2009).

RESULTS

Air and soil environmental conditions

The growing season average soil temperature was 12.1 ± 0.1°C and 11.9 ± 0.2°C and soil moisture was 28.3 ± 0.008 v/v% and 29.1 ± 0.004 v/v% in 2019 and 2020 in the control treatment, respectively. Unfortunately, all HOBOs were placed too close to the ground in 2019, rather than at 15 cm above ground (Sherry et al., 2007), thus the air temperature measurements between warmed and ambient treatments were not significantly different due to shading by the plant canopy (Appendix S1: Figure S2a). However, the air temperature was significantly higher early in the growing season prior to canopy development (Appendix S1: Figure S3a). Nevertheless, soil temperatures were higher under warming chambers compared with ambient plots in 2019 (Appendix S1: Figures S2c, S3b, Table S2). Hence, the air temperature recorded in 2019 did not reflect the actual warming that occurred under the open-topped chambers. We corrected this error in the second growing season, and found that warming increased air temperature by 0.9°C in 2020 (Appendix S1: Figure S2b).

As expected, warming significantly increased soil temperature and decreased soil moisture, although results differed across years during our experiment (Appendix S1: Figure S2c–f, Table S2). Specifically, warming increased soil temperature by an average of 1.2°C and decreased soil moisture by an average of 5.6% relative to the control across both years (Appendix S1: Figure S2e,f, Appendix S1: Figure S2). The open-topped chambers produced a larger warming effect on air and soil temperature early in the growing season (May–June) relative to middle season temperatures (July–August; Appendix S1: Figure S3a,b). Precipitation reduction and addition decreased soil moisture by an average of 3.7% and increased soil moisture by 3.3% relative to the control across both years, respectively (Appendix S1: Figure S2e,f). Meanwhile, the precipitation treatments had no significant effects on soil temperature and air temperature, but there was an interaction effect with the warming on soil temperature (Appendix S1: Table S2). Relative to the control, air temperature was increased by 0.7°C and 0.4°C in warming + drought plots and warming + wet treatments in 2020 (Appendix S1: Figure S2b), respectively. Meanwhile, soil temperature increased by 1.1°C and 0.8°C (Appendix S1: Figure S2c,d), and soil moisture decreased by 5.4% and 2.2% across both years, respectively, under experimental warming (Appendix S1: Figure S2e,f).

Responses of flowering phenology among species to climatic treatments

At the species-level, the first and last flowering days of all 10 species were significantly affected by year and warming (Figure 2; Appendix S1: Tables S3 and S4).

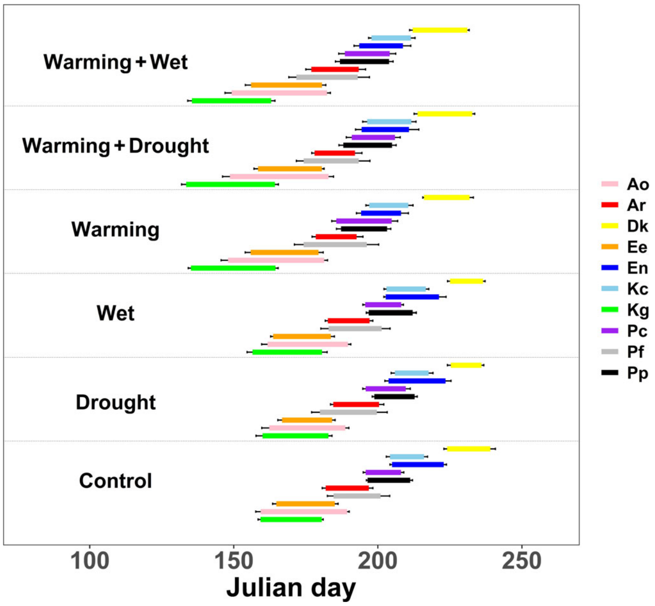

FIGURE 2 Timing and duration of the flowering period for 10 common alpine species (color coded by species listed in Table 1) under six warming and precipitation treatments from 2019 through 2020 growing seasons. First and last flowering day, and flowering duration for all 10 species are provided in Appendix S1: Table S3. The rightmost end of each bar represents the date of last flowering with its standard error for each species, and the leftmost end represents the mean date of the first flowering with its standard error. Julian day: January 1 is the 1st day of the year.

