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RESEARCH ARTICLE

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Asymmetric winter warming advanced plant phenology to a greater extent than symmetric warming in an alpine meadow

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Abstract

1. The warming of terrestrial high-latitude ecosystems, while increasing, will likely be asymmetric across seasons—where winter non-growing seasons will warm more than summer-growing seasons. Asymmetric winter warming in temperature-sensitive ecosystems may delay spring phenological events by reducing the opportunity that a plants' chilling requirement is met. Similarly, symmetric warming can advance spring phenology.
2. To explore the impact of asymmetric warming on plant phenology, we applied a year-round warming and a winter warming treatment to our experimental plots. Over a 2-year period, we monitored leaf-out and flowering phenology for 11 plant species.
3. There was variation among species, however, both winter and year-round warming, advanced the leaf-out day and the first flowering day relative to the control treatment. Winter warming advanced leaf-out and flowering phenology by 11.1 (±2.4) and 12.6 (±2.9) days respectively. However, year-round warming had less of an impact advancing leaf-out and flowering phenology by 5.1 (±2.1) and 10.0 (±3.0) days respectively.
4. Our study provides direct evidence that asymmetric winter warming has a larger impact on plant phenology than symmetric year-round warming. Increasing soil temperature in the winter from below to above freezing temperatures advanced the spring phenology of alpine plants. Winter warming increased soil temperature more than year-round warming, which explains why phenology advanced under winter warming more than under year-round warming. In addition, early or mid-season flowering plant species displayed different phenology strategies in warmer winters.
5. Relative to other ecosystems, alpine ecosystems such as the Tibetan Plateau will likely respond to asymmetric warming given the higher amplitude of winter temperature increases due to climatic warming. Our data indicate that seasonal variation in warming should be considered when predicting and modelling the response of alpine ecosystems to climatic change.

KEYWORDS
climate change, early spring flowering plants, mid-summer flowering plants, reproductive phenology, Tibetan Plateau

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1 | INTRODUCTION

Climate change is projected to increase average surface temperatures globally from 0.3 to 0.7°C in next 20 years (Stocker et al., 2013); however, warming patterns will not be equal across seasons. Non-growing winter seasons are predicted to warm to a greater extent than summer growing seasons (Piao et al., 2010; Stocker et al., 2013). The difference between summer and winter warming will likely be amplified in cold, high latitude, temperature-sensitive areas such as the Arctic, Antarctic and the Tibetan Plateau (Chen et al., 2013; Root et al., 2003; Stocker et al., 2013). In fact, since the 1960s winter temperatures on the Tibetan Plateau have increased 0.3°C per decade and summer temperatures have increased 0.2°C per decade (Chen et al., 2013; Lu & Liu, 2010). We know that winter and summer are warming at different rates (i.e. asymmetric warming), yet how these differences increase or decrease biological processes and community interactions in important ecosystems remains uncertain.

Spring phenology, plant leaf out and flowering date are important developmental stages in plant life cycles as well as a sensitive indicator of global change (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007; Menzel et al., 2006; Parmesan & Yohe, 2003). Many factors control the timing of spring phenology in ecosystems, yet temperature is the most studied. While numerous studies reveal that symmetric warming advanced the phenology of plants (Cleland, Chiariello, Loarie, Mooney, & Field, 2006; Dunne, Harte, & Taylor, 2003; Miller-Rushing & Primack, 2008; Morin, Roy, Sonié, & Chuine, 2010; Norby, Hartz-Rubin, & Verbrugge, 2003; Parmesan & Yohe, 2003; Peñuelas & Filella, 2001; Schwartz, 1998), asymmetric warming in winter was found to delay plant development (Guo et al., 2014; Körner & Basler, 2010; Luedeling, Guo, Dai, Leslie, & Blanke, 2013). Warming during the ecodormancy phase, the period a plant remains dormant due to external, environmental conditions, can increase plant development and advance spring phenology (Cleland et al., 2006; Dunne et al., 2003; Menzel et al., 2006). Temperature increases during the endodormancy phase, the period a plant remains dormant due to plant internal factors, can lead to later spring phenology because the chilling requirements for plant development have not been met (Chuine, Morin, & Bugmann, 2010; Guo et al., 2014; Körner & Basler, 2010; Luedeling et al., 2013; Naor, Flaishman, Stern, Moshe, & Erez, 2003). The projected asymmetric seasonal warming could change temperatures during these critical periods for plant development and thus impact plant phenology.

