Research

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Climate warming reshapes seasonal flowering but stabilizes species interactions in a Tibetan alpine grassland

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Summary

- Climate warming commonly drives asymmetric shifts in flowering phenology among species, potentially disrupting plant–plant interactions and threatening ecosystem stability. However, the mechanisms driving these species-specific phenological responses, and the extent to which resulting asynchrony destabilizes interspecific interactions, remain poorly understood.
- Using a 3-yr *in situ* warming experiment in a Tibetan alpine grassland, we monitored seasonal flowering patterns of 29 species and quantified interaction potentials across 812 species pairs from their flowering-time overlap.
- Warming advanced the start of the flowering season in 75.9% of species and the end of the flowering season in 69.0%, with greater phenological shifts in late- than early-flowering species, in insect- than wind-pollinated species, and with more similar shifts in closely related species than in distantly related species. By contrast, warming significantly altered the interaction potential in only 6.8% of species pairs (55/812), independent of the pairwise phylogenetic distance.
- Our results advance understanding of species-specific phenological shifts in alpine grasslands and reveal that warming may induce substantial phenological reassembly without necessarily disrupting plant–plant interactions, suggesting resilience of ecological networks to phenological change.

Introduction

Global air temperatures are rising rapidly, with predictions indicating an increase of 3.3°C to 5.7°C above pre-industrial levels by the end of this century (IPCC, 2023). Such warming has profound impacts on flowering phenology – the seasonal timing of a key reproductive event in plants – with implications for reproductive success, biodiversity, and ecosystem stability (Cleland *et al.*, 2012; Piao *et al.*, 2019; Park & Post, 2022). However, flowering phenological responses to warming vary considerably among species (Sherry *et al.*, 2007; Qiu *et al.*, 2024), potentially reshaping flowering overlapping periods and altering species interactions (Burkle *et al.*, 2013; de Manincor *et al.*, 2023). Few studies, to date, have investigated the mechanisms underlying species-specific phenological responses to warming and their consequences on species interactions (CaraDonna *et al.*, 2014; Austin *et al.*, 2024). Addressing this knowledge gap is essential for improving predictions of climate change impacts on biodiversity and ecosystem stability.

Previous studies have indicated that species-specific responses to warming are related to their different flowering timings (Meng *et al.*, 2017; Prevéy *et al.*, 2019). For instance, in tundra ecosystems, late-flowering species have advanced their flowering more than early-flowering species in response to warmer summer temperatures, likely driven by increased water stress in the mid-to-late season (Prevéy *et al.*, 2019). Additionally, pollination mode may regulate the response of flowering phenology to warming. Insect-pollinated species, which rely on synchrony with their pollinators, may exhibit more constrained adjustments in flowering time than wind-pollinated species under climate warming (Fuccillo Battle *et al.*, 2022; de Manincor *et al.*, 2023). Phylogenetic relatedness may also influence interspecific variation in flowering phenological responses, with closely related species tending to exhibit similar phenological shifts due to conserved genetic architectures and physiological traits (Davies *et al.*, 2013; Cirtwill *et al.*, 2020). However, these potential biotic and abiotic mechanisms underlying species-specific phenological responses to warming still require experimental validation.

Synchronous flowering is commonly observed in species-rich plant communities with short growing seasons, such as alpine and subalpine grasslands (CaraDonna *et al.*, 2014; Richman *et al.*, 2020). This overlap in flowering phenology may promote interspecific interactions, including both mutualism and competition, as coflowering species often share pollinators and, in some cases, other limiting resources such as water and nutrients (Encinas-Viso *et al.*, 2012; Burkle *et al.*, 2013). Given the potential phylogenetic conservatism of flowering time (Kochmer & Handel, 1986), closely related species may exhibit greater overlap in flowering periods, thereby intensifying interspecific interactions. Under climate warming, if closely related species undergo similar phenological shifts due to shared evolutionary constraints (Davies *et al.*, 2013), their coflowering durations may remain relatively stable, leading to limited alterations in interspecific interactions compared with more distantly related species. Nevertheless, how phylogenetic distance shapes interspecific interactions and their responses to warming remains poorly understood.

The Tibetan Plateau, with 64% of its area covered by alpine grasslands, has warmed at twice the global average rate over the past five decades (Chen *et al.*, 2013). While numerous studies have documented warming effects on alpine plant flowering phenology (Meng *et al.*, 2017; Chen *et al.*, 2022), the mechanisms underlying species-specific responses remain unresolved. In species-rich alpine grasslands with short growing seasons, flowering periods often overlap extensively among species (Chen *et al.*, 2022), potentially promoting interspecific interactions. However, how phenological responses to warming reorganize these interactions remains unknown. Here, we conducted an *in situ* warming experiment in an alpine grassland on the Tibetan Plateau, monitoring the flowering phenology of 29 species and assessing interaction potential based on their temporal coflowering overlap (CaraDonna *et al.*, 2014). We tested two hypotheses: (1) Flowering onset, pollination mode, and phylogenetic relatedness jointly regulate asymmetric flowering phenological responses to warming among species; and (2) closely related species exhibit stronger interaction potential but show weaker warming-induced changes in that potential than distantly related species.

Materials and Methods

Study site

Our study site locates at the Qinghai Haibei National Field Research Station of Alpine Grassland in the northeastern edge of the Tibetan Plateau (101°35 ′E, 37°60 ′N, 3200 m asl). The site has a typical monsoon climate with short cool summers and long cold winters. From 1981 to 2014, the mean annual air temperature was −1.1°C, with monthly mean temperatures ranging from −14.4°C to 10.5°C (Wang *et al.*, 2020). The mean annual precipitation was 487.8 mm, with *c.* 84% of precipitation falling in the growing season from May to September. The alpine grassland community at this site typically comprises 20–50 plant species per square meter, with staggered flowering primarily occurring between May and September. Additionally, species in the Cyperaceae and Poaceae families lack petals and predominantly depend on wind pollination, while species in the Gentianaceae and Asteraceae families feature vibrant petals and prominent stamens and pistils to attract pollinators, primarily relying on insect pollination (Du *et al.*, 2017; Wang *et al.*, 2024).

Experimental design

In April 2021, we started an *in situ* warming experiment using a completely randomized block design with six blocks (Fig. 1a). Each block contained six 2.5 m × 1.8 m plots, with two plots assigned to control and year-round warming treatments. The warming plots were designed to simulate a 2°C increase in temperature above pre-industrial levels, in line with the target set by the Paris Agreement (UNFCCC, 2015), achieving this using infrared radiation heaters (220 V, 1500 W, 1 m long, 0.03 m wide; KR85-1040, Heraeus Holding GmbH, Hanover, Germany). The control plots were equipped with dummy heaters to account for potential structural effects of the experimental setup.

