# Plants with lengthened phenophases increase their dominance under warming in an alpine plant community

Ji Chen[1], Yiqi Luo[2], Yuxin Chen[3], Andrew J. Felton [4], Kelly Hopping[5], Rui-Wu Wang[6], Shuli Niu[7], Xiaoli Cheng[8], Yuefang Zhang[9], Junji Cao[10], Jørgen Olesen[1], Mathias Neumann Andersen[1], and Uffe Jørgensen[1]

[1]Aarhus Universitet
[2]Northern Arizona University
[3]Sun Yat-sen University
[4]Utah State University
[5]Boise State University
[6]Center for Ecological and Environmental Sciences
[7]Institute of Geographic Sciences and Natural Resources Research Chinese Academy of Sciences
[8]Yunnan University
[9]Ministry of Agriculture and Rural Affairs
[10]Institute of Earth Environment Chinese Academy of Sciences

April 28, 2020

## Abstract

Predicting how warming-induced shifts in plant species-specific phenology affect species dominance remains challenging. Here, we investigated the effects of experimental warming on plant species-specific phenology and dominance as well as their relations in an alpine meadow on the Tibetan Plateau. Warming significantly advanced phenological firsts (leaf out and first flower dates) for most species, while having variable effects on phenological lasts (leaf senescence and last flower) and full phenological periods (growing season and flower duration). Experimental warming reduced community evenness and differentially impacted the species-specific dominance. Specifically, warming-induced shifts in phenological lasts and full phenological periods, rather than the single phenological firsts, are associated with changes in species dominance. Species with lengthened full phenological periods under warming increased their dominance. Our results advance our understanding of how altered species-specific phenophases can be related to changes in community structure in response to climate change.

**Graphical abstract**

1
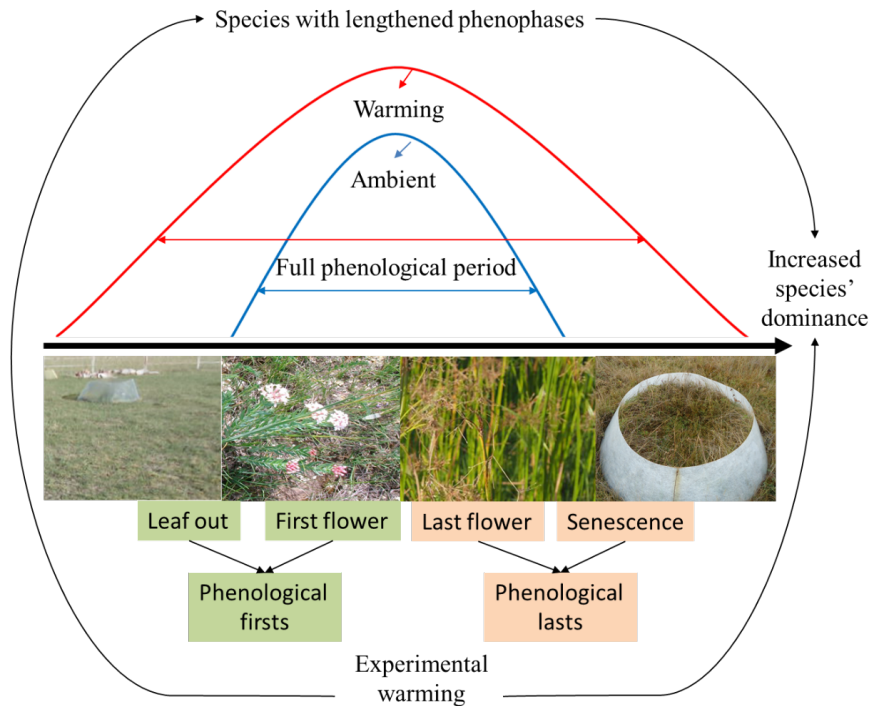
## 1. Introduction

Shifts in plant phenology under climate warming alter the competitive environment experienced by the individuals and species (Cleland *et al.* 2007), potentially affecting species dominance and reshaping plant community composition (Smith & Knapp 2003; Parmesan 2006; Forrest & Miller-Rushing 2010). Whereas rising temperatures may have substantial impacts on plant phenology and species dominance (Root *et al.* 2003; Thuiller *et al.* 2005; Cleland *et al.* 2007), predicting how warming-induced shifts in plant species-specific phenology affect species dominance remains challenging (Rudolf 2019). Our current understanding of warming impacts on plant phenology and its linkages with species dominance mainly stems from the focus on the 'phenological firsts' (e.g., leaf out and first flower) (Dunne *et al.* 2003; Sherry *et al.* 2007; Leblans *et al.* 2017). However, several recent studies have shown that 'phenological lasts' (e.g., leaf senescence and last flower) respond asymmetrically or even contrastingly to climate warming, as compared to the phenological firsts (CaraDonna *et al.* 2014; Gallinat *et al.* 2015; Prevéy *et al.* 2019). The impacts of shifts in 'phenological lasts' on species dominance, however, remained unresolved. Indeed, a better understanding of the underlying drivers for shifts in species-specific phenological firsts and lasts will help determine the effects of warming on the full phenological periods, as well as on the implications for variations in species dominance.

Plant phenology is highly sensitive to climate warming and finely tuned to the changing environment (Parmesan 2006; Cleland *et al.* 2007). However, the underlying driving factors and their importance for shifts in species-specific phenology to climate warming remain unclear (Tang *et al.* 2016; Chmura *et al.* 2019), hindering an improved understanding of the potential links between plant phenology and species dominance. Rising temperatures could advance leaf out date of some species due to faster accumulation of growing-degree days (Cayton *et al.* 2015; Suonan *et al.* 2017), or could delay leaf out date for other species due to delayed or even failed fulfillment of winter chilling requirements (Marchin *et al.* 2015; Guo *et al.* 2019).

Apart from the direct effects of rising temperatures, warming-induced changes in soil moisture and soil nutrient availability could also have significant indirect effects on plant phenology (Estiarte & Peñuelas 2015; Gill *et al.* 2015; Marchin *et al.* 2015). For example, warming-induced reductions in soil moisture could potentially cause delayed reproductive phenology (Sherry *et al.* 2007; Dorji *et al.* 2013) or declines in flower

duration (de Valpine & Harte 2001). Furthermore, phenological firsts and lasts are likely controlled by different environmental factors due to niche differentiation among various plant growth stages (Ernakovich *et al.* 2014; Bahuguna & Jagadish 2015; Gill *et al.* 2015), further heightening the challenges to predict the impacts of warming on species-specific phenology, species dominance, and ecosystem structure.

Assessments of shifting plant phenology and species-specific dominance have largely proceeded independently (Diez*et al.* 2012; Rudolf 2019). This is, in part, because larger-scale phenology assessments, primarily derived from satellite remote sensing, have limited power in representing species-specific phenological patterns (Zhang *et al.* 2003). However, species have consistently shown divergent movements in their phenological patterns to climate warming, rather than shifting unidirectionally (Sherry *et al.*2007). These highly differed species-specific phenological patters may have substantial but underexplored impacts on species dominance, invasion, and community composition (Fridley *et al.* 2016; Post *et al.* 2016; Zohner *et al.* 2018), as the timing of phenological events often determines the competitive conditions experienced during each developmental phase (Parmesan 2006; Forrest & Miller-Rushing 2010; Augspurger 2013). Therefore, it is critical to integrate species-specific phenological firsts and lasts to better understand the phenological responses to climate warming, and the consequences this may have for plant species dominance.