Warming advanced the average first and last flowering dates for the 10 species by 10.3 ± 3.2 and 7.5 ± 2.6 days across both years, respectively, resulting in the entire flowering period occurring earlier in the season. Moreover, year and warming interacted to alter flowering patterns (Appendix S1: Figure S4, Table S3). Specifically, warming advanced the average first flowering dates for the 10 species by 11.4 ± 1.1 days in 2019 and 9.2 ± 1.1 days in 2020, and the average last flowering date advanced 8.7 ± 0.9 and 6.4 ± 0.8 days, respectively (Appendix S1: Figure S4). Surprisingly, neither precipitation changes alone nor with warming had significant effects on flowering events for any species (Appendix S1: Tables S3, S4).

We found that the first and last flowering dates among species advanced differently under warming (Appendix S1: Figure S4, Tables S3, S4). That is, flowering duration showed no consistent results across species because of species-specific first and last flowering date responses (Figure 2; Appendix S1: Figure S4, Table S3). For example, warming advanced the average first and last flowering of *K. graminifolia* by 24.6 ± 2.2 and 16.7 ± 1.7 days respectively, and significantly extended average flowering duration by 6.1 ± 2.1 days (Appendix S1: Table S4). However, warming advanced the average first and last flowering times of *P. pachyantha* by 9.1 ± 1.7 and 7.2 ± 1.7 days, respectively, resulting in no significant change in flowering duration and flowering events (including the first and last flowering date and flowering duration), whereas flowering time of *A. rivularis* did not change under any climatic treatment (Appendix S1: Table S4).

Responses of flowering synchrony among species to climatic treatments

We found that warming had different effects on the first and last flowering dates of the three flowering functional groups and that these effects varied between years (Appendix S1: Table S5). The first and last flowering dates of early-flowering species were more sensitive to warming than those of mid- or late-flowering species (Figure 3; Appendix S1: Figure S6, Tables S5, S6). Early-flowering species extended their flowering durations more than mid- and late-flowering species under warming (Figure 3c). Meanwhile, differences in responses of flowering events to warming for early-, mid-, and late-flowering species were greater in 2019 than in 2020 (Appendix S1: Figure S5, Table S5). This divergence in phenological responses of different flowering functional groups to warming decreased flowering synchrony among species by an average of 2.7 ± 0.6 days across both years (Figure 4a; Appendix S1: Figure S7, Table S5), similar to the second scenario shown in our schematic (Figure 1b). However, precipitation treatments and their interaction with warming had no significant effect on the flowering phenology or synchrony of the three functional groups (Figure 4a; Appendix S1: Table S5).