The phenology of plant species that develop at different points in the season (i.e. early-, mid- and late-flowering plants) respond differently to seasonal temperature changes. The phenology of early spring flowering species was less sensitive to warming than mid-summer flowering plant species (Meng et al., 2016; Wang, Meng, et al., 2014; Wang, Wang, et al., 2014). However, other studies found different results that plant species that flower before the community flowering peak, were more sensitive to warming than species that flower after flowering peak (Castro Marin et al., 2011; Richardson et al., 2013; Sherry et al., 2007; Wolkovich et al., 2012). The time when the floral primordium differentiates for early- and mid-season flowering plants can determine their sensitivity to warming (Wang, Meng, et al., 2014). Thus, warmer winters might differentially induce the flowering process that are regulated by exposure to long periods of cold in the winter in some species but not in others leading to changes in the phenology of different flowering functional groups (Cook et al., 2012). Manipulative experiments with asymmetric seasonal warming can explore the various mechanisms that may be influencing these processes. However, few studies have been conducted in cold-sensitive regions where changes in plant phenology could be an early signal of climate change impacts on ecosystems (Chen, An, Inouye, & Schwartz, 2015).

The Tibetan Plateau is the highest and largest plateau in the world (Qin, Yang, Liang, & Guo, 2009). Covering an area of 2.5 million km^2 with an average altitude >4000 m a.s.l., it is characterized by cold temperatures and a short growing season (He et al., 2006). Thus, alpine vegetation on the Tibetan Plateau is sensitive to temperature changes (Wang, Liu, et al., 2014; Wang, Wang, et al., 2014). Spring phenological changes on the Tibetan Plateau have been assessed using remote sensing and the results from these studies have been inconsistent. Some studies reported an advance in spring phenology from the early 1980s until the mid-1990s, followed by a rapid delay in spring phenology until 2006 (Yu, Luedeling, & Xu, 2010). These studies speculated that the observed delay in plant phenology was due to winter warming leading to unfulfilled chilling requirements (Yu et al., 2010). However, other remote sensing studies found a different pattern — that spring phenology has continuously advanced since 1982 (Zhang, Zhang, Dong, & Xiao, 2013). Clearly, there has been a lot of debate about what mechanisms are responsible for the changes in spring phenology on the Tibetan Plateau (Chen, Zhu, Wu, Wang, & Peng, 2011; Dong, Zhang, Zhang, & Xiao, 2013; Luedeling, Yu, & Xu, 2011; Shen et al., 2013; Wang, Peng, Lin, & Chang, 2013; Zhang, Dong, Zhang, & Xiao, 2013). After summarizing the available remote sensing datasets, it appears that spring phenology has advanced over the past 30 years at large-spatial scales, but there is substantial spatial heterogeneity in response across the landscape (Shen et al., 2015). The observed remote sensing patterns are interesting, yet they are unable to tease apart the mechanisms driving the observed changes in phenology because they are not experimental and they cannot detect flowering (Shen et al., 2015; Wang, Meng, et al., 2014). Moreover, some experimental and observational studies have revealed that warming accelerated the phenology on the Tibetan Plateau (Chen et al., 2015; Meng et al., 2016; Wang, Meng, et al., 2014; Wang, Wang, et al., 2014; Zhou et al., 2014). Given asymmetric warming on plant phenology has been unexplored, it remains unclear how differences in winter and spring temperatures control spring phenology.

Understanding spring phenological changes and the mechanisms driving them is essential to accurately evaluate the impacts of warming on plant growth and ecosystem function. To explore how asymmetric winter warming altered plant phenology, we conducted a warming study with an asymmetric winter warming treatment, a constant warming treatment and a non-warmed control treatment in an alpine meadow on the Tibetan Plateau. Over 2 years, we measured the leaf-out day and the first flowering day of 11 common alpine species. We asked two related questions: (1) How does symmetric year-round warming and asymmetric winter warming affect the phenology of alpine meadow plants; (2) How the phenology of different flowering functional groups responds to warming?

2 | MATERIALS AND METHODS

2.1 | Study site and experiment design

We conducted the experiment at the Haibei Alpine Grassland Ecosystem Research Station that was managed by the Chinese Academy of Sciences (Haibei Station, 101°12′E, 37°30′N, 3200 m. a.s.l.). The experimental area is dominated by alpine grassland and has a continental monsoon climate, with severe, long winters and short, cool summers. From 1983 to 2013, the mean annual air temperature was 1.1°C and the mean annual precipitation was 485 mm. Over 84% of the precipitation occurred during the relatively short summer-growing season from May to September (Zhao & Zhou, 1999). Soils at the site are classified as Mat-Gryic Cambisols (Chinese Soil Taxonomy) and as *borolls* (USDA Soil Taxonomy). The dominant plant species at the site were *Kobresia humilis*, *Stipa alinea*, *Festuca ovina*, *Elymus nutans*, *Poa pratensis*, *Carex scabrirostris*, *Tibetia himalaica*, *Melilotoides archiducis-nicolai*, *Gentiana straminea*, *Gentiana lawrencei*, *Leontop odiumnanum*, *Potentilla nivea*, *Saussurea superba*, *Aster diplostephioides* and *Dasiphora fruticosa*. For more details on the experimental site see (Wang, Liu, et al., 2014; Zhao & Zhou, 1999).