To close this knowledge gap, a three-year field-manipulative warming experiment using open top chambers (OTCs) was conducted in an alpine meadow grassland on the Tibetan Plateau to study the responses of various plant phenological events and the consequent impacts on species dominance. To assess and compare the species-specific responses of plant phenology and species dominance, eight common plant species were monitored across the three growing seasons, which were the only common species observed in all experimental plots at the study site. Furthermore, the Tibetan Plateau is warming at a faster rate than the global average due to its relative high altitude (Deutsch *et al.* 2008; You *et al.* 2016). Studies of plant phenology within temperature-limited regions, such as the Tibetan Plateau, are especially valuable, given that species within these regions are highly sensitive to climate change and may respond to climate warming in unexpected ways (Arft*et al.* 1999; Khorsand Rosa*et al.* 2016; Prevéy *et al.*2017). Two key questions motivated our work: (1) what are the species-level impacts of warming on plant phenology? and (2) do species-level impacts of warming on plant phenology scale up to affect species dominance, and if so, what are the underlying mechanisms for such changes?

## 2. Materials and methods

### 2.1 Study site

A field-manipulative warming experiment was performed at the Haibei Grassland Ecological Monitoring Station (Xihai Town, Qinghai province, 100°51´E, 36°57´N, 3,140 m a.s.l.). The study site has been used as a winter grazing grassland since 1976, with moderate grazing intensity during the non-growing season. Based on meteorological records from 1995 to 2013, the mean annual precipitation is 408 mm, and the mean annual temperature is 1.3 oC (Chen *et al.* 2016). Relatively high air temperature and rainfall occur from mid-April to mid-October (growing season), while low rainfall (< 5% of annual) and low temperatures occur during the non-growing season. Additional long-term, detailed information about the study site can be found in (Chen *et al.* 2015b; Guo *et al.* 2018; Li *et al.* 2019) (Fig. S1). The dominant species are *Stipa krylovii, Poa crymophila, Koeleria cristata, Medicago ruthenica,* and *Kobresia humilis* (Fig. S1 and Table S1).

### 2.2 Experimental design

The study site (200 m × 400 m) was fenced off for three years before the initiation of experimental warming to exclude disturbance by herbivores. All mammalian herbivores were completely removed for the whole experiment duration. In August 2010, the entire study site was divided into six blocks with 10-m buffer zones between each edge of adjacent blocks. Each block was then divided into two plots (5 m × 10 m), one of which was randomly selected for experimental warming. In each of the experimental warming plots, one OTC (with a base area of 2.1 m2, six OTCs in total) was installed to achieve a passively warmed environment (Fig. S1). Protocols for the OTCs used in this study are described in detail for previous studies at this site (Chen *et al.* 2017a; Chen *et al.* 2017b), as well as at other sites (Dorji *et al.* 2013; Baruah *et al.* 2017).

## 2.3 Measurements

The main objective is to study the species' specific phenological responses as well as their links with species dominance. To meet this objective, eight commonly shared plant species were selected and monitored across the three growing seasons, covering all plant functional groups at the study site (three grasses, one sedge, one legume, three forbs). Based on our preliminary field investigations, those eight species were the only common species observed in all experimental plots at the study site (Fig. S1 and Table S1). The total aboveground biomass of those eight species occupied more than 85% of the total community biomass and the total cover of those eight species occupied more than 90% of the total community cover (Table S1) (Chen *et al.* 2017a; Chen *et al.* 2018).

To avoid the edges effects caused by OTCs, a quadrat (0.5 m × 0.5 m) was selected from the center area within each OTC as well as from the center area in each ambient plot for the species' phenology and dominance measurements. To reduce the heterogeneity and uncertainties associated with variations among individual plants, six individuals of each commonly shared species were selected and marked in each quadrat after the first leaf out. These marked individuals for each species in each quadrat were monitored every 2 to 4 days during the whole growing season. Phenological observations of each species in each quadrat were the average of those marked individuals, in case that some individuals got lost or died during the growing seasons. The first flower dates were documented when the flower buds had broken and anthers/stigmas were visible for the marked plants (Suonan*et al.* 2017). The last flower dates were measured when all petals had dropped off (Iler *et al.*2013; CaraDonna *et al.* 2014). Leaf senescence was defined as more than 50% of a plant's leaves having changed color (Marchin *et al.*2015). The duration of the growing season was calculated as the difference between leaf out and leaf senescence dates, and the length of flower duration was calculated as the difference between first and last flower dates. Phenological observations for each species in each quadrat were recorded every 2 to 4 days during the growing seasons from 2011 to 2013. All phenological observations were transformed into Julian days for further analysis.

Height, abundance and cover for each species within the quadrats in ambient and warming plots were recorded during the peak biomass period, which was usually in mid-August (apart from *Gentiana squarrosa* , which is in mid-July). Height for each species was calculated as the mean of the marked individuals. Species abundance was calculated as the total number of each species within the quadrat. A gird frame (0.5 m × 0.5 m) with 25 grid cells (0.1 m × 0.1 m) was placed in each quadrat to help estimating the total areal cover of each focal species in each plot (Penuelas *et al.* 2004; Damgaard 2014).

Soil temperature during the whole year and soil volumetric moisture during the growing season (frozen during the non-growing season) for each plot were documented using HOBO data loggers at a depth of 10 cm (Onset Computer Company, USA) (Chen*et al.* 2016). For each plot, three soil cores (0-10 cm) adjacent to the quadrats were collected and combined to make a composite soil sample in mid-August. Soil inorganic N content was measured using a flow injection auto-analyzer (FIAstar 5000 Analyzer, Denmark).

## 2.4 Data analyses

All data analysis and plotting were performed in R 3.5.1 (https://www.r-project.org/) using the *nlme* , *vegan,*and *ggplot2* packages. All original data were tested for normality prior to the statistical analysis using the Shapiro-Wilk normality method, and log-transformed if necessary. All data used in this study are available from the figshare (https://figshare.com/s/4e7061a904f66d1a4504) and from the online supplementary file.

Relative height (RH), relative abundance (RA) and relative cover (RC) were calculated by normalizing the species-specific absolute height, abundance and cover against the total height, abundance and cover for each plot. Simpson's evenness index (?) (Simpson 1949) was adopted to evaluate the community evenness. Species' importance value (IV) was used to assess species-specific dominance, which is quantified as the mean of relative height, relative abundance, and relative coverage (Whittaker 1965).

$$RH = \frac{\text{Height of a species}}{\text{Height of all species}} \times 100\% (1),$$

$$RA = \frac{\text{Abundance of a species}}{\text{Abundance of all species}} \times 100\% (2),$$

4

$RC = \frac{\text{Coverage of a species}}{\text{Coverage of all species}} \times 100\% (3),$

$E = \frac{D^{'}}{S} \ (4),$

$D^{'} = 1/\sum_{i=1}^{S} \text{RA}_i^2 \ (5),$

$IV = \frac{RH+RA+RC}{3} \ (6),$

where $D^{'}$ is the Simpson's reciprocal indices of diversity (Simpson 1949), S is the total number of species studied in this study (eight) and $\text{RA}_i$ is the relative abundance for each species in each plot. Experimental warming-induced changes in each variable were calculated from the paired plots per block:

$Warming - induced\ changes = \frac{W_v - A_v}{A_v} \times 100\%(7),$

where $W_v$ and $A_v$ were observed values from warming and ambient treatments, respectively.

We used linear mixed-effects (LME) models (Zuur *et al.* 2009) to assess the effects of warming on soil temperature, soil moisture, soil inorganic N, species-specific phenology, Simpson's evenness index and species dominance. All these variables were continuously observed from 2011 to 2013. In these LME models, we set warming, year, and their interactions as fixed effects and plot nested within block as random effects, because. We assessed the impacts of warming on plant phenology phases and species dominance separately for each species. Residuals and residual variances for all variables satisfied the assumptions of normality and homogeneity.