Flowering phenology monitoring

During the flowering seasons from 2021 to 2023, we monitored flower abundance every 5 d for 29 species that were consistently present in both the control and warming treatments (Fig. 2, Supporting Information Fig. S1; Table S1), within a fixed 2.5 m × 0.9 m observation area in each experimental plot (Fig. S2). For each species and year, we interpolated the seasonal data to estimate daily flower abundance. We then calculated the total flower count for the entire flowering season. The start of the flowering season (SOF) and end of the flowering season (EOF) were defined as the dates when the cumulative flower abundance reached 10% and 90% of the total flower count, respectively (Valencia *et al.*, 2016; Ahmad *et al.*, 2023). The length of the flowering season (LOF) was defined as the time interval between EOF and SOF.

Phenological shifts were calculated for each block as the difference in flowering phenologies between warming and control plots, with negative and positive values indicating advancements and delays under warming, respectively. We further quantified phenological sensitivity by dividing these shifts by the warming-induced change in soil temperature at 5 cm depth.

Quantification of interaction potential

To quantify interaction potential among coflowering species, we employed the methodology established by CaraDonna *et al.* (2014), which provides a robust framework for assessing the potential strength of two-species interactions, such as competition or mutualism, that arise from the utilization of shared resources (e.g. pollinators, water, and nutrient availability) under coflowering conditions (Encinas-Viso *et al.*, 2012).

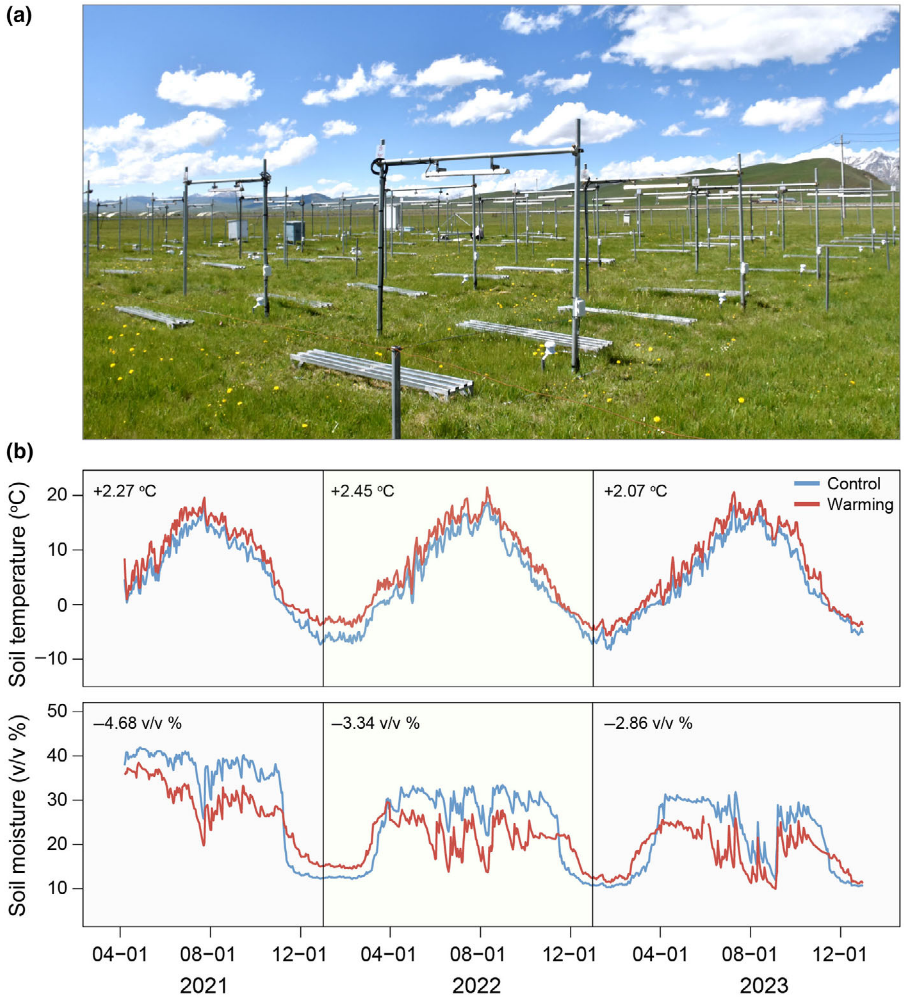

Fig. 1 Alpine grassland warming experiment and treatment effects on soil microclimate. (a) Warming experiment landscape. (b) Soil temperature and moisture at 5 cm depth under control and warming treatments from 2021 to 2023.

The interaction potential is a composite metric that integrates two critical dimensions: (1) the absolute strength of the interaction, quantified by the cumulative flower abundance during the overlapping flowering period, and (2) the relative impact of the absolute interaction on the two species, assessed by the proportion of flower abundance during the overlapping period relative to each species' total flower count. Mathematically, this is represented as the ratio of the overlapping area between the flower abundance curves of two species to the total area under the flower abundance curve of the focal species. For example, for focal *Species A* interacting with *Species B*, the interaction potential is calculated as (Fig. S3): S_{AB}/S_A, where S_A is the total abundance of *Species A* (i.e. the area under the *Species A* curve), and S_{AB} represents the cumulative flower abundance during the overlapping period (i.e. the area of overlap between the curves of *Species A* and *Species B*). We analyzed all 812 species pairs (each of the 29 species paired with any of the remaining 28) and found that 230 pairs had zero interaction potential due to a lack of overlapping flowering periods.

Seed number and seed mass measurement

Seeds of 13 species, including six insect-pollinated and seven wind-pollinated species, were collected during autumn 2023 (Fig. S4). These species together accounted for *c.* 56% of the total community biomass. Within each experimental plot, seeds were sampled from three individual plants per species. Mature seeds were collected using mesh bags positioned to intercept naturally dispersed seeds during the seed-shedding period. Collected seeds were air-dried in the laboratory, then counted and weighed.

Statistical analysis

We employed linear mixed-effects modeling to examine the effects of warming and observation year on flowering phenologies, while accounting for species-specific responses, using the *lme* function from the NLME package (v.3.1.166). Warming (W), observation year (Y), and species identity (S) were treated as fixed effects to evaluate their main effects and interactions (W × Y and W × S), testing whether warming effects varied over time and among species. Block was included as a random intercept (1|Block) to account for spatial heterogeneity in flowering phenology responses potentially induced by different blocks. Similarly, a linear mixed-effects model with the same structure was applied to assess the effects of warming and observation year on interaction potential, incorporating species pair identity (SP) as a fixed effect alongside W and Y, with interactions (W × Y and W × SP).