Our study was conducted within a larger experimental warming × precipitation multi-factor infrastructure that was established in July 2011. The larger experiment manipulated warming (+2°C, ambient) and precipitation (addition, drought, ambient) in a fully factorial completely randomized design with six experimental blocks (n = 6). However, in this study we focused our data collection on the warming manipulations; the precipitation manipulations were not included. Experimental plots were 2.2 × 1.8 m with a 2.5 m among the treatment plots. In October 2011, we added an asymmetric winter warming treatment (n = 5, for a total of 15 experimental plots) using the same spacing and randomized design as the year-round warming and control plots in the larger study. Relative to the control plots, we aimed to increase soil temperature (5 cm) in the year-round warming plots by 1.5–1.8°C above ambient. To disentangle the effects of year-round and winter warming on plant phenology we kept mean annual temperature the same in both treatments. Thus, soil temperatures in the winter warming plots were 1°C higher than in the year-round warming plots during the non-growing season (2.5–2.8°C above ambient) and 1°C lower than the year-round warming plots during the growing season (0.5–0.8°C above ambient). We defined the start of the non-growing season as the first day the 7 day smoothed daily mean air temperature remained <0°C for at least five consecutive days (Wang, Liu, et al., 2014). Similarly, we defined the onset of the growing season as the first day the 7 day smoothed daily mean air temperature remained >0°C for at least five consecutive days (Wang, Liu, et al., 2014). Non-growing seasons were 20 October 2012–11 April 2013; 18 October 2013–3 April 2014; Growing seasons were 12 April 2013–17 October 2013; 4 April 2014–17 October 2014.

For the experimental warming treatments, infrared heating structures were established above all of the plots as a control, but only the warmed plots were warmed. Two medium-wave infrared heaters (1200W, 220V, 1 m long and 0.22 m wide) or their light-free control boxes, were fixed 1.5 m above the ground within each of the plots with stainless steel posts. In two plots within each treatment temperature and moisture probes (EM 50, Decagon Devices Inc., Pullman, WA, USA) were installed. Air temperature probes were installed 30 cm above the soil surface and soil temperature and moisture probes were installed at 5, 10 and 20 cm in the soil profile; all data were automatically recorded hourly and stored in a data logger.

2.2 | Phenology measurements

We used a pool of 11 common plant species, to explore how warming altered plant phenology. Each species was monitored every 3–4 days during the growing season from March to September in 2013 and 2014. All species were classified into three functional groups based on their life history as early spring (Early; flower before June), mid-summer (Mid; flower between June and July) and late autumn (Late; flower after August) flowering plants (Wang, Meng, et al., 2014; Table 1). The selected pool of eleven species made up 70–80% of the relative cover and 74.4% of the total biomass in the plant community

TABLE 1 Alpine meadow species examined in this study. The 11 species monitored accounted for 74.4% of the total above-ground biomass

Species	Abbreviation	Functional group	Flowering functional group	Contribution to community biomass (%)
Stipa alinea	Sa	Grass	Mid	44.62
Elymus nutans	En	Grass	Mid	3.13
Poa pratensis	Pp	Grass	Mid	2.75
Kobresia humilis	Kh	Sedge	Early	3.59
Tibetia himalaica	Th	Legume	Mid	4.73
Melilotoides archiducis-nicolai	Ma	Legume	Mid	1.53
Gentiana lawrencei	Gl	Forb	Late	4.60
Aster diplostephioides	Ad	Forb	Late	3.65
Potentilla nivea	Pn	Forb	Mid	3.54
Gentiana straminea	Gs	Forb	Late	1.24
Saussurea superba	Ss	Forb	Late	0.97