Linear mixed effects models was also used to explore the relation between warming-induced shifts in species-specific plant phenology and the corresponding changes in species dominance. To account for the variations, block, year and species were considered as random effects in those LME models. Redundancy analysis (RDA) with treatment (ambient and warm) and environmental factors (soil temperature, soil moisture, and soil inorganic N) as explanatory variables was utilized to explore the potential factors affecting species phenology and dominance. The importance of each explanatory variable was calculated by forward selection with 999 unrestricted permutations. The RDAs were performed separately for each plant phenological event and for species dominance.

### 3. Results

### 3.1 Soil microclimate and soil N availability

Averaged across the three consecutive years, experimental warming by OTCs significantly increased upper (0-10 cm) soil temperature by 1.1 oC, increased soil inorganic N by 10.% (Fig. 1), and significantly decreased soil volumetric moisture by 2.8% unit. The interactive effects of warming and year on soil temperature and soil inorganic N were not statistically significant (Table S2). However, the warming effects on soil volumetric moisture differed significantly among years, with warming-induced decreases in soil volumetric moisture of 4.8, 2.6, and 1.2% unit in 2011, 2012, and 2013, respectively (Table S2).

### 3.2 Leaf out, leaf senescence and growing season length

The effects of warming on leaf out, leaf senescence, and growing season length differed greatly among species (Table S3 and Fig. S2). Warming significantly advanced leaf out dates for six of the eight species by 4.7 to 7.4 days, while warming had no effect on leaf out date of *Artemisia scoparia* and *Heteropappus altaicus* (Table 1 and Fig. 2). Warming significantly delayed leaf senescence for *Kobresia humilis* , *Artemisia scoparia* , and *Heteropappus altaicus* by 3.2, 4.2 and 5.7 days, respectively, while warming advanced leaf senescence for *Gentiana squarrosa* by 6.7 days. Warming significantly extended growing season length by 5.4 to 9.0 days for five of the eight species, while warming did not affect growing season length for *Artemisia scoparia* , *Heteropappus altaicus* , and *Gentiana squarrosa* .

When soil temperature, soil moisture, soil inorganic N, and warming treatment were used to constrain the ordination of species-specific phenology with RDA, the full RDA model accounted for 57, 70, and 66% of variation in leaf out, leaf senescence, and growing season length, respectively (Fig. S3).

### 3.3 First flower, last flower and flower duration

Warming significantly advanced first flower dates for six of the eight species by 3.8 to 7.3 days, while warming significantly delayed it by 3.9 days for *Heteropappus altaicus* (Table 1 and Figs. 3 and S2). Warming significantly delayed last flower date for *Poa crymophila* , *Koeleria cristata* , *Artemisia scoparia* and*Heteropappus altaicus* by 3.0, 3.7, 4.8 and 6.3 days, respectively, while it was significantly advanced for *Gentiana squarrosa* by 7.7 days. Warming significantly lengthened flower duration for five of the eight species by 5.0 to 8.8 days, while it did not significantly affect flower duration for *Artemisia scoparia* ,*Heteropappus altaicus* , and *Gentiana squarrosa* (Fig. 3).

The RDA analysis showed that soil temperature and soil moisture played more important roles than soil inorganic N in driving flower phenology. Soil temperature and soil moisture together explained 54, 64, and 62% of the variation in first flower, last flower, and flower duration, respectively (Fig. S4).

### 3.4 Plant species dominance

Warming significantly decreased plant community evenness, but warming had differential impacts on species dominance (Fig. 4, and Tables S4 and S5). The RDA analysis with treatment and environmental variables accounted for 41% of the variation in species dominance (Fig. S5). In general, species with a greater extension in growing season length and flower duration tended to increase their dominance (Fig. 5). The positive relations were also observed between warming-induced shifts in last flower and leaf senescence dates and warming-induced changes in species dominance (Fig. 5). Specifically, warming-induced changes in last flower, leaf senescence, flower duration and growing season length explained 16, 8, 27 and 22% variance of warming-induced changes in species dominance, respectively. By contrast, there was no relation between warming-induced changes in leaf out and first flower dates and warming-induced changes in species dominance (Fig. S6).

### 4. Discussion

Our results reveal that species-specific phenological firsts (leaf out and first flower) and lasts (leaf senescence and last flower) are differentially sensitive to climate warming on the cold Tibetan Plateau. Importantly, warming-induced shifts in phenological lasts and full phenological periods (growing season length and flower duration), rather than the single phenological firsts, drive changes in species dominance. Some studies have reported no relation between shifts in plant phenology and community change by solely linking phenological firsts and community coverage (McLean *et al.* 2016; Block *et al.* 2019), whereas our results can advance the understanding of the relationship between plant phenology and community by linking the phenological lasts as well as the full phenological periods with species dominance. Our results therefore stress that (1) the current trend toward observations of only the first dates of plant phenology provide an incomplete picture for assessing and predicting response of plant phenology and plant community turnover to climate warming and (2) shifts in the full phenological periods provide powerful indicators of how climatic warming alters species dominance, and by extension community structure.

### 4.1 Shifts in plant phenology drive species dominance

Warming was differentially advantageous to some species and increased their relative dominance, while warming was disadvantageous to other species and decreased their relative dominance. Warming-induced shifts in species-specific full phenological periods and phenological lasts were significant predictors of warming-induced changes in species dominance. Specifically, species that increased their relative dominance experienced a significantly longer full phenological periods or extended phenological lasts. On the other hand, for species which experienced a decrease in dominance, all underwent a directional shift in their phenology, without significantly altering the duration of their growing season length or flower duration. Our results agree with other studies that shifts in plant phenology could cause either more differentiation or similarity among species' timing (Nicotra *et al.* 2010; Petitpierre *et al.* 2012), having cascading impacts on species dominance (Kraft *et al.* 2015; Godoy *et al.* 2018).

We propose three non-exclusive hypotheses for how shifts in species-specific plant phenology may impact

species dominance. First, a relatively longer growing season or flower duration could mitigate potential phenological mismatches between plant growth and optimal environmental factors (e.g. temperature and moisture) (Augspurger 2013; Wheeler *et al.* 2015). Plants with the ability to adapt their phenology to capture favorable conditions could thus have a competitive advantages over others (Ernakovich *et al.* 2014). However, if a longer growing season or flower duration results from a substantial advance in phenological firsts, this could still leave them vulnerable to adverse conditions at the shoulders of the growing season. For example, warming-induced substantial advancement of leaf out and first flower dates could increase the likelihood of exposure to spring frost damage or herbivory by spring active insects (Richardson *et al.* 2018), which could decrease species' dominance in the community.

Second, warming-induced lengthening of the growing season or flower duration could help species avoid potential trophic mismatches (CaraDonna *et al.* 2014; Fridley *et al.* 2016; Renner & Zohner 2018). For mutualistic plant-animal relationships, for example, phenological mismatches between flowers and pollinators could have crucial effects on plant community composition through reduced plant fitness over time (Elzinga *et al.* 2007; Wheeler *et al.* 2015; Schmidt *et al.* 2016). A similar study conducted in three natural deciduous forests in northern Japan showed that species with shortened flower duration could experience pollination failure, leading to lower seed production and consequently reduced dominance within the community (Kudo & Ida 2013). Conversely, a lengthened growing season or flower duration could help plants remain in sync with their pollinators, despite an advance or delay in the pollinators' own phenology.