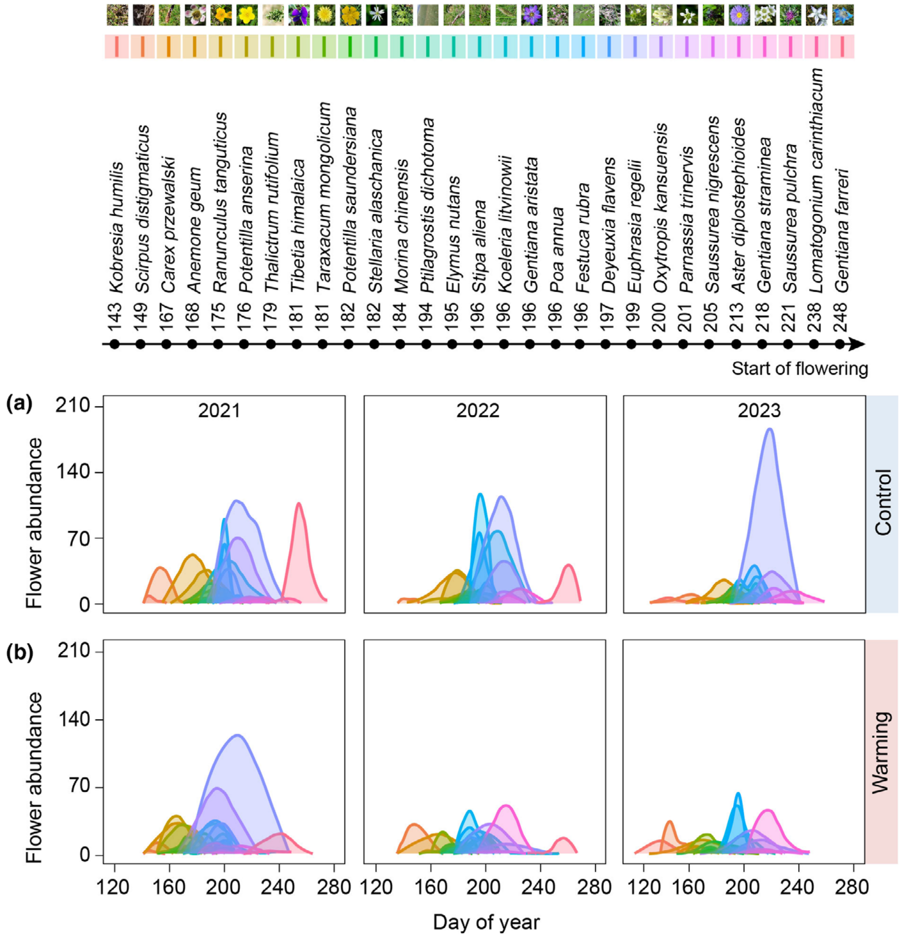

Fig. 2 Seasonal dynamics of flower abundance for 29 species under control and warming treatments from 2021 to 2023. (a) Control. (b) Warming. Species are ordered by the timing of flowering onset.

Finally, we tested the effects of warming on seed number and seed mass using a linear mixed-effects model with W and S as fixed effects (including W × S interaction) and block as a random intercept.

To control the false discovery rate across analyses of flowering phenology, interaction potential, and seed traits, given the large number of species or species pairs examined, *P*-values were adjusted using the Benjamini–Hochberg procedure, implemented via the *summary* function with the ‘test = adjusted(“BH”)’ option in the MULTCOMP package (v.1.4.25) in R (Hothorn *et al.*, 2008), thereby limiting the inflation of Type I errors.

A phylogenetic tree comprising the 29 focal species was generated by extracting relevant lineages from the global angiosperm phylogenetic supertree (GBOTB.extended) using the *phylo.maker* function in the V.PHYLOMAKER package (v.0.1.0) (Smith & Brown, 2018; Jin & Qian, 2019). Species absent from the supertree were inserted according to their respective genera or families. Branch lengths for these inserted species were assigned following the approach used in Phylomatic and BLADJ (Webb & Donoghue, 2005), distributing branch lengths evenly across unresolved nodes to maintain temporal calibration consistency. To assess whether phylogenetic relatedness influences flowering phenology responses to warming, Pagel’s λ was calculated using the *phylosig* function in the PHYTOOLS package (v.2.4.4) (Pagel, 1999; Revell, 2024). This index evaluates the conservatism of species’ phenological responses within the phylogeny (Blomberg *et al.*, 2003; Münkemüller *et al.*, 2012). A Pagel’s λ value of 0 indicates that phenological responses are independent of phylogeny, whereas a value of 1 indicates that phenological responses follow a Brownian motion evolution along the phylogenetic tree. Additionally, we calculated the phylogenetic distance between two interacting species for all species pairs using the *cophenetic* function from the APE package (v.5.8.1) (Paradis & Schliep, 2019). Linear regression was used to examine the relationships between species interaction potentials and phylogenetic distance, as well as the influences of phylogenetic distance and baseline interaction potential on warming-induced change in interaction potential.

We conducted linear mixed-effects modeling to examine the effects of flowering functional group (FFG; early-, mid-, and late-flowering) and pollination functional group (PFG; wind- and insect-pollinated) on phenological responses (Table S1). In this model, W × FFG or W × PFG was treated as fixed effects, with block and species identity included as random effects. If significant differences ($P < 0.05$) were detected for the fixed effects, we further conducted multiple comparisons using the *emmeans* function.

Table 1 Results of linear mixed-effects models on flowering phenology.

Factor	df	*F*	*P*
Start of flowering season (SOF)			
Warming	1681	895.6	< 0.001
Year	2681	0.4	0.6
Species	28 681	487.8	< 0.001
Warming × year	2681	9.5	< 0.001
Warming × species	28 681	7.3	< 0.001
End of flowering season (EOF)			
Warming	1681	492.3	< 0.001
Year	2681	2.9	0.06
Species	28 681	461.2	< 0.001
Warming × year	2681	7.4	< 0.001
Warming × species	28 681	5.5	< 0.001
Length of flowering season (LOF)			
Warming	1681	36.1	< 0.001
Year	2681	1.5	0.2
Species	28 681	26.9	< 0.001
Warming × year	2681	0.4	0.7
Warming × species	28 681	2.5	< 0.001

The models assess the individual and interactive effects of warming, observation year, and species identity on flowering phenology. df, degrees of freedom (numDF and denDF, respectively).

We also employed linear mixed-effects modeling to test the relationships between changes in interaction potential and seed mass or seed number. Species identity (13 focal species measured in 2023) was included as a random intercept to account for interspecific variation. Interaction potential for each focal species was calculated as the sum of its interaction potentials with all interacting species (Fig. S4).

In this study, all analyses were conducted in R 4.4.2 (R Development Core Team, 2024).