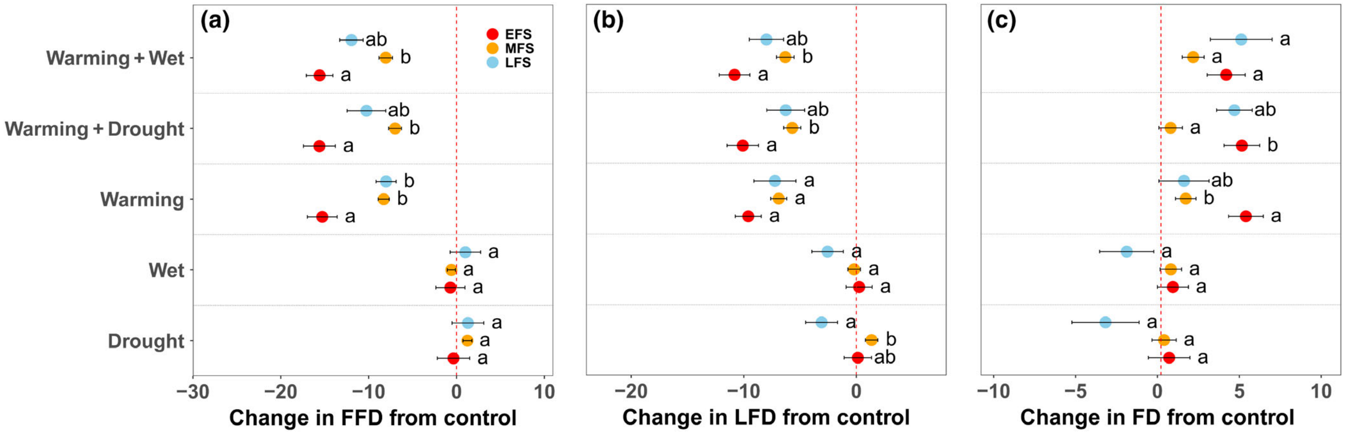

FIGURE 3 Average first flowering day (FFD), last flowering day (LFD) and flowering duration (FD) of early- (EFS), mid- (MFS), and late-flowering (LFS) functional groups from 2019 through 2020 growing seasons that were advanced or delayed by warming and precipitation treatments relative to the control (panel a: FFD; panel b: LFD; panel c: FD). A negative value indicates earlier flowering day and shorter FD relative to the control; a positive value indicates later flowering day and extended FD relative to the control. Mean ± standard error is shown in the figures. Linear mixed models were used to test the effects of warming, precipitation changes and flowering functional groups on FFD ($F = 26.91$, $p < 0.0001$), LFD ($F = 6.10$, $p = 0.0024$), and FD ($F = 13.39$, $p < 0.0001$). See Appendix S1: Table S5 for model details. Tukey's tests were used to compare the differences in phenology among early-, mid-, and late-flowering functional groups within treatments in pairs. The different lowercase letters indicate significant differences ($p < 0.05$) among flowering functional groups in the same climatic treatment based on Tukey's tests.