Third, longer growing season and delayed leaf senescence would allow for longer periods of photosynthetic activity, nutrient acquisition, and therefore more resources allocation to growth, fecundity, or survival mechanisms, which could eventually increase the relative cover and abundance of a plant species (Ernakovich *et al.* 2014; Fridley *et al.* 2016). Similarly, species with extended last flower and flower duration could support increased seed production and reproductive success, which could also lead to increased abundance (Craufurd & Wheeler 2009; CaraDonna *et al.* 2014). Both patterns suggest that ongoing climate warming will reshape community structure towards dominance by species with lengthened phenophases.

Species with lengthened phenophases and increased dominance are basically the dominant species at our study. This suggests that the observed shifts in plant phenology with warming scenarios would likely cause gradual biodiversity losses of non-dominant and rare species, and thus could move the community towards a biotic homogenization (McKinney & Lockwood 1999; Dawson *et al.* 2011; Savage & Vellend 2015). For example, community evenness index was negatively related to dominance value of species experienced longer growing season and flower duration (Fig. S7). In addition, there are only eight common species investigated in this study, which may potentially leave some uncertainties when evaluating the community level phenology and species composition as a whole. However, neither the rare species nor the community biodiversity losses are the objectives of this study. Our goals are to stress the importance of the phenological lasts and the full phenological periods in understanding the warming impacts on plant phenology and species dominance.

### 4.2 Advanced leaf out and first flower dates

Warming significantly advanced leaf out and first flower dates for six of the eight species. Higher temperatures with climatic warming will primarily decrease the growing degree days required for a certain phenological event, and this is particularly critical in cold environment such as the Tibetan Plateau (Piao *et al.* 2015; Suonan *et al.* 2017). Open top chambers were installed year-round across the whole experimental period. During the growing season, increased soil temperature stimulated decomposition and nutrient cycling (Chen *et al.* 2015a; Estiarte & Penuelas 2015), which could facilitate plant growth through promoting increased soil N availability. At the beginning of the growing season, higher temperatures would prevent soil water from freezing and support both plant and microbial activities (Chen *et al.* 2017a; Suonan *et al.* 2017). During the non-growing season, higher temperature may also have positive effects on leaf out, despite a certain period of chilling requirements may also be critical prior to initiation of leaf out (Marchin *et al.* 2015; Guo *et al.* 2019). This is because the mean soil temperature was quite low during winter at our study site (Chen *et al.* 2017b), and thus it is less likely that OTCs raised soil temperature enough to break the winter chilling requirements threshold (Suonan *et al.* 2017).

### 4.3 Species-specific responses of leaf senescence and last flower dates

Warming-induced changes in leaf senescence and last flower dates were highly variable among species. First, unlike leaf out and first flower dates, leaf senescence and last flower dates are more likely jointly controlled by the complex interactions among multiple factors, such as soil temperature, soil moisture, soil nutrient availability, and photoperiod (Ernakovich *et al.*2014; Estiarte & Penuelas 2015; Gill *et al.* 2015). Changes in these factors may advance or delay the last dates of plant phenology, depending on their balanced effects. Second, the underlying driving mechanisms for plant growth and maintenance of plant metabolic activities are also highly variable among species (Myers-Smith *et al.* 2015). For example, some legumes are reported to be sensitive to reductions in soil moisture, while forbs are expected to be more responsive to warming-induced changes in soil N availability (White *et al.* 2000; Engelbrecht *et al.* 2007). Third, even species within the same plant functional group were also highly varied in their responses of leaf senescence and last flower dates to experimental warming. For example, warming advanced leaf senescence and last flower dates for *Gentiana squarrosa* but delayed them for*Heteropappus altaicus* and *Artemisia scoparia* , despite the fact that they are all forbs. The advancement of leaf senescence and last flower dates of *Gentiana squarrosa* in the early-growing could confer a competitive advantage by allowing this species to avoid the shading effects induced by other taller species later in the growing season. In addition, plant functional traits (e.g., leaf morphology and plant height) are also reported to have critical impacts on plant phenology even within the same plant function group (Guerin *et al.* 2012; Dorji *et al.* 2013). These results call for caution when using plant functional group as a predictor of the effects of warming on last dates of plant phenology.

Our results from the cold Tibetan Plateau stress that warming-induced shifts in phenological firsts are inadequate to predict the ecological consequences of climatic warming on plant phenology and plant community turnover. Rather, we find considerable variability among species in how warming impacts the first and last dates of their phenological patterns. As a consequence, it is warming-induced changes in full phenological periods and phenological lasts, and how this varies among species that drive how warming reshapes species dominance. Our results provide novel insights for understanding the effects of climate warming on plant phenology and plant community turnover in a climatically sensitive ecosystem, and underscore the need to assess how climatic warming will impact the phenological lasts and the full phenological periods.

### Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article.

**Conflict interests** The authors declare no conflict of interest.

### ORCID

Ji Chen, https://orcid.org/0000-0001-7026-6312

Yuxin Chen, https://orcid.org/0000-0003-0658-7562

Andrew J. Felton, https://orcid.org/0000-0002-1533-6071

Kelly A. Hopping, https://orcid.org/0000-0002-0557-0526

Shuli Niu, https://orcid.org/0000-0002-2394-2864

Jørgen Eivind Olesen, https://orcid.org/0000-0002-6639-1273

### Reference

Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M. *et al.* (1999). Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecol. Monogr.* , 69, 491-511. https://doi.org/10.1890/0012-9615(1999)069[0491:rotpte]2.0.co;2

Augspurger, C.K. (2013). Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. *Ecology* , 94, 41-50. https://doi.org/10.1890/12-0200.1

Bahuguna, R.N. & Jagadish, K.S.V. (2015). Temperature regulation of plant phenological development.*Environ. Exp. Bot.* , 111, 83-90. https://doi.org/10.1016/j.envexpbot.2014.10.007

Baruah, G., Molau, U., Yang, B. & Alatalo, J.M. (2017). Community and species-specific responses of plant traits to 23 years of experimental warming across subarctic tundra plant communities. *Sci. Rep.* , 7, 2571. https://doi.org/10.1038/s41598-017-02595-2

Block, S., Alexander, J.M. & Levine, J.M. (2019). Phenological plasticity is a poor predictor of subalpine plant population performance following experimental climate change.*Oikos* . https://doi.org/10.1111/oik.06667

CaraDonna, P.J., Iler, A.M. & Inouye, D.W. (2014). Shifts in flowering phenology reshape a subalpine plant community. *P. Natl. Acad. Sci.* , 111, 4916-4921. https://doi.org/10.1073/pnas.1323073111

Cayton, H.L., Haddad, N.M., Gross, K., Diamond, S.E. & Ries, L. (2015). Do growing degree days predict phenology across butterfly species? *Ecology* , 96, 1473-1479. https://doi.org/10.1890/15-0131.1

Chen, J., Luo, Y., Xia, J., Jiang, L., Zhou, X., Lu, M. *et al.* (2015a). Stronger warming effects on microbial abundances in colder regions. *Sci. Rep.* , 5, 18032. https://doi.org/10.1038/srep18032

Chen, J., Luo, Y., Xia, J., Shi, Z., Jiang, L., Niu, S. *et al.* (2016). Differential responses of ecosystem respiration components to experimental warming in a meadow grassland on the Tibetan Plateau. *Agr. Forest Meteorol.* , 220, 21-29. http://dx.doi.org/10.1016/j.agrformet.2016.01.010

Chen, J., Luo, Y., Xia, J., Wilcox, K.R., Cao, J., Zhou, X. *et al.* (2017a). Warming Effects on Ecosystem Carbon Fluxes Are Modulated by Plant Functional Types.*Ecosystems* , 20, 515-526. https://doi.org/10.1007/s10021-016-0035-6