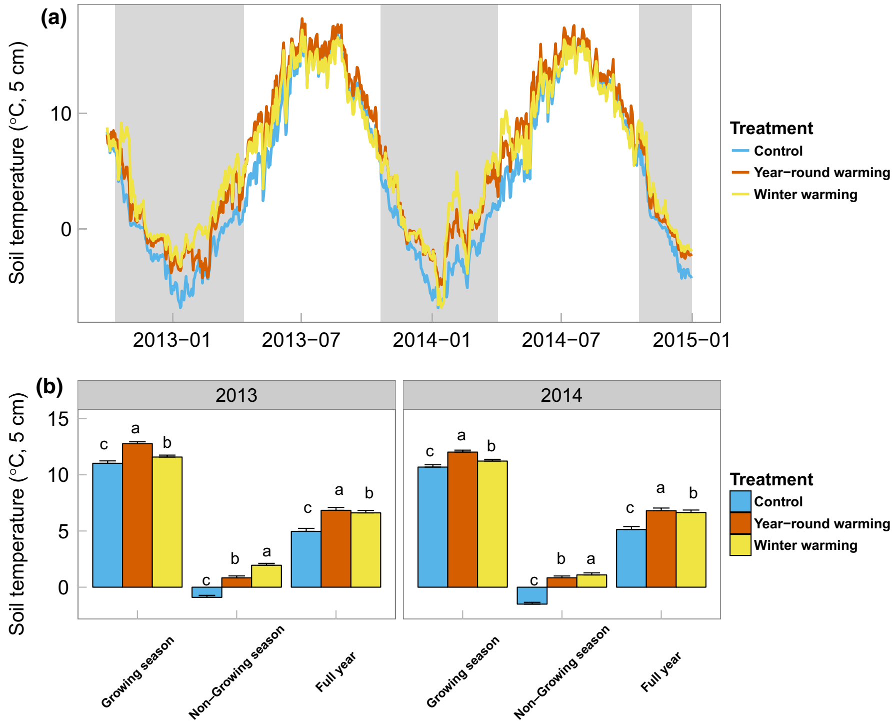

FIGURE 1 Daily average soil temperature (°C, 5 cm) (a) under control, year-round warming and winter warming treatments from October 2012 to December 2014. Mean (±*SE*) soil temperature (°C, 5 cm) (b) for the whole year, the growing season and the non-growing season under control, year-round warming and winter warming treatments in 2013 and 2014 (Non-growing seasons are 20 October 2012–11 April 2013; 18 October 2013–3 April 2014). We applied the linear mixed effects models to test the effects of treatment (control, year-round warming and winter warming) on soil temperature separately in 2013 and 2014. We set treatment as fixed factor, and time as a random factor in each model to account for variation among repeated measurements of temperature or moisture. Next, we used Tukey's tests to conduct pairwise comparisons of differences in soil temperature among control, year-round warming and winter warming treatments. We applied the same statistical strategy—using linear mixed effects models followed by Tukey's tests for each year—when analysing soil temperature during non-growing season, soil temperature during the growing season, air temperature and soil moisture. Different letters indicate significant differences at .05 level. Shading periods represent the non-growing season

monitored (Table 1). To track leaf-out day, individuals in each plot were marked when the first leaf was observed. Once all the plants had leafed out, six individuals for forbs and legumes and six stems for grasses and sedges were randomly selected, marked and monitored for the growing season. We were unable to identify the leaves of *Stipa alinea* and *Poa pratensis* grass species during their leaf-out phase, thus we tracked nine out of the 11 species for leaf-out day over the course of the study. The first date a flower was observed for each of the marked individuals was recorded as the first flowering day. Flowering rates were low for two out of the 11 species monitored (*Saussure superba* and *Aster diplostephioides*), thus we monitored the first flowering day for nine species across the 2 years. Leaf-out day and first flowering day events were averaged for six individuals of each species within each plot.

2.3 | Statistical analyses

We performed all analyses in this study in R version 3.3.1 (R Development Core Team, 2016) with package "NLME" (Pinheiro, Bates, DebRoy, & Sarkar, 2007). We applied linear mixed effects models using "lme" function to test the effects of treatment (control, year-round warming and winter warming) on soil temperature separately in 2013 and in 2014. We set treatment as fixed effects, time as a random effect in each model to account for variation among repeated measurements of temperature or moisture. Next, we used Tukey's tests to conduct pairwise comparisons of differences in soil temperature among control, year-round warming and winter warming treatments. We applied the same statistical strategy—using linear mixed effects models followed by Tukey's tests for each year—when analysing soil temperature during non-growing season, soil temperature during the growing season, air temperature and soil moisture. Linear mixed effects models were used to examine the effect of treatment (control, year-round warming and winter warming) on plant phenology (leaf-out day, first flowering day) for each year. Treatment was treated as fixed effects, and species nested within block was treated as a random effect to account for variation among species within block. We selected linear mixed effects models based on Akaike information criterion (AIC). We compared a null model (only intercept as the fixed effect) and the model with treatment and intercept as fixed effects using "Maximum likelihood (ML)" method. The linear mixed effects models with treatment as fixed effect are the better fit. Therefore, we reported the ANOVA result of the