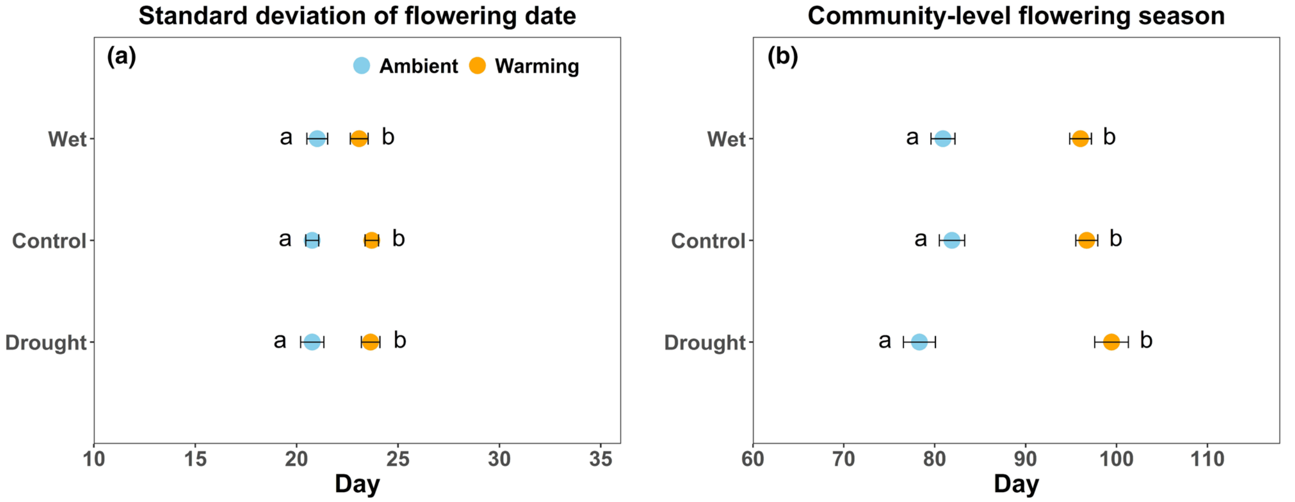

FIGURE 4 Average standard deviation of first flowering date (flowering synchrony) (a) and length of community-level flowering season (b) under six warming and precipitation treatments from 2019 through 2020 growing seasons. Mean ± standard error is shown in the figures. High standard deviation for first flowering date indicates low flowering synchrony. Linear mixed-effects models were used to assess the effects of warming and precipitation changes on flowering synchrony ($F = 56.803$, $p < 0.0001$) and community-level flowering season length ($F = 192.154$, $p < 0.0001$). See Appendix S1: Table S7 for model details. Tukey's tests were used to conduct pairwise comparisons of differences in flowering synchrony and community-level flowering season between all treatments. The different lowercase letters indicate significant differences ($p < 0.05$) among each treatment based on Tukey's tests.

Responses of community-level flowering season to climatic treatments

The average length of the community-level flowering season was significantly extended by 15.5 ± 2.1 days across both years under warming (Figure 4b; Appendix S1: Figure S7, Table S7), which is consistent with the hypothesis that warming will extend the flowering season as shown in our second scenario (Figure 1b). In contrast, precipitation treatments separately or with warming had no significant effects on community-level flowering season length. (Figure 4b; Appendix S1: Table S7).

DISCUSSION

We found warming altered flowering phenology at both the species and community levels. However, precipitation change and its interactions with warming had no significant effects on flowering phenology of this alpine plant community. Warming advanced flowering of species differently in that early-flowering species were more sensitive to warming than mid- and late-flowering species. Together, these responses decreased flowering synchrony among species and extended the community-level flowering season. Warming mediated the flowering phenology of alpine meadow plants, and species-specific phenological shifts reshaped community-level phenological patterns to further affect community structure and ecosystem functioning.

Effects of warming and precipitation changes on flowering phenology

Consistent with our expectation, the average first and last flowering dates of species advanced under warming, leading to an earlier flowering period. This finding is consistent with much research that warming advances the flowering phenology of alpine meadow plants (Jabis et al., 2020; Meng et al., 2016; Suonan et al., 2019). Advanced flowering phenology may be explained by increased preseason soil temperature. Most of the Tibetan Plateau lacks a persistent snowpack in the nongrowing season because of a monsoon-dominated climate (Wang, Liu, et al., 2014). Thus, soil temperature influences spring plant growth. In our study, the warming treatment significantly increased air and soil temperature, which promoted plant development and advanced phenology (Appendix S1: Table S6, Figure S6). Hulber et al. (2010) also found that temperature degree days were an important driver of flowering phenology in alpine species. However, shifts in first flowering date were inconsistent with shifts in last flowering date for all measured species. That is, some species only advanced first flowering date while the end of the flowering date did not change under warming. This variation may be explained by differences in the sensitivity of different flowering phenological events to environmental cues within species (CaraDonna et al., 2014). Alternatively, the timing of last flowering may be driven by more complex environmental cues including day length, temperature, traits and especially flowering onset timing (Li et al., 2020), or by underlying phylogenetic constraints (Li, Li, et al., 2016; Semenchuk et al., 2016). Our study confirmed that the first flowering date was more sensitive to warming than the last flowering date, suggesting that studies based only on the first flowering date may not fully represent the response of flowering phenology to climate change. That is, understanding how phenology responds to climate change requires consideration across the entire sequence of phenological events.