Chen, J., Luo, Y., Xia, J., Zhou, X., Niu, S., Shelton, S. *et al.* (2018). Divergent responses of ecosystem respiration components to livestock exclusion on the Qinghai Tibetan Plateau. *Land Degrad. Dev.* , 29, 1726-1737. https://doi.org/org/10.1002/ldr.2981

Chen, J., Shi, W. & Cao, J. (2015b). Effects of Grazing on Ecosystem CO2 Exchange in a Meadow Grassland on the Tibetan Plateau During the Growing Season. *Environ. Manage.* , 55, 347-359. https://doi.org/10.1007/s00267-014-0390-z

Chen, J., Zhou, X., Hruska, T., Cao, J., Zhang, B., Liu, C. *et al.* (2017b). Asymmetric Diurnal and Monthly Responses of Ecosystem Carbon Fluxes to Experimental Warming.*Clean-Soil Air Water* , 45, 1600557. https://doi.org/10.1002/clen.201600557

Chmura, H.E., Kharouba, H.M., Ashander, J., Ehlman, S.M., Rivest, E.B. & Yang, L.H. (2019). The mechanisms of phenology: the patterns and processes of phenological shifts. *Ecol. Monogr.* , 89, e01337. https://doi.org/10.1002/ecm.1337

Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007). Shifting plant phenology in response to global change. *Trends Ecol. Evol.* , 22, 357-365. https://doi.org/10.1016/j.tree.2007.04.003

Craufurd, P.Q. & Wheeler, T.R. (2009). Climate change and the flowering time of annual crops. *J. Exp. Bot.* , 60, 2529-2539. https://doi.org/10.1093/jxb/erp196

Damgaard, C. (2014). Estimating mean plant cover from different types of cover data: a coherent statistical framework. *Ecosphere* , 5, 1-7. https://doi.org/10.1890/ES13-00300.1

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.M. (2011). Beyond predictions: biodiversity conservation in a changing climate. *Science* , 332, 53-58. https://doi.org/10.1126/science.1200303

de Valpine, P. & Harte, J. (2001). Plant responses to experimental warming in a montane meadow.*Ecology* , 82, 637-648. https://doi.org/10.1890/0012-9658(2001)082[0637:PRTEWI]2.0.CO;2

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. *et al.* (2008). Impacts of climate warming on terrestrial ectotherms across latitude.*P. Natl. Acad. Sci.* , 105, 6668-6672. https://doi.org/10.1073/pnas.0709472105

Diez, J.M., Ibáñez, I., Miller-Rushing, A.J., Mazer, S.J., Crimmins, T.M., Crimmins, M.A.*et al.* (2012). Forecasting phenology: from species variability to community patterns. *Ecol. Lett.* , 15, 545-553. https://doi.org/10.1111/j.1461-0248.2012.01765.x

Dorji, T., Totland, O., Moe, S.R., Hopping, K.A., Pan, J. & Klein, J.A. (2013). Plant functional traits mediate reproductive phenology and success in response to experimental warming and snow addition in Tibet. *Global Change Biol.* , 19, 459-472. https://doi.org/10.1111/gcb.12059

Dunne, J.A., Harte, J. & Taylor, K.J. (2003). Subalpine meadow flowering phenology responses to climate change: Integrating experimental and gradient methods. *Ecol. Monogr.* , 73, 69-86. https://doi.org/10.1890/0012-9615(2003)073[0069:smfprt]2.0.co;2

Elzinga, J.A., Atlan, A., Biere, A., Gigord, L., Weis, A.E. & Bernasconi, G. (2007). Time after time: flowering phenology and biotic interactions. *Trends Ecol. Evol.* , 22, 432-439. https://doi.org/10.1016/j.tree.2007.05.006

Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L. *et al.*(2007). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* , 447, 80. https://doi.org/10.1038/nature05747

Ernakovich, J.G., Hopping, K.A., Berdanier, A.B., Simpson, R.T., Kachergis, E.J., Steltzer, H. *et al.* (2014). Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Global Change Biol.* , 20, 3256-3269. https://doi.org/10.1111/gcb.12568

Estiarte, M. & Peñuelas, J. (2015). Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: effects on nutrient proficiency.*Global Change Biol.* , 21, 1005-1017. https://doi.org/10.1111/gcb.12804

Forrest, J. & Miller-Rushing, A.J. (2010). Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philos. T. R. Soc. B.* , 365, 3101-3112. https://doi.org/10.1098/rstb.2010.0145

Fridley, J.D., Lynn, J.S., Grime, J.P. & Askew, A.P. (2016). Longer growing seasons shift grassland vegetation towards more-productive species. *Nat. Clim. Change* , 6, 865. https://doi.org/10.1038/nclimate3032

Gallinat, A.S., Primack, R.B. & Wagner, D.L. (2015). Autumn, the neglected season in climate change research. *Trends Ecol. Evol.* , 30, 169-176. https://doi.org/10.1016/j.tree.2015.01.004

Gill, A.L., Gallinat, A.S., Sanders-DeMott, R., Rigden, A.J., Gianotti, D.J.S., Mantooth, J.A.*et al.* (2015). Changes in autumn senescence in northern hemisphere deciduous trees: a meta-analysis of autumn phenology studies.*Ann. Bot.* , 116, 875-888. https://doi.org/10.1093/aob/mcv055

Godoy, O., Bartomeus, I., Rohr, R.P. & Saavedra, S. (2018). Towards the integration of niche and network theories. *Trends Ecol. Evol.* , 33, 287-300. https://doi.org/10.1016/j.tree.2018.01.007

Guerin, G.R., Wen, H. & Lowe, A.J. (2012). Leaf morphology shift linked to climate change. *Biol. Letters* , 8, 882. https://doi.org/10.1098/rsbl.2012.0458

Guo, L., Chen, J., Luedeling, E., He, J.-S., Cheng, J., Wen, Z. *et al.* (2018). Early-spring soil warming partially offsets the enhancement of alpine grassland aboveground productivity induced by warmer growing seasons on the Qinghai-Tibetan Plateau. *Plant Soil* , 425, 177-188. https://doi.org/10.1007/s11104-018-3582-0

Guo, L., Wang, J., Li, M., Liu, L., Xu, J., Cheng, J. *et al.* (2019). Distribution margins as natural laboratories to infer species' flowering responses to climate warming and implications for frost risk. *Agr. Forest Meteorol.* , 268, 299-307. https://doi.org/10.1016/j.agrformet.2019.01.038

Iler, A.M., Høye, T.T., Inouye, D.W. & Schmidt, N.M. (2013). Nonlinear flowering responses to climate: are species approaching their limits of phenological change? *Philos. T. R. Soc. B.* , 368, 20120489. https://doi.org/10.1098/rstb.2012.0489

Khorsand Rosa, R., Oberbauer, S.F., Starr, G., Inga, P.L.P., Pop, E., Ahlquist, L. *et al.* (2016). Plant phenological responses to a long-term experimental extension of growing season and soil warming in the tussock tundra of Alaska.*Global Change Biol.* , 21, 4520-4532. https://doi.org/10.1111/gcb.13040

Kraft, N.J.B., Godoy, O. & Levine, J.M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *P. Natl. Acad. Sci.* , 112, 797-802. https://doi.org/10.1073/pnas.1413650112

Kudo, G. & Ida, T.Y. (2013). Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology* , 94, 2311-2320. https://doi.org/10.1890/12-2003.1

Leblans, N.I.W., Sigurdsson, B.D., Vicca, S., Fu, Y., Penuelas, J. & Janssens, I.A. (2017). Phenological responses of Icelandic subarctic grasslands to short-term and long-term natural soil warming. *Global Change Biol.* , 23, 4932-4945. https://doi.org/10.1111/gcb.13749