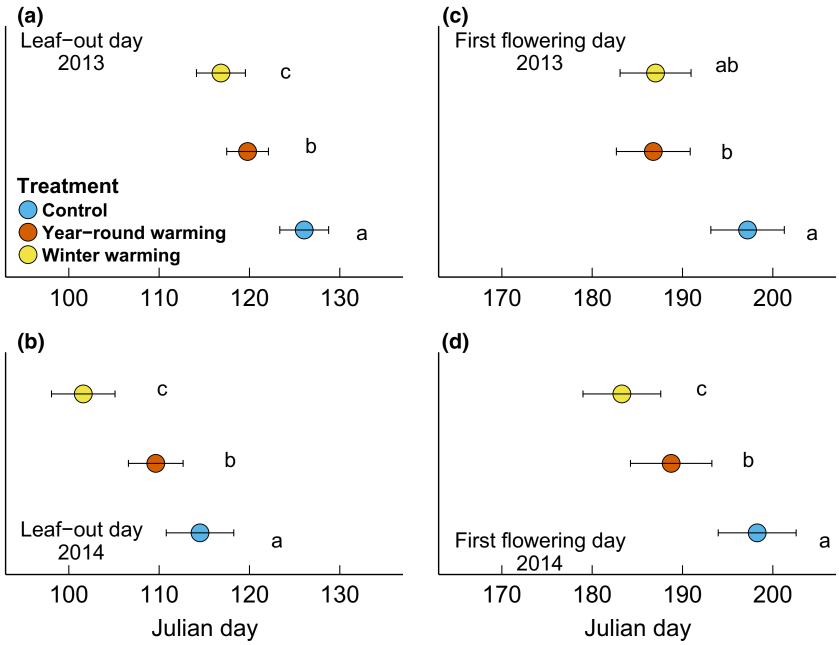

FIGURE 2 Average leaf-out day and the first flowering day for all species monitored in the control, year-round warming and winter warming treatments in 2013 and 2014 (a: Leaf-out day in 2013; b: Leaf-out day in 2014; c: First flowering day in 2013; d: First flowering day in 2014). Mean ± *SE* are shown in the Figures. All the analyses were performed using the linear mixed models to test the effect of treatment (control, year-round warming and winter warming) on plant phenology (leaf-out day, first flowering day) for each year. Treatment was treated as fixed effects, and species nested within block was treated as a random effect to account for variation among species within block. Tukey's tests were used to conduct pairwise comparisons of differences in plant phenology among control, year-round warming and winter warming treatments in each year. Different letters indicate significant differences at 0.05 level

linear mixed effects model with treatment as fixed effect and species nested within block as random effect using "Restrict maximum likelihood (REML)" method. In addition, we used Tukey's tests to conduct pairwise comparisons of differences in plant phenology among control, year-round warming and winter warming treatments in each year.

Linear mixed effects models were used to test the independent effects of treatment (control, year-round warming and winter warming), species and year and the interactive effects of these three factors on plant phenology (leaf-out day, first flowering day). Treatment, species and year were treated as fixed effects and block was treated as a random effect to account for variation among blocks. Linear mixed effects models were also used to test the independent effects of treatment (control, year-round warming and winter warming), function (early-, mid- or late-flowering functional groups) and year, and the interactive effects of these three factors on plant phenology (leaf-out day, first flowering day). Treatment, function and year were treated as fixed effects and block was treated as a random effect to account for variation among blocks. Next, two-way ANOVAs were applied to test the effects of treatment (year-round warming and winter warming) and function (early-, mid- or late-flowering functional groups) on leaf-out day and first flowering day (advanced or delayed in year-round warming than control: $\triangle$ year-round warming, advanced or delayed in winter warming than control: $\triangle$ winter warming). Finally, we used Tukey's tests to compare the differences in phenology among early-, mid- and late-flowering functional groups within treatments in pairs, and between $\triangle$ year-round warming and $\triangle$ winter warming within functional groups in pairs. Differences were defined as significant when $p < .05$.

3 | RESULTS

3.1 | Soil environmental conditions

Our experimental warming treatments warmed our ecosystem as expected ($F_{2,3648} = 1380.77$, $p < .001$; Figure 1). Relative to control treatments, the symmetric year-round warming (year-round warming) treatment increased yearly average soil temperature by 1.77°C in both 2013 and 2014 ($p < .001$; Figure 1). In the asymmetric winter warming (winter warming) treatment, soil temperature was, on average, 1.57°C warmer than soils in the control treatment across both years ($p < .001$; Figure 1). Average soil temperature in the control treatment was 5.05°C across both years (Figure 1).