Unexpectedly, different species exhibited inconsistent responses to warming in that some species extended their flowering season while others did not as a result of differences in the response of the first and last flowering time. Our results differ from an elevation transplant experiment in alpine grassland on the Tibetan Plateau, which found that warming prolonged flowering duration, and resulted in a longer reproduction period (Li, Jiang, et al., 2016). Some experiments also found that warming advanced flowering date but did not change flowering duration, indicating that flowering time is sensitive to warming, but flower duration may be a conserved trait (Jabis et al., 2020; Lessard-Therrien et al., 2014; Semenchuk et al., 2016). These different phenological responses among species may differ based among life forms or functional groups (Rollinson & Kaye, 2012). For example, early-flowering species extended their flowering durations more so than mid- and late-flowering species under warming. Furthermore, it should be noted that annual variation and significant interaction effects of year and warming on plant phenology in this study may result from interannual climate variability (Elmendorf et al., 2016; Oberbauer et al., 2013). For example, 2019 was relatively warmer and drier than 2020 at our study site, and this climate variability may cause differences to occur within treatments over the study period (Appendix S1: Figure S2). This variation in the flowering period among species suggests a diversity of patterns in the responses of alpine plants to warming, which may alter the intra- and interspecific interactions of co-occurring species and affect the structure of existing alpine plant communities.

Contrary to our hypothesis, there was no interactive effect between warming and precipitation change on flower phenology. Precipitation addition and reduction did not change the effects of warming on flowering phenology in our study. This differs from a study in the drier alpine ecosystems on the Tibetan Plateau, where precipitation addition led to earlier leaf-out and flowering (Ganjurjav et al., 2020). Warming delayed flowering in an alpine grassland on the central Tibetan Plateau but increased snow addition reversed this response (Dorji et al., 2013). However, our results were consistent with an experiment in more humid alpine meadow, in which warming and precipitation had no interactive effect on the start of flowering (Suonan et al., 2019). This is consistent with remote sensing findings on the Tibetan Plateau that showed that phenology is more sensitive to temperature in humid regions and more sensitive to precipitation in dry regions (Shen et al., 2015). In North American tallgrass prairie warming and precipitation addition had no interactive effects on phenology (Sherry et al., 2007). Together, these results indicated that precipitation in combination with warming may not regulate flowering phenology in cold or wet alpine meadow ecosystems (Inouye & Wielgolaski, 2013; Jabis et al., 2020), and that temperature may be the main driver of plant phenology in alpine meadow ecosystems on the Tibetan Plateau (An et al., 2020; Ma et al., 2020).

Warming reduced flowering synchrony among species

In our study, although warming clearly advanced flowering of all the functional groups, early-flowering species were more sensitive to warming than mid- and late-flowering species. Surprisingly, this finding differs from other research on the Tibetan Plateau that found that late-flowering species were more sensitive to warming than early-flowering species (Meng et al., 2016; Suonan et al., 2017; Wang, Meng, et al., 2014). However, our results are consistent with global meta-analyses of phenology manipulation experiments and long-term observational data, which reported that early-flowering species are most responsive to climate warming (Menzel et al., 2006; Richardson et al., 2013; Sherry et al., 2007; Wolkovich et al., 2012). This divergence may be explained by decreased soil moisture due to warming and asymmetric competition for resources during the growing season among species. In our study, warming caused a significant decrease in soil moisture in the middle and late growing seasons (Appendix S1: Figure S3b), during a time when light and nutrient availability decreases at the onset of peak growth in alpine meadow communities (Niu et al., 2014). Thus, competition between plants for water, light, and nutrient resources may increase later in the growing season, which may weaken the positive effect of warming and cause divergent responses of different functional groups to warming (Cleland et al., 2006; Temperton et al., 2007). Additionally, Wolkovich et al. (2012) concluded that sensitivity of flowering to temperature decreased throughout the growing season. Temperature at the beginning of the growing season increased more than at the end of the year in our experiment resulting in stronger responses in flowering phenology by early-season compared with late-season flowering species (Appendix S1: Table S6, Figure S6). Sherry et al. (2007) also found divergent responses in flowering among species perhaps due to increased growth rate or earlier budbreak in early-flowering compared with late-flowering species under warming. This divergence of flowering phenology shows species-specific adaptation to climate change, and reveals substantial plasticity in the flowering period of alpine plant species.