Li, X., Guo, W., Chen, J., Ni, X. & Wei, X. (2019). Responses of vegetation green-up date to temperature variation in alpine grassland on the Tibetan Plateau. *Ecol. Indic.* , 104, 390-397. https://doi.org/10.1016/j.ecolind.2019.05.00

Marchin, R.M., Salk, C.F., Hoffmann, W.A. & Dunn, R.R. (2015). Temperature alone does not explain phenological variation of diverse temperate plants under experimental warming. *Global Change Biol.* , 21, 3138-3151. https://doi.org/10.1111/gcb.12919

McKinney, M.L. & Lockwood, J.L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* , 14, 450-453. https://doi.org/10.1016/S0169-5347(99)01679-1

McLean, N., Lawson, C.R., Leech, D.I. & van de Pol, M. (2016). Predicting when climate-driven phenotypic change affects population dynamics. *Ecol. Lett.* , 19, 595-608. https://doi.org/10.1111/ele.12599

Myers-Smith, I.H., Elmendorf, S.C., Beck, P.S.A., Wilmking, M., Hallinger, M., Blok, D. *et al.*(2015). Climate sensitivity of shrub growth across the tundra biome.*Nat. Clim. Change* , 5, 887. https://doi.org/10.1038/nclimate2697

Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U. *et al.*(2010). Plant phenotypic plasticity in a changing climate. *Trends Plant Sci.* , 15, 684-692. https://doi.org/10.1016/j.tplants.2010.09.008

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* , 37, 637-669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Penuelas, J., Gordon, C., Llorens, L., Nielsen, T., Tietema, A., Beier, C. *et al.* (2004). Nonintrusive field experiments show different plant responses to warming and drought among sites, seasons, and species in a north–south European gradient. *Ecosystems* , 7, 598-612. https://doi.org/10.1007/s10021-004-0179-7

Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C. & Guisan, A. (2012). Climatic niche shifts are rare among terrestrial plant invaders. *Science* , 335, 1344-1348. https://doi.org/10.1126/science.1215933

Piao, S., Tan, J., Chen, A., Fu, Y.H., Ciais, P., Liu, Q. *et al.* (2015). Leaf onset in the northern hemisphere triggered by daytime temperature. *Nat. Commun.* , 6, 6911. https://doi.org/10.1038/ncomms7911

Post, E., Kerby, J., Pedersen, C. & Steltzer, H. (2016). Highly individualistic rates of plant phenological advance associated with arctic sea ice dynamics. *Biol. Letters* , 12. https://doi.org/10.1098/rsbl.2016.0332

Prevey, J., Vellend, M., Ruger, N., Hollister, R.D., Bjorkman, A.D., Myers-Smith, I.H. *et al.* (2017). Greater temperature sensitivity of plant phenology at colder sites: implications for convergence across northern latitudes. *Global Change Biol.* , 23, 2660-2671. https://doi.org/10.1111/gcb.13619

Prevey, J.S., Rixen, C., Ruger, N., Hoye, T.T., Bjorkman, A.D., Myers-Smith, I.H. *et al.* (2019). Warming shortens flowering seasons of tundra plant communities.*Nat. Ecol. Evol.* , 3, 45. https://doi.org/10.1038/s41559-018-0745-6

Renner, S.S. & Zohner, C.M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annu. Rev. Ecol. Evol. Syst.* , 49, 165-182. https://doi.org/10.1146/annurev-ecolsys-110617-062535

Richardson, A.D., Hufkens, K., Milliman, T., Aubrecht, D.M., Furze, M.E., Seyednasrollah, B. *et al.* (2018). Ecosystem warming extends vegetation activity but heightens vulnerability to cold temperatures. *Nature* , 560, 368-+. https://doi.org/10.1038/s41586-018-0399-1

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003). Fingerprints of global warming on wild animals and plants. *Nature* , 421, 57. https://doi.org/10.1038/nature01333

Rudolf, V.H.W. (2019). The role of seasonal timing and phenological shifts for species coexistence.*Ecol. Lett.* https://doi.org/10.1111/ele.13277

Savage, J. & Vellend, M. (2015). Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography* , 38, 546-555. https://doi.org/10.1111/ecog.01131

Schmidt, N.M., Mosbacher, J.B., Nielsen, P.S., Rasmussen, C., Hoye, T.T. & Roslin, T. (2016). An ecological function in crisis? The temporal overlap between plant flowering and pollinator function shrinks as the Arctic warms.*Ecography* , 39, 1250-1252. https://doi.org/10.1111/ecog.02261

Sherry, R.A., Zhou, X., Gu, S., Arnone, J.A., Schimel, D.S., Verburg, P.S. *et al.* (2007). Divergence of reproductive phenology under climate warming. *P. Natl. Acad. Sci.* , 104, 198-202. https://doi.org/10.1073/pnas.0605642104

Simpson, E.H. (1949). Measurement of diversity. *Nature* , 163, 688. https://doi.org/10.1038/163688a0

Smith, M.D. & Knapp, A.K. (2003). Dominant species maintain ecosystem function with non-random species loss. *Ecol. Lett.* , 6, 509-517. https://doi.org/10.1046/j.1461-0248.2003.00454.x

Suonan, J., Classen, A.T., Zhang, Z. & He, J. (2017). Asymmetric winter warming advanced plant phenology to a greater extent than symmetric warming in an alpine meadow.*Funct. Ecol.* https://doi.org/10.1111/1365-2435.12909

Tang, J., Korner, C., Muraoka, H., Piao, S., Shen, M., Thackeray, S.J. *et al.* (2016). Emerging opportunities and challenges in phenology: a review. *Ecosphere* , 7. https://doi.org/10.1002/ecs2.1436

Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T. & Prentice, I.C. (2005). Climate change threats to plant diversity in Europe. *P. Natl. Acad. Sci.* , 102, 8245-8250. https://doi.org/10.1073/pnas.0409902102

Wheeler, H.C., Hoye, T.T., Schmidt, N.M., Svenning, J.-C. & Forchhammer, M.C. (2015). Phenological mismatch with abiotic conditions-implications for flowering in Arctic plants.*Ecology* , 96, 775-787. https://doi.org/10.1890/14-0338.1

White, T.A., Campbell, B.D., Kemp, P.D. & Hunt, C.L. (2000). Sensitivity of three grassland communities to simulated extreme temperature and rainfall events. *Global Change Biol.* , 6, 671-684. https://doi.org/10.1046/j.1365-2486.2000.00344.x

Whittaker, R.H. (1965). Dominance and diversity in land plant communities: numerical relations of species express the importance of competition in community function and evolution. *Science* , 147, 250-260. https://doi.org/10.1126/science.147.3655.250

You, Q., Min, J. & Kang, S. (2016). Rapid warming in the Tibetan Plateau from observations and CMIP5 models in recent decades. *Int. J. Climatol.* , 36, 2660-2670. https://doi.org/10.1002/joc.4520

Zhang, X., Friedl, M.A., Schaaf, C.B., Strahler, A.H., Hodges, J.C.F., Gao, F. *et al.* (2003). Monitoring vegetation phenology using MODIS. *Remote Sens. Environ.* , 84, 471-475. https://doi.org/10.1016/S0034-4257(02)00135-9

Zohner, C.M., Mo, L. & Renner, S.S. (2018). Global warming reduces leaf-out an flowering synchrony among individuals. *Elife* , 7. https://doi.org/10.7554/eLife.40214

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R* . Springer Science & Business Media.