Results

Warming effects on microclimate and flowering phenology

Mean air temperatures during the growing season (May to September) were 7.8°C in 2021, 8.7°C in 2022, and 8.0°C in 2023, with corresponding total precipitation of 428.8, 431.5, and 295.9 mm, respectively (Fig. S5). Over the three study years, experimental warming increased soil temperatures at 5 cm depth by an average of 2.3°C (2.1–2.5°C) and reduced soil moisture by 3.6% (2.9–4.7%; Fig. 1b). Such warming, overall, advanced SOF by 10.7 d ($P < 0.001$; Table 1) and EOF by 8.5 d across species and years ($P < 0.001$), while prolonging LOF by 2.2 d ($P < 0.001$; Fig. 3a). Corresponding phenological sensitivities to warming were $-4.8\ \mathrm{d}\ ^\circ\mathrm{C}^{-1}$ for SOF, $-3.9\ \mathrm{d}\ ^\circ\mathrm{C}^{-1}$ for EOF, and $+1.0\ \mathrm{d}\ ^\circ\mathrm{C}^{-1}$ for LOF (Fig. 3b).

The magnitude of warming effects on SOF and EOF varied among years ($P < 0.001$ for the 'Warming × Year' interaction; Table 1). Warming led to greater advancement of SOF and EOF in 2021 and 2023 than in 2022 (Fig. S6), likely due to higher baseline spring temperatures in 2022, which attenuated the relative impact of experimental warming (Fig. S7). There was no evidence that soil moisture before or during the growing season contributed to the observed interannual variation in SOF and EOF responses (Fig. S8).

Warming effects on flowering phenology varied among species ($P < 0.001$ for the 'Warming × Species' interaction; Table 1). Under warming, SOF advanced in 75.9% of species and remained unchanged in 24.1%, while EOF advanced in 69.0% of species and remained unchanged in 31.0% (Figs S9, S10, S11). Significant Pagel's λ values were detected for species-specific shifts in SOF ($\lambda = 0.31$, $P = 0.04$) and EOF ($\lambda = 0.54$, $P = 0.009$), but not for LOF ($\lambda = 0.00$, $P = 1.0$; Fig. 4a). The Gentianaceae family showed the greatest advancement in SOF, with an average shift of 14.5 d ($P < 0.001$), while the Asteraceae family exhibited the strongest response in EOF, advancing by 10.8 d on average ($P < 0.001$; Fig. S12).

Phenological responses to warming also differed among functional groups. Late-flowering species advanced their SOF and EOF more than early- and mid-flowering species ($P < 0.05$; Fig. 4b), whereas insect-pollinated species showed stronger advances than wind-pollinated species ($P < 0.05$; Fig. 4c). Late-flowering, insect-pollinated species *Saussurea pulchra* exhibited the largest advances in SOF and EOF, with shifts of 22.8 and 16.8 d, respectively ($P < 0.001$; Fig. S10). By contrast, LOF responses did not differ significantly between pollination modes ($P = 0.7$; Fig. 4c).

Changes in flowering interaction potentials

Of all 812 species pairs examined, 582 pairs (71.7%) exhibited overlapping flowering periods, indicating potential interactions (Fig. 5a). These interaction potentials were modulated by phylogenetic distance, with a reduction in interaction potentials as phylogenetic distance increased ($P < 0.001$; Fig. 5a).

Across 2021–2023, warming significantly affected interaction potential ($P = 0.003$; Table S2). This effect varied among species pairs ($P < 0.001$ for the 'W × SP' interaction), with 4.1% (33/812 pairs) showing increased interaction potential, 2.7% (22/812 pairs) showing decreased potential (Table S3), and 93.2% (757/812 pairs) showing no significant change ($P > 0.05$; Fig. S13). Furthermore, warming effects on interaction potential were not significantly associated with phylogenetic distance ($P = 0.57$; Fig. 5b). Changes in interaction potential were negatively correlated with baseline values, with warming shifting responses from increases to decreases as baseline interaction potential increased (Fig. 5b).

Seed trait changes linked to interaction potentials

Across 13 species observed in 2023, warming did not significantly affect seed mass ($P = 0.94$; Fig. S14a), except for significant decreases in *Oxytropis kansuensis* ($P = 0.004$) and *Carex przewalskii* ($P = 0.04$). Warming also had no significant effect on seed number across species ($P = 0.56$; Fig. S14b).

Although warming-induced changes in interaction potential did not significantly affect seed mass ($P = 0.65$) or seed number ($P = 0.28$) across all focal species (Fig. 6), detectable effects were

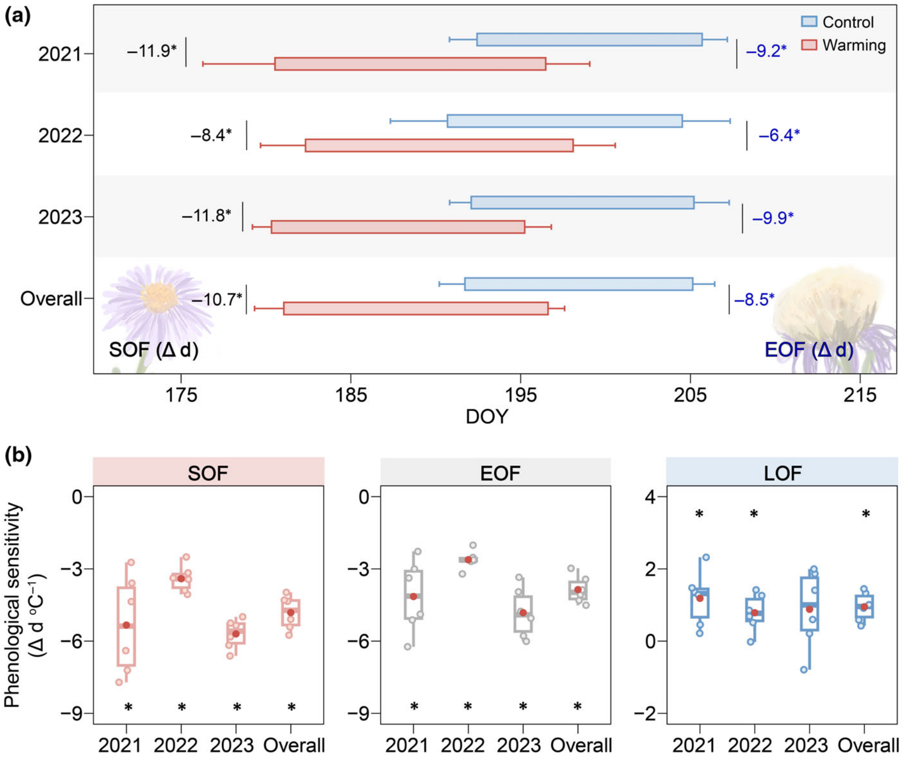

Fig. 3 Warming effects on flowering phenology across species from 2021 to 2023. (a) Flowering phenology under control and warming treatments. The left side of each boxplot shows the start of flowering (SOF), and the right side shows the end of flowering (EOF). Numbers indicate warming-induced shifts in SOF and EOF, respectively. (b) Phenological sensitivities of SOF, EOF, and length of flowering season (LOF). In panel (a), error bars represent one SE of the mean ($n = 6$ plots). In panel (b), box center lines indicate the median; box limits show the upper and lower quartiles; whiskers extend to 1.5× the interquartile range from the 25th and 75th percentiles; red dots mark the mean; and jittered points denote six plots. Linear mixed-effects models were used to assess warming effects on flowering phenology. Asterisks denote statistical significance (*, $P < 0.05$).