Winter warming soil temperatures were, on average, 0.99°C cooler than year-round warming soil temperatures during the growing season across both of the years measured ($F_{2,1937} = 603.18$, $p < .001$). However, during the non-growing season, average soil temperatures in the winter warming treatment were 0.70°C higher than in the year-round warming treatment ($F_{2,1708} = 2032.98$, $p < .001$). Specifically, soil temperature was increased from below 0°C in the control plots (2013: −1.60 ± 0.07; 2014: −1.38 ± 0.13) to above 0°C in year-round warming plots (2013: 2.01 ± 0.10; 2014: 2.06 ± 0.19) and winter warming treatment plots (2013: 2.82 ± 0.10; 2014: 2.64 ± 0.19) during the non-growing season (Figure 1b). Average air temperatures were 0.53°C warmer in the year-round warming and 0.46°C warmer in the winter warming treatment than in the control treatment (−0.47°C; $F_{2,3633}$ = 1458.01, p < .001). Across the two growing seasons, average soil moisture was 27%, 21% and 22% in control, year-round warming and winter warming treatments respectively ($F_{2,1932}$ = 1231.78, p < .001).

3.2 | Warming effects on plant phenology

Asymmetric winter warming and symmetric year-round warming advanced plant leaf-out day and the first flowering day relative to the control treatment. Winter warming had a larger effect on the leaf-out day and the first flowering day than year-round warming. Year-round warming and winter warming advanced the average leaf-out day for nine species by 6.3 ± 2.3 days and by 9.2 ± 2.7 days, respectively, relative to the control treatment in 2013 ($F_{2,84}$ = 59.682, p < .0001; Figure 2a,b). Year-round warming and winter warming advanced the average leaf-out day for nine species by 4.9 ± 3.0 days and by 12.9 ± 3.5 days, respectively, relative to the control treatment in 2014 ($F_{2,80}$ = 38.997, p < .0001; Figure 2a,b). Average first flowering day for all nine species advanced 10.4 (±4.1 *SE*) days and 10.1 (±3.9 *SE*) days, respectively, in the year-round warming and winter warming relative to the control treatment in 2013 ($F_{2,81}$ = 126.608, p < .0001; Figure 2c,d). The average first flowering day advanced 9.5 ± 4.5 days and 15.0 ± 4.3 days in the year-round warming and winter warming treatment, respectively, relative to the control treatment in 2014 ($F_{2,84}$ = 109.861, p < .0001; Figure 2c,d).

Phenology patterns were often species specific (leaf-out day: F_8 = 647.456, p < .0001; first flowering day: F_8 = 2379.044, p < .0001); however, warming advanced the leaf-out day (F_2 = 152.258, p < .0001) and the first flowering day (F_2 = 393.159, p < .0001) for all nine species (Figure S1, Supporting Information). Furthermore, this effect was greater in the winter warming treatment where leaf-out day and first flowering day were significantly earlier than in the year-round warming treatment (except first flowering day in 2013; Figure 3a,b). Moreover, the interactive effects of treatment, species and year were significant for both leaf-out day and first flowering day (Table S1). In addition, after 2 years, both warming treatments significantly advanced leaf-out day and first flowering day. Surprisingly, in 2014, leaf-out day was accelerated in all treatments, but first flowering day was not (Figure S2).

3.3 | The responses of different flowering functional groups

Three flowering functional groups in our study showed significantly different phenological changes in response to warming (Table 2, Figure 3). Especially in the winter warming plots, the phenology of mid-summer (mid-flowering) and late-autumn (late-flowering) groups were more sensitive than early-spring (early-flowering) groups (Figure 3a,b). In the year-round warming plots, the leaf-out day of mid-season flowering plants was more sensitive to warming than the leaf-out day of early-season flowering group (p = .019; Figure 3a). However, the warming impacts on the first flowering day of mid- and late-season flowering plants were similar to those of the early-season