**Table 1. *F* values for linear mixed-effects models of warming (W), year (Y) and their interactive (W x Y) effects on plant phenology for each species.**

| Species | Treat | num DF | den DF | Leaf out | Leaf senescence | Growing days | First flower | Last flower | Flower du |
|---|---|---|---|---|---|---|---|---|---|
| Sk | W | 1 | 5 | 22.78** | 4.29 | 24.54** | 28.55** | 2.75 | 31.34** |
| | Y | 2 | 20 | 0.36 | 8.79** | 5.09* | 0.83 | 0.51 | 1.42 |
| | W * Y | 2 | 20 | 0.16 | 0.25 | 0.50 | 0.20 | 0.05 | 0.19 |
| Pc | W | 1 | 5 | 61.87*** | 0.75 | 18.11** | 25.49** | 7.39* | 28.89** |
| | Y | 2 | 20 | 0.30 | 1.03 | 1.07 | 1.61 | 2.14 | 1.87 |
| | W * Y | 2 | 20 | 0.04 | 0.07 | 0.10 | 0.41 | 0.27 | 0.62 |
| Kc | W | 1 | 5 | 21.68** | 0.03 | 9.23* | 10.28* | 15.22* | 52.03*** |
| | Y | 2 | 20 | 0.66 | 0.79 | 0.75 | 1.40 | 4.79* | 4.42* |
| | W * Y | 2 | 20 | 0.66 | 0.04 | 0.48 | 0.86 | 0.38 | 2.59 |
| Mr | W | 1 | 5 | 27.32** | 0.23 | 14.92* | 41.53** | 0.14 | 30.05** |
| | Y | 2 | 20 | 2.69 | 0.35 | 1.73 | 2.90 | 1.89 | 3.13 |
| | W * Y | 2 | 20 | 0.36 | 0.07 | 0.05 | 0.22 | 0.33 | 0.56 |
| Kh | W | 1 | 5 | 25.67** | 9.89* | 42.02** | 45.98** | 0.20 | 12.70* |
| | Y | 2 | 20 | 7.09** | 12.44*** | 1.78 | 5.43* | 1.48 | 4.64* |
| | W * Y | 2 | 20 | 0.10 | 0.44 | 0.17 | 0.03 | 0.60 | 0.36 |
| As | W | 1 | 5 | 0.75 | 11.65* | 2.01 | 4.50 | 16.60** | 1.14 |
| | Y | 2 | 20 | 0.57 | 0.78 | 1.05 | 1.26 | 0.68 | 0.28 |
| | W * Y | 2 | 20 | 0.12 | 0.10 | 0.16 | 0.18 | 0.04 | 0.03 |
| Ha | W | 1 | 5 | 3.96 | 32.63** | 5.22 | 8.97* | 39.56** | 2.03 |
| | Y | 2 | 20 | 5.18* | 0.39 | 3.49* | 2.20 | 12.58*** | 2.73 |
| | W * Y | 2 | 20 | 0.32 | 0.34 | 0.53 | 0.14 | 0.47 | 0.03 |
| Gs | W | 1 | 5 | 41.92** | 34.75** | 0.26 | 47.43** | 39.98** | 0.06 |
| | Y | 2 | 20 | 3.04 | 5.69* | 0.45 | 5.27* | 0.24 | 2.08 |
| | W * Y | 2 | 20 | 0.12 | 1.42 | 0.40 | 0.92 | 1.61 | 0.22 |

numDF: numerator degrees of freedom. denDF: denominator degrees of freedom. Linear mixed-effects models were conducted separately for each species for each phenological observation. Warming (W), year (Y) and their interaction (W * Y) were considered as fixed factors, while plot nested within block was considered as a random factor. Asterisks indicate significant differences at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***). Sk: *Stipa krylovii* . Pc: *Poa crymophila* . Kc: *Koeleria cristata* . Mr: *Medicago ruthenica* . Kh: *Kobresia humilis* . As: *Artemisia scoparia* . Ha: *Heteropappus altaicus* . Gs: *Gentiana squarrosa* .
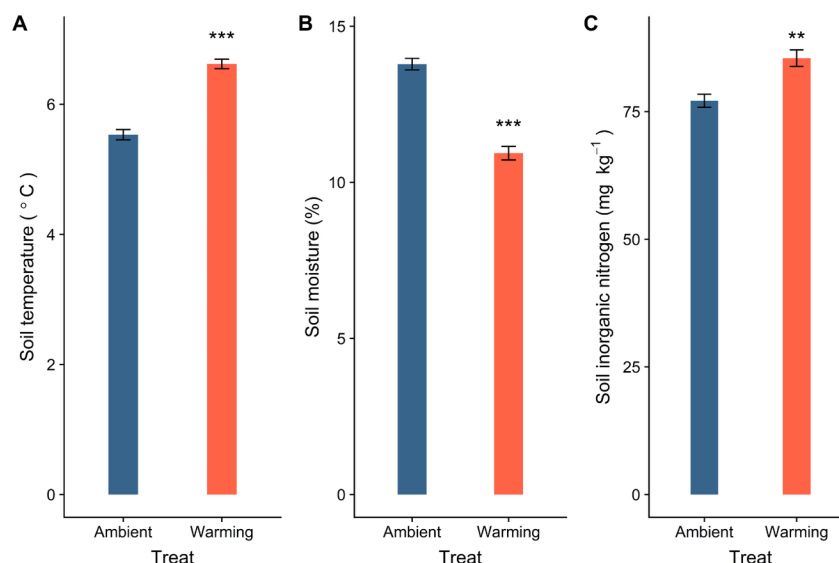
**Figure 1. Effects of warming treatment on (A) soil temperature, (B) soil volumetric moisture and (C) soil inorganic nitrogen content.** Asterisks indicate significant difference at $P < 0.01$ (**) and $P < 0.001$ (***). Values are mean ± standard errors across years.
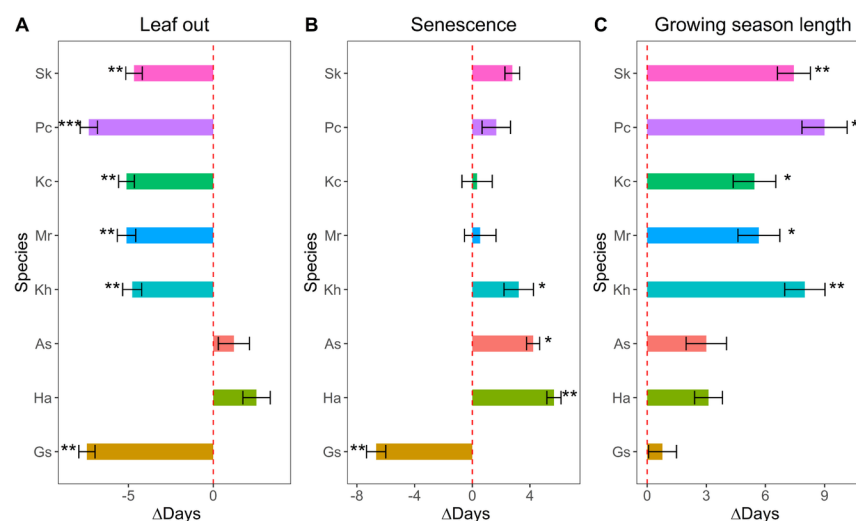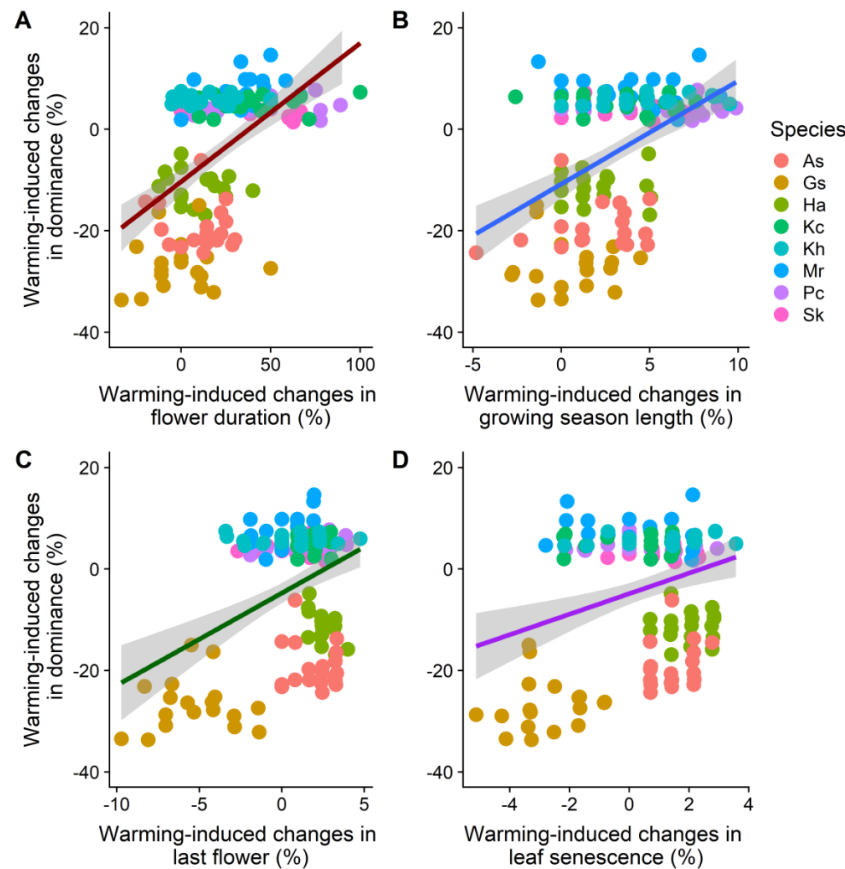