observed in a few insect-pollinated species. Specifically, in *Ranunculus tanguticus* and *Saussurea nigrescens*, seed mass decreased as interaction potential increased under warming ($P < 0.05$; Fig. 6a). By contrast, seed mass in *O. kansuensis* increased with rising interaction potential ($P = 0.04$; Fig. 6a). Additionally, seed number in *R. tanguticus* reduced with increased interaction potential ($P = 0.03$; Fig. 6b).

Discussion

Elucidating how species-level flowering phenology responds to global climate change is fundamental for projecting future changes in the terrestrial biosphere (Wolkovich *et al.*, 2012; Collins *et al.*, 2021). Our study provides compelling evidence that climate warming generally advanced flowering timing but induced asymmetric phenological shifts among species. Consistent with our first hypothesis, we found that flowering onset, pollination mode, and phylogenetic position collectively influenced species-specific phenological responses to warming. However, our results only partially support the second hypothesis: Closely related species pairs exhibited greater interaction potential, but the warming-induced changes in their interaction potential did not differ significantly from those of distantly related pairs.

Warming effects on flowering phenology and underlying mechanisms

Our result of the advancement in SOF under warming aligns with previous findings in Tibetan alpine grasslands (Suonan *et al.*, 2017; Chen *et al.*, 2022). This finding may be attributed to an accelerated fulfillment of plants' heat accumulation requirement in spring, which breaks ecological dormancy and promotes earlier green-up, ultimately leading to earlier flowering (Fu *et al.*, 2014; Wang *et al.*, 2014). By contrast, limited changes in LOF were observed due to a concurrent advancement in EOF, indicating that the duration required for flowering may be relatively conserved, ensuring sufficient time for successful pollination.

We observed that both SOF and EOF advanced less under warming in 2022 than in 2021 and 2023, likely reflecting modulation by interannual climate variability. The reduced phenological response in 2022 may be attributed to its warmer spring, which could have alleviated cold-temperature constraints on early plant development, thereby diminishing the relative impact of experimental warming. Given that warming often reduces soil moisture availability (Dorji *et al.*, 2013) and that flowering typically requires substantial water (Gallagher & Campbell, 2017), we further examined whether interannual variation in soil moisture modulated the phenological responses to warming. However, the observed weak correlations between shifts in SOF and EOF and soil moisture before or during the growing season suggest that water availability likely plays a limited role in shaping the interannual variation in phenological responses. This result could be explained by the high baseline growing-season soil moisture in this alpine mesic meadow (*c.* 30.9 v/v%), which rendered the modest experimental warming (*c.* 1.5°C) insufficient to induce water stress during flowering.

The observed shifts in SOF and EOF under warming were asymmetric among species, with late-flowering species advancing more than early-flowering species–a pattern also observed in