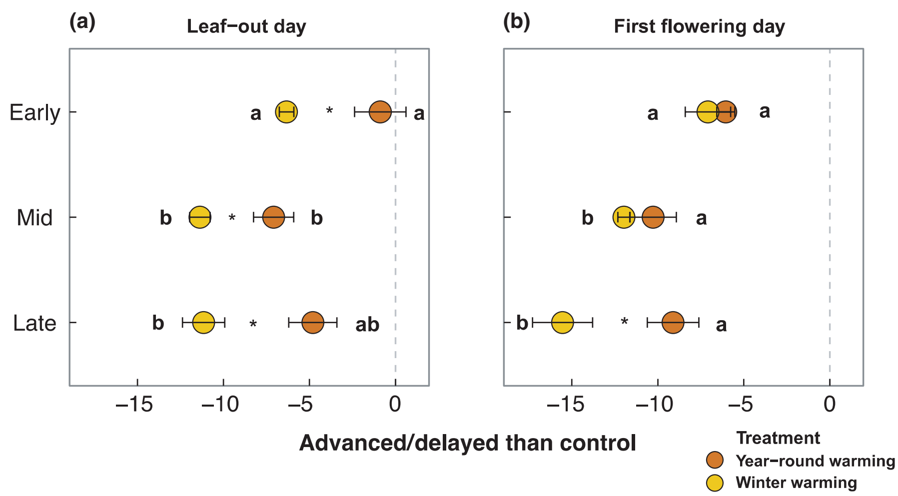

FIGURE 3 Average leaf-out day and first flowering day of early-, middle- and late-flowering functional groups that was advanced or delayed in the year-round warming and in the winter warming treatments relative to the control treatments (a: Leaf-out day; b: First flowering day). A negative value indicates earlier leaf-out day or first flowering day relative to the control treatment; a positive value indicates later leaf-out day or first flowering day relative to the control treatment. Two-way ANOVAs were applied to test the effects of treatment (year-round warming and winter warming) and function (early-, mid- or late-flowering functional groups) on leaf-out day and first flowering day (advanced or delayed in year-round warming than control: △ year-round warming, advanced or delayed in winter warming than control: △ winter warming). We used Tukey's tests to compare the differences in phenology among early-, mid- and late-flowering functional groups within treatments in pairs, and between △ year-round warming and △ winter warming within functional groups in pairs. Mean ± *SE* are shown in the figures. Different letters indicate significant differences among early-, mid- and late-flowering functional groups at .05 level; an asterisk indicates significant differences between winter warming and year-round warming at .05 level. Red represent year-round warming and yellow represent winter warming

TABLE 2 Two-way ANOVAs showing the effects of treatment and function (early-, mid- or late-flowering functional groups) and their interactional effects on leaf-out day, first flowering day. *df*, *F* value and *p* value are shown. Bold values and *** both indicate significance at .001 level

	Leaf-out day			First flowering day		
	df	*F*	*p*	*df*	*F*	*p*
Treatment (T)	1	34.016	**5.153×10^{-6}***	1	9.06	**.006***
Function (F)	2	13.72	**.0001***	2	11.95	**.0003***
T × F	2	0.42	.659	2	2.80	.081

flowering plants (Figure 3b). The leaf-out day of the three functional groups changed consistently among warming treatments. While both treatments shifted the leaf out day earlier, the winter warming treatment shifted that day earlier than the year-round warming treatment did (Figure 3a,b). The first flowering day of early- and mid-flowering species did not differ significantly between the winter warming and the year-round warming treatments. In general, the leaf-out day was controlled by treatment, function and year, and the first flowering day was controlled by treatment, function and the interaction of function and year (Table S2).

4 | DISCUSSION

Global change driven warming during winter and summer periods will alter important plant phenology events such as plant leaf-out or flowering date. Our manipulative experiment with symmetric year-round warming and asymmetric winter warming in an alpine meadow found that asymmetric winter warming advanced the leaf and flower phenology of plants to a greater extent than symmetric year-round warming did. In addition, the phenology of mid-summer and late-autumn flowering plants was more sensitive to winter warming than early spring flowering plants. Clearly in our study, and in others, asymmetric warming in the winter advanced plant phenology (Chen et al., 2015; Fu, Campioli, Deckmyn, & Janssens, 2012; Zhang, Zhang, Dong, et al., 2013)—a pattern that will have cascading impacts on ecosystem structure and function in a warming world.

4.1 | Warming treatment impacts on plant phenology

In our study, asymmetric winter warming advanced plant phenology to a greater extent than symmetric year-round warming did. Winter soil temperatures in the warming treatments might explain this result. The mean non-growing season soil temperature in control plots was below 0°C, and 0°C is the freezing threshold temperature for many organisms and processes (Went, 1953). The warming treatments in our study raised the winter temperature above the freezing threshold temperature in the year-round warming plots and increased temperatures more in the winter warming plots. Since most of the Tibetan Plateau has no persistent snowpack in the winter due to the monsoon-dominated climate (Wang, Liu, et al., 2014), soil temperature regulates many below-ground activities and thus spring plant growth. By preventing the soil water from freezing in winter, processes such as decomposition could occur year-round under warming (Campbell, Mitchell, Groffman, Christenson, & Hardy, 2008; Post & Aastrup, 2009; Sturm et al., 2005) enhancing spring growth. Winters on the Tibetan Plateau are extremely cold and thus warmer winter soil temperature explains why warming in the winter advanced the date for leaf out and flowering earlier than year-round warming did. It is important to note that our results may be specific to ecosystems with similar temperature ranges; other ecosystems where winter temperatures are always above freezing or are always below freeing may respond differently.

Our study did not find that asymmetric winter warming delayed the leaf-out day and the first flowering day of alpine plants. Winter mean daily temperatures on the Tibetan Plateau are lower than 0°C, thus our experimental warming treatment may not have warmed the soil enough to overcome the winter chilling threshold for leaf-out day and first flowering day (Zhang, Zheng, & Yang, 1982) or the chilling requirement might be flexible so that plants could meet their chilling requirements over shorter periods of low temperature (Went, 1953).