**Figure 2. Warming-induced changes in (A) leaf out, (B) leaf senescence and (C) growing season length for each species.** Asterisks indicate significant differences at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***). Values are mean ± standard errors. Sk: *Stipa krylovii* . Pc:*Poa crymophila* . Kc: *Koeleria cristata* . Mr: *Medicago ruthenica* . Kh: *Kobresia humilis* . As: *Artemisia scoparia* . Ha: *Heteropappus altaicus* . Gs: *Gentiana squarrosa* .
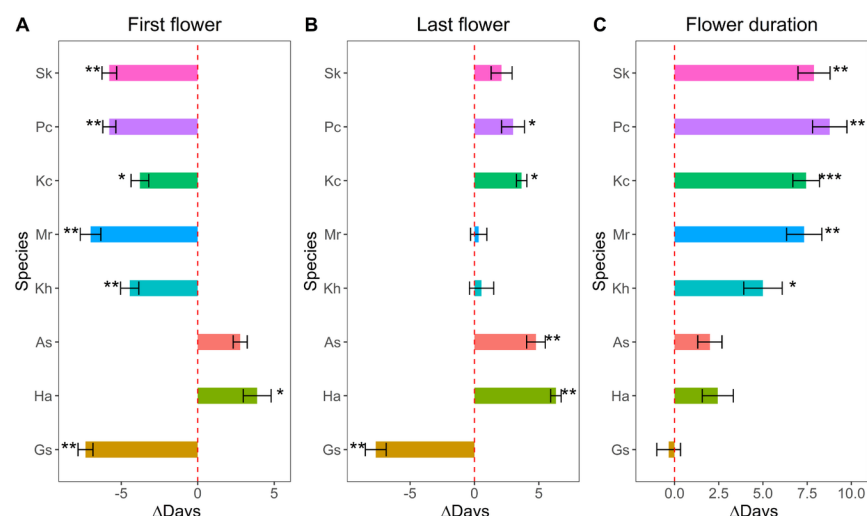
**Figure 3. Warming-induced changes in (A) first flower, (B) last flower and (C) flower duration for each species.** Asterisks indicate significant differences at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***). Values are mean ± standard errors. Sk: *Stipa krylovii* . Pc: *Poa crymophila* . Kc: *Koeleria cristata* . Mr: *Medicago ruthenica* . Kh: *Kobresia humilis* . As: *Artemisia scoparia* . Ha: *Heteropappus altaicus* . Gs: *Gentiana squarrosa* .
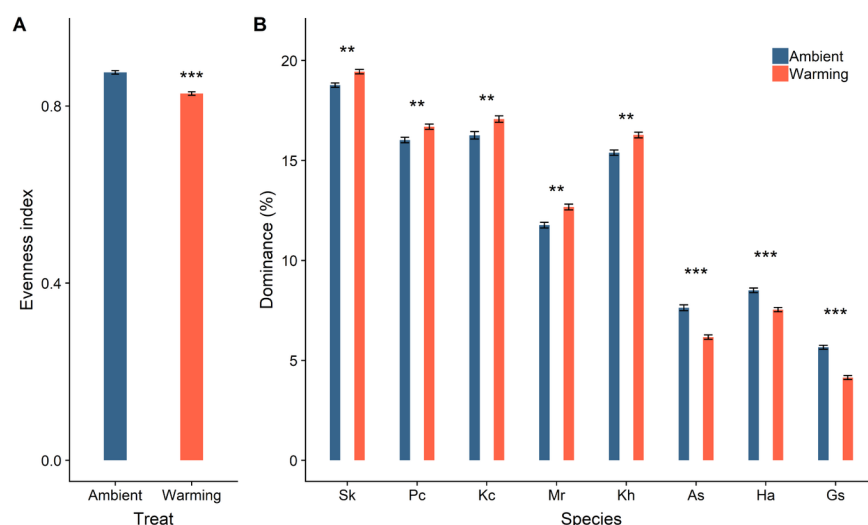


**Figure 4. Warming effects on (A) Simpson evenness index and (B) species dominance.** Asterisks indicate significant differences at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***). Values are mean ± standard errors. Sk: *Stipa krylovii* . Pc: *Poa crymophila* . Kc: *Koeleria cristata* . Mr: *Medicago ruthenica* . Kh: *Kobresia humilis* . As: *Artemisia scoparia* . Ha: *Heteropappus altaicus* . Gs: *Gentiana squarrosa* .

15

**Figure 5. Relation between warming-induced changes in species dominance and warming-induced shifts in species-specific (A) flower duration, (B) growing season length, (C) last flower and (D) leaf senescence.** Positive relations were observed between warming-induced changes in species dominance and warming-induced shifts in flower duration (Slope = 0.27, confidence interval (CI) = 0.20 to 0.35,$p < 0.001$, marginal $R2$ = 0.27), growing season length (Slope = 2.03, CI = 1.40 to 2.66, $p <$ 0.001, $R2$ = 0.22), last flower (Slope = 1.82, CI = 1.12 to 2.52, $p < 0.001$,$R2$ = 0.16) and leaf senescence (Slope = 2.02, CI = 0.92 to 3.12, $p < 0.001$,$R2$ = 0.08). The solid lines denote significant model slopes of the linear mixed effects models, and shaded areas show the 95% CI for slops. Sk: *Stipa krylovii* . Pc: *Poa crymophila* . Kc: *Koeleria cristata* . Mr: *Medicago ruthenica* . Kh: *Kobresia humilis* . As: *Artemisia scoparia* . Ha: *Heteropappus altaicus* . Gs: *Gentiana squarrosa* .