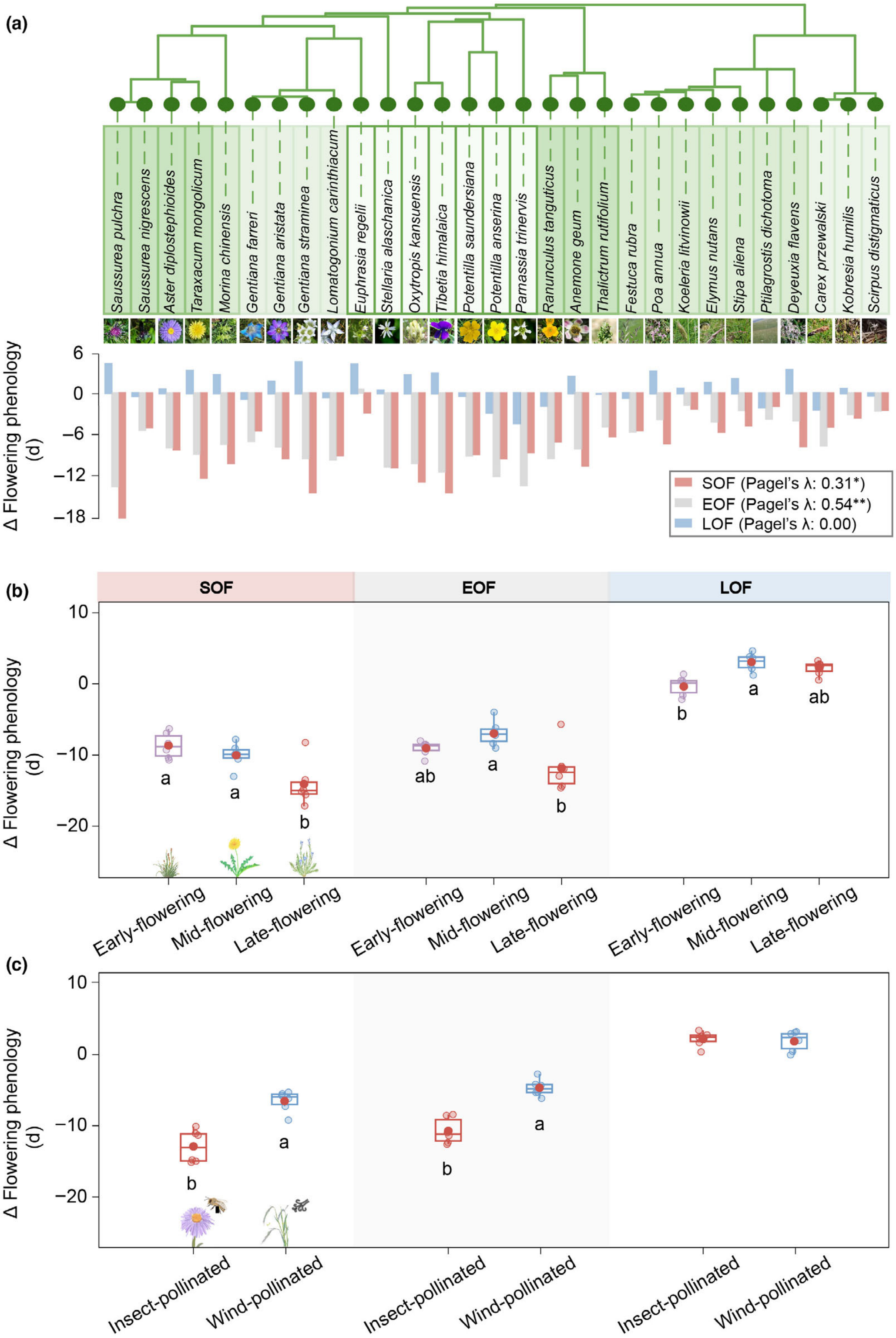

Fig. 4 Influence of phylogenetic relatedness and functional groups on warming effects on flowering phenology. (a) Phylogenetic relatedness. (b) Flowering functional group. (c) Pollination functional group. SOF, EOF, and LOF represent the start, end, and length of the flowering season, respectively. Asterisks denote statistical significance for Pagel's λ, indicating that warming effects are significantly regulated by phylogenetic relatedness (*, $P < 0.05$; **, $P < 0.01$). In panels (b, c), box center lines indicate the median; box limits show the upper and lower quartiles; whiskers extend to 1.5× the interquartile range from the 25th and 75th percentiles; red dots mark the mean; and jittered points denote six plots. Linear mixed-effects models were used to assess the effects of functional groups on phenological responses. Different lowercase letters indicate significant differences among functional group categories at $P < 0.05$.

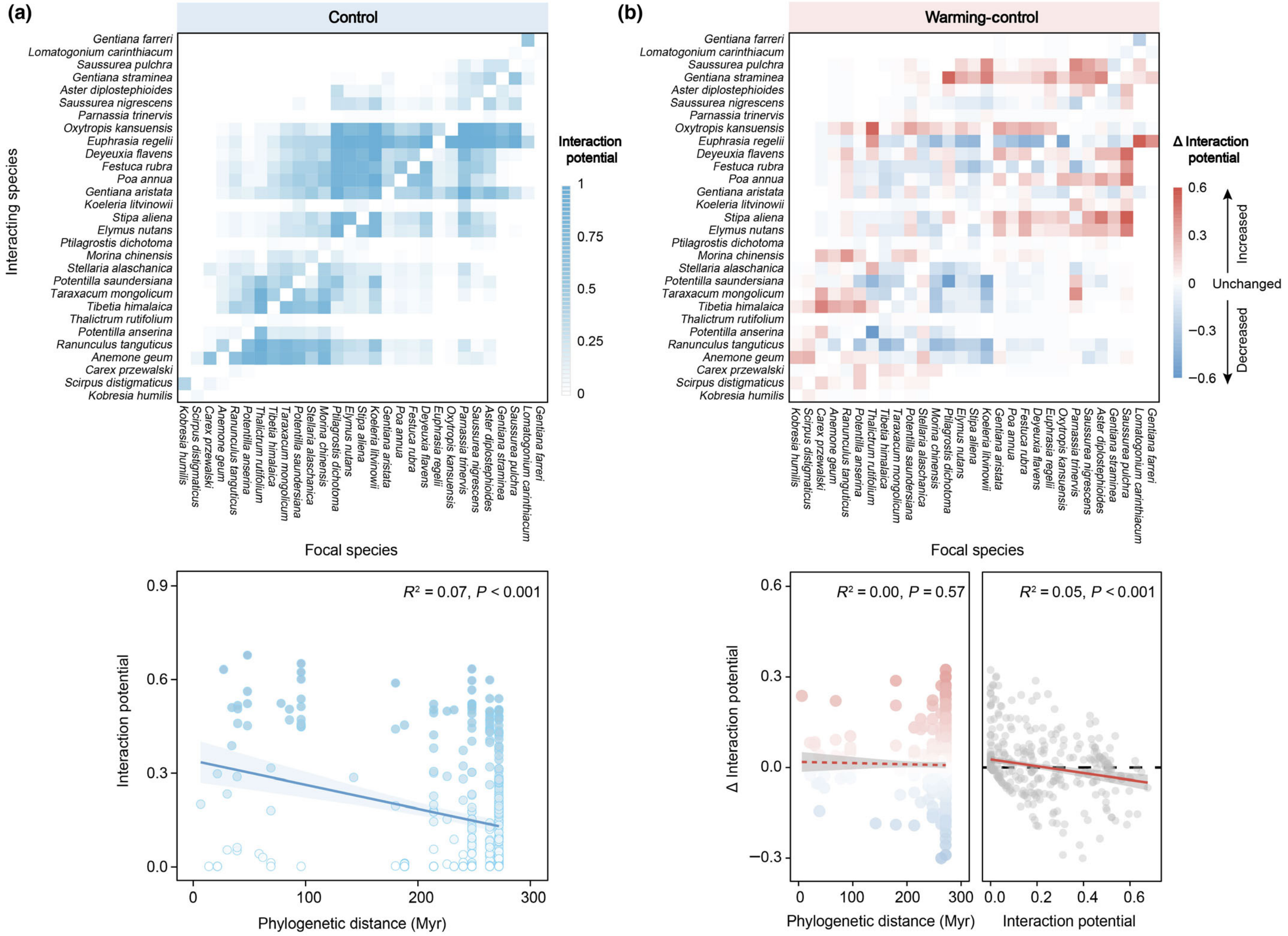

Fig. 5 Phylogenetic regulation of species interaction potentials and their response to warming. (a) Interaction potential in relation to phylogenetic distance under control treatment. (b) Warming-induced changes in interaction potential in relation to phylogenetic distance and baseline interaction potential. For a species pair consisting of *Species A* and *Species B*, the interaction potentials, whether *Species A* or *Species B* is considered as the focal species, correspond to the same phylogenetic distance between the two species. Linear regression was used to examine these relationships. The analysis considered only species pairs in which both members co-occurred under both control and warming treatments.

other alpine grasslands and tundra ecosystems (Suonan *et al.*, 2017; Prevéy *et al.*, 2019). We observed the greatest advancement in SOF and EOF in the late-flowering species *S. pulchra* (Asteraceae). This finding may be related to differences in the timing of floral primordium differentiation among species. Early-flowering species often form floral primordia during the previous winter or early spring and rely on vernalization or photoperiod cues, which reduce their sensitivity to warming (Körner, 2003). By contrast, late-flowering species may develop floral primordia closer to the growing season and consequently show stronger temperature responses (Wang *et al.*, 2014; Bai *et al.*, 2024).

Insect-pollinated species showed stronger shifts in flowering phenology than wind-pollinated species, consistent with previous observations in tree species from Northwest China and the Northeastern United States (Dai *et al.*, 2013; Fuccillo Battle *et al.*, 2022). For instance, the insect-pollinated *S. pulchra* (Asteraceae) exhibited a greater advancement in EOF than the wind-pollinated *Elymus nutans* (Poaceae) in response to warming. This asymmetry between PFGs is likely because insect-pollinated species rely heavily on synchronizing with pollinators (Rusman *et al.*, 2025), which often advance their activity earlier under climate warming (Burkle *et al.*, 2013). By contrast, wind-pollinated plants, which depend on wind for pollen dispersal, are often less influenced by warming.