4.2 | The phenology of flowering functional groups

In our study, the phenology of mid- and late-flowering plant species was more sensitive to winter warming than the early spring-flowering species. This finding is counter to what other studies in other ecosystems found (Castro Marin et al., 2011; Richardson et al., 2013; Sherry et al., 2007; Wolkovich et al., 2012); however, it was consistent with a reciprocal translocation experiment along an elevation gradient on the Tibetan Plateau (Meng et al., 2016; Wang, Meng, et al., 2014; Wang, Wang, et al., 2014). Typically, early-flowering plants complete their floral primordia in the former autumn and winter, whereas middle- and late-flowering plants, differentiate the floral primordium before flowering, that synchronized with vegetative growth (Körner, 2003; Wang, Meng, et al., 2014). With manipulative warming treatment in winter, our study further confirmed that temperature increase in winter might have delayed the completion of cold exposure that can regulate flowering process in early-flowering plants (Cook et al., 2012). Therefore, the phenology of early-season flowering plant species was less sensitive to winter warming than the mid-season flowering plants. These different phenological strategies may change functional group composition, leaf area and productivity of different flowering functional groups in the community. Thus, warming driven impacts on phenology can directly and indirectly impacting on species' distribution, interactions and productivity in the future (Cleland et al., 2007; Morin et al., 2009; Penuelas, Rutishauser, & Filella, 2009; Richardson et al., 2013).

4.3 | Winter warming and plant reproductive phenology

In our study, winter warming advanced flowering phenology, which is consistent with leaf-out phenology. Previous studies exploring winter warming and phenology focused on leaf phenology (Fu, Piao, et al., 2015; Fu, Zhao, et al., 2015; Morin et al., 2009; Shen et al., 2015), and few monitored how winter warming alters flower phenology (Bokhorst et al., 2008). First flowering occurs when a plant starts its reproductive phase, a phase that requires adequate chilling conditions (vernalization) during endodormancy (Bykova, Chuine, Morin, & Higgins, 2012). Therefore, flowering phenology is expected to be more sensitive to winter warming than leaf phenology. However, the first flowering day changed consistently with leaf-out day in winter warming in our study. In fact, winter warming in this system may result in higher plant reproductive fitness because earlier flowering leads to a longer fruit maturation time (Inouye & Wielgolaski, 2013). Yet, earlier flowering may also increase the risk of frost damage and possible mismatches with pollinators (Jia, Bayaerta, Li, & Du, 2011). In addition, other phenological components such as the peak and end of flowering may respond differently than first flowering to asymmetric winter warming, thus leading to increases or decreases in plant reproductive output (CaraDonna, Iler, & Inouye, 2014; Miller-Rushing & Primack, 2008). Given asymmetric warming is already happening on the Tibetan Plateau, winter warming impacts on plant reproductive phenology and reproductive output should be an emphasis in future studies.

4.4 | Implications

Winter daily temperatures on the Tibetan Plateau are, on average, lower than 0°C (Wang, Liu, et al., 2014). Our results suggest that increasing winter temperatures above the freezing threshold under asymmetric winter warming will advance the spring phenology events of alpine plants to a greater extent than year-round warming will. Furthermore, we clearly show that plants who leaf out or bloom early or late in the growing season have differential responses to warming. If leaf phenology shifts at different rates among species in the community, then the plant community composition may also shift under warming, especially winter warming, towards plants who leaf out and bloom earlier in the season. Thus, alpine plants with different life histories will likely display different strategies when coping with warmer temperatures leading to new alpine plant communities that might have different functions.

Our results suggest that warmer winters will advance leaf phenology, extend the growing season and advance the growth and reproduction of alpine plants. However, earlier phenology can come at a cost for plant growth and reproduction—such as an increased frost risk and possible mismatches with pollinators. In addition, the phenology of early-flowering functional group was less sensitive to a warmer winter than mid- and late-season flowering plants. Winter warming may lead to declines in soil moisture, which can reduce plant growth and reproduction. Changes in plant phenology, whether a cost or benefit to plant growth, will result in changes in plant interactions, community composition, biomass production, carbon balance and nutrient cycling. Therefore, the effects of asymmetric growing season warming should continue to be explored with experiments and models that aim to predict how ecosystems will function in the future.

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AUTHORS' CONTRIBUTIONS

J.-S. H. conceived the ideas; J.S. designed methodology, collected the data and analysed the data; J.S. and A.T.C. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data associated with this article can be found in the Dryad Digital Repository at https://doi.org/10.5061/dryad.q2g41 (Suonan, Classen, Zhang, & He, 2017).

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