Warming reduced flowering synchrony and increased differences in flowering time among species within this alpine meadow community. This is contrary to phenological records from Europe where increasing synchrony of leaf-out and first flowering day occurred with a rapid increase in temperature (Wang et al., 2016), but consistent with a different study in which warming reduced leaf-out and flowering synchrony among individuals by up to 55% (Zohner et al., 2018). Decreased flowering synchrony is likely to have resulted from different sensitivity to warming among species, such as the early- versus mid- and late-flowering species in our study (Figures 1b and 4a). Furthermore, differences in the sensitivity to winter cold and day length among species also contribute to changes in flowering synchrony under warming (Laube et al., 2014; Zohner et al., 2016, 2018). Less synchronized flowering among species may affect the reproductive success of plants by altering competition among species for abiotic resources and pollination services (Bogdziewicz, Pesendorfer, et al., 2020; Forrest et al., 2010; Ghazoul, 2006). Thus, further understanding of the effects of climate warming on the structure and function of alpine ecosystems should consider shifts in flowering synchrony among species.

Effects of warming and precipitation changes on community-level flowering season

Contrary to our predication, we found an extended community-level flowering season under warming, and there was no significant interactive effect between warming and precipitation on flowering. This is consistent with the analysis of a 39-year flowering phenology study in Colorado, which reported that the community-level flowering season was extended with increasing summer temperature (CaraDonna et al., 2014). However, increased summer temperature in alpine tundra led to a shorter community-level flowering duration due to greater advancement in flowering times of late-flowering species relative to early-flowering species (Prevéy et al., 2019). Our finding of an expansion of community-level flowering season was attributed to species-level phenological shifts because early-flowering species were more sensitive to warming than mid- and late-flowering species, which confirmed the second scenario shown in our schematic (Figure 1b). This divergent response of flowering phenology within and among species to warming caused the differentiation of phenological niches within this alpine plant community. This further indicates that diversity of species-level shifts in phenology under warming will ultimately lead to altered flowering patterns at the community-level, which will be further modified by species-specific responses to climate warming.

Changes in community-level flowering season in response to warming may lead to phenological mismatches between plants and pollinators or herbivores (Edwards & Richardson, 2004; Schmidt et al., 2016). Temporal divergence may affect the strength of competition among plants and potentially promote coexistence among species within this community (Tiusanen et al., 2020). Moreover, an extended community-level flowering season may result in the redistribution of flower abundance during the flowering season and changes in peak flowering time (Aldridge et al., 2011; Bogdziewicz, Szymkowiak, et al., 2020; CaraDonna et al., 2014; Høye et al., 2013). Thus, changes in community-level phenology should be combined with measurements of floral abundance and pollination resources to explore the effects of phenological shifts on trophic interactions under future climate change.

CONCLUSIONS

We found that warming significantly advanced the flowering season and caused the entire flowering period to begin earlier in the growing season. However, precipitation variability did not influence the effects of warming on flowering phenology. Overall, the responses of first and last flowering time, and flowering duration to warming varied within and among species in this alpine meadow. Early-flowering species were more sensitive to warming than mid- and late-flowering plants, which resulted in decreased flowering synchrony among species and an extended community-level flowering season. Our results suggest that divergence of flowering phenology among species may regulate the response of community-level flowering phenology in alpine ecosystems to climate warming, and that such changes may alter trophic interactions. Future research should consider the impacts of phenological shifts on trophic interactions in alpine ecosystems to better understand the lasting effects of phenological shifts under future climate changes.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data (Chen et al., 2022) are available in Figshare at https://doi.org/10.6084/m9.figshare.20394414.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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