Closely related species exhibited more similar phenological responses to warming than distantly related species, consistent with previous evidence of phylogenetic conservatism in flowering time across 23 sites in the Northern Hemisphere (Davies *et al.*, 2013). This pattern likely reflects shared genetic architectures being expressed in floral traits that govern flowering responses to temperature cues (Li *et al.*, 2016). In this study, species in the Gentianaceae family showed the greatest advancement in SOF, while those in the Cyperaceae family exhibited the

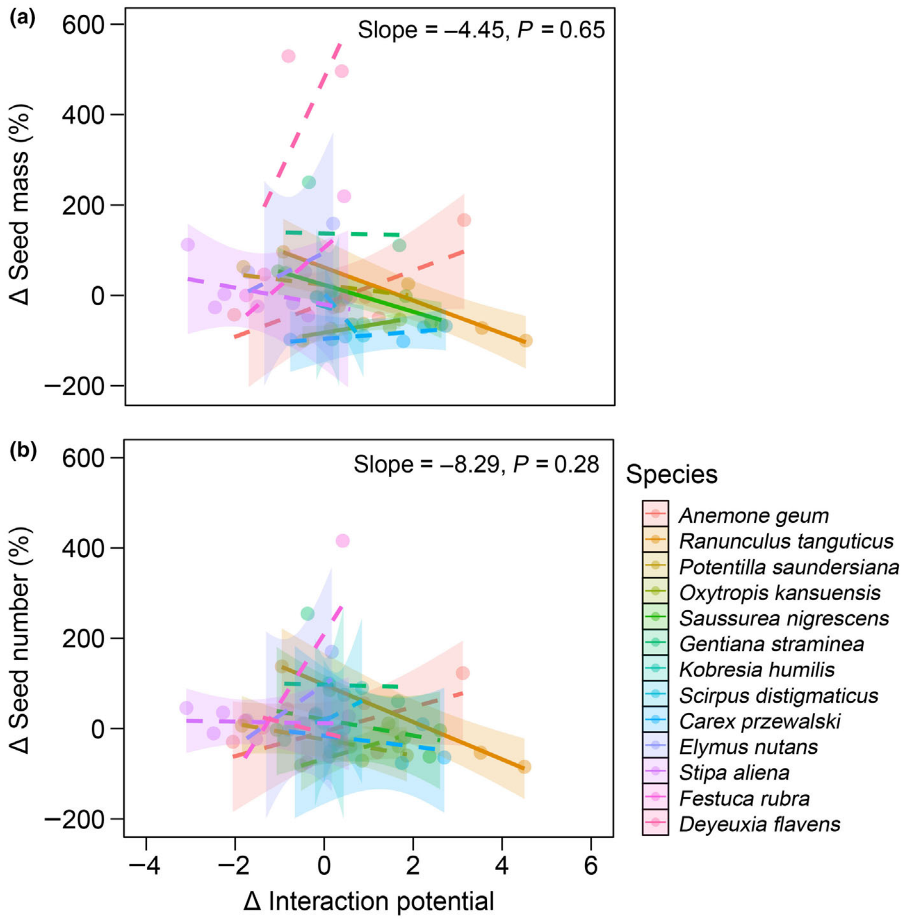

Fig. 6 Relationships between warming-induced changes in seed traits and interaction potential. (a) Seed mass. (b) Seed number. Statistical results shown in the upper right corner are from linear mixed-effects models based on data from all species, with species treated as a random effect. Solid and dashed lines indicate significant and nonsignificant species-level relationships, respectively ($P < 0.05$). Each dot represents a species-level observation per plot in 2023 (n = 3–6 plots).

smallest. Members of these families may share similar floral traits such as size, structure, and investment in reproductive tissues, which influence pollination strategies and promote coordinated flowering responses to climate warming (Westoby *et al.*, 1995; Davies *et al.*, 2013).

Phylogenetic distance shapes interaction potential, not its response to warming

In the species-rich alpine grassland we studied, 71.7% of species pairs exhibited pronounced interaction potential due to overlapping flowering periods, suggesting potential competition or mutualism through shared pollinators, water, or nutrient resources (Veresoglou & Fitter, 1984; Johnson *et al.*, 2022). Furthermore, interaction potential decreased with increasing phylogenetic distance across species pairs. Among all pairs, the highest interaction potential was observed between *Stipa aliena* (Poaceae) and *E. nutans* (Poaceae), while the lowest was between *Gentiana farreri* (Gentianaceae) and *O. kansuensis* (Fabaceae). These results support the Phylogenetic Limiting Similarity Hypothesis, which suggests that closely related species, due to niche conservatism, tend to share similar resource use strategies, thereby intensifying interspecific competition (Macarthur & Levins, 1967; Cirtwill *et al.*, 2020). Conversely, distantly related species may exhibit niche differentiation, potentially reducing such competition.

We observed that only 6.8% of species pairs altered their interaction potential under warming, largely driven by asynchronous shifts between the SOF and EOF within individual species. For example, in the pair *Tibetia himalaica* and *Gentiana aristata*, the warming-induced decline in interaction potential was mainly due to a greater advancement in SOF than EOF in *T. himalaica* (Fig. S10). Changes in interaction potential can also be driven by differential phenological shifts between species. For example, the warming-induced decrease in the interaction potential of the pair *E. nutans* and *R. tanguticus* was mainly due to a greater advancement in SOF in *R. tanguticus* (Fig. S15). A 39-year study in the Colorado Rocky Mountains supports this finding, reporting that species-specific phenological responses shape interaction potential in subalpine plant communities (CaraDonna *et al.*, 2014).

However, we found no evidence that phylogenetic distance modulated the response of interaction potential to warming, as both closely and distantly related species pairs showed similarly small changes in potential on average. For closely related species pairs, such limited change may reflect similar phenological responses to warming due to shared genetic architectures and conserved traits (Violle *et al.*, 2011; Williams *et al.*, 2021). For example, in the pair *Kobresia humilis* (Cyperaceae) *and Scirpus* *distigmaticus* (Cyperaceae), comparable advances in both SOF and EOF led to negligible changes in interaction. By contrast, distantly related species pairs tended to exhibit more divergent phenological responses, driving stronger but directionally inconsistent changes in interaction potential. In the pair *E. nutans* (Poaceae) and *Euphrasia regelii* (Orobanchaceae), a greater EOF advancement in *E. nutans* than in *E. regelii* led to a marked decrease in potential. Conversely, in the pair *S. pulchra* (Asteraceae) and *Deyeuxia flavens* (Poaceae), greater advancement in *S. pulchra* resulted in a strong increase in potential. These contrasting shifts across distantly related species pairs may have canceled each other out, resulting in an overall average response close to zero.

Moreover, we found that as baseline interaction potential increased, the initially positive effect of warming on interaction potential gradually weakened and then reversed, becoming negative. This pattern likely reflects the species interaction shifting from facilitation or commensalism to competition as the baseline interaction intensity increases. At low baseline levels, the positive effects of warming may be driven by the emergence or enhancement of facilitative or commensal relationships. For instance, warming may increase flowering synchrony between insect-pollinated species, thereby enhancing their attractiveness to pollinators (Lázaro *et al.*, 2009; de Manincor *et al.*, 2023). However, as baseline interaction potential increases, warming may gradually shift interactions from being dominated by positive associations to being driven by competition, resulting in a net decline in interaction potential. For instance, climate warming often reduces soil moisture availability (Sherry *et al.*, 2007; Dorji *et al.*, 2013), and under conditions of flowering synchrony, this can intensify competition for limiting resources such as water and nutrients. Additionally, statistical constraints may also contribute to this pattern. For species pairs with no initial overlap (i.e. interaction potential = 0), random phenological shifts under warming are more likely to maintain or increase flowering overlap, resulting in increased interaction potential. By contrast, for highly synchronized pairs, further increases in flowering overlap are limited, and stochastic shifts are more likely to reduce synchrony, lowering interaction potential. Further research is needed to disentangle the relative contributions of ecological mechanisms and statistical effects.

Cascading effect of changing interaction potential on reproductive outcomes

We observed cascading effects of warming-induced changes in interaction potential on reproductive outcomes in only a subset of insect-pollinated species. In both *R. tanguticus* and *S. nigrescens*, increasing interaction potential with other species was associated with reductions in seed mass, and in *R. tanguticus*, also in seed number. This negative cascading effect may be because increased floral overlap under warming increases the probability of heterospecific pollen transfer, thereby reducing pollination purity and fertilization efficiency (Waser *et al.*, 1996; Brown *et al.*, 2002). By contrast, *O. kansuensis* showed increased seed mass with rising interaction potential, suggesting a positive cascading effect. In this case, enhanced flowering overlap may have attracted more pollinators and improved pollination success (Lázaro *et al.*, 2009; de Manincor *et al.*, 2023). Additionally, we found no evidence for such cascading effects in wind-pollinated species, suggesting that abiotic pollen dispersal may not play as pivotal a role as pollinator-mediated processes in linking changes in flowering overlap to reproductive outcomes under warming. However, given that our observations were limited to 13 species monitored during a single growing season, longer term studies across a broader range of taxa are needed to assess the generality of these findings and to uncover the underlying mechanisms.

It should be noted that our finding in an alpine grassland plant community may not be generalizable across all ecosystems. The community studied here exhibited strong phenological sensitivity to warming – a pattern also observed in many subalpine meadows (CaraDonna *et al.*, 2014), Arctic tundra (Prevéy *et al.*, 2019), and temperate woodlands (Miller-Rushing & Primack, 2008). However, species-specific phenological responses often vary across systems. For example, we found that late-flowering species advanced more than early-flowering ones, whereas in temperate woodlands (Miller-Rushing & Primack, 2008) and another alpine meadow (Chen *et al.*, 2022), early-flowering taxa were more sensitive to temperature (Miller-Rushing & Primack, 2008; Chen *et al.*, 2022). Moreover, closely related co-occurring species in temperate woodlands, such as those in the genera *Betula* and *Solidago*, exhibited divergent phenological responses to warming (Miller-Rushing & Primack, 2008), in contrast to our finding of phylogenetic conservatism in phenological shifts.

In addition, despite relatively modest changes in interspecies interaction potential observed in our study, more pronounced changes in flowering overlap have been reported in other ecosystems, such as in a Mediterranean shrub community (Pareja-Bonilla *et al.*, 2025), in tallgrass prairies and bottomland forests where 94% of species showed changes (Austin *et al.*, 2024), and in a subalpine meadow where 23% of species pairs altered their interaction potential (CaraDonna *et al.*, 2014). However, the metrics used to quantify phenology-driven changes in plant–plant interactions vary across studies, with some relying solely on flowering overlap, and others incorporating both temporal overlap and flower abundance (i.e. interaction potential). Standardizing these metrics in future research will be essential for improving cross-system comparisons and for advancing our understanding of how climate change is reshaping biotic interactions.

Conclusions

In sum, our 3-yr field experiment reveals that climate warming induced substantial shifts in flowering phenology yet has limited effects on interspecific interaction potential in an alpine grassland on the Tibetan Plateau, suggesting a degree of resilience in ecological networks to phenological change. These findings offer key insights into the asymmetric nature of species' phenological responses and their consequences for plant–plant interactions under climate change. In particular, our identification of flowering onset, pollination mode, and phylogenetic relatedness as key predictors of phenological shifts advances mechanistic understanding of species-specific responses and improves projections of alpine ecosystem trajectories in a warming world.

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Competing interests

None declared.

Author contributions

HW conceived and developed the research. JZ conducted the experiments and performed data compilation and analysis. JZ wrote the first draft. JZ, JW, JM, CL, SN, HZ, LS, CS, XJ, ZZ, HL, J-SH and HW contributed to the writing and discussion of the paper.

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Data availability

The data that support the findings of this study are openly available in the Figshare repository at doi: 10.6084/m9.figshare.29945399.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Seasonal dynamics of flower abundance for 29 species under control and warming treatments.

Fig. S2 Close-up of the observation area for seasonal flower abundance in the experimental plot.

Fig. S3 Conceptual representation of the calculation of interaction potential in flowering species pairs.

Fig. S4 Responses of overall interaction potential to warming for 13 species with observed seed traits in 2023.

Fig. S5 Seasonal climate dynamics from 2021 to 2023.

Fig. S6 Sensitivities of flowering season start, end, and length to warming from 2021 to 2023.

Fig. S7 Cumulative growing degree-days under control and warming treatments from 2021 to 2023.

Fig. S8 Relationships between warming effects on flowering phenology and soil moisture before and during the growing season.

Fig. S9 Flowering phenology of 29 species under control and warming treatments across years.

Fig. S10 Effect of warming on flowering phenology of 29 species across years.

Fig. S11 Proportion of species exhibiting different phenological responses to warming.

Fig. S12 Effect of warming on flowering phenology at the family level across years.

Fig. S13 Proportion of species pairs exhibiting different responses of interaction potential to warming.

Fig. S14 Effects of warming on seed mass and seed number of 13 species in 2023.

Fig. S15 Regression coefficients linking changes in interaction potential to phenological shifts under warming.

Table S1 Species information.

Table S2 Results of linear mixed-effects models on interaction potential.

Table S3 Changes in interaction potential under warming.

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