What's in flower? Phenological temperature sensitivities in a restricted alpine flora

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Abstract

As climate warming continues, cues for shifts in plant reproductive timing will be a key mediator of species success. To examine the links between temperature and flowering time in the Australian alpine, we used climate records and 18,000 flowering observations spanning 12 years for 52 alpine plant species from the Snowy Mountains, Australia. We modelled three phenological traits (flowering onset, peak, and end) against climate to determine species that exhibit an expansion, contraction or shift in their temporal niche. Ninety-four percent of species in our dataset were phenologically sensitive to temperature. Flowering onset was most influenced by October mean temperature, with mean flowering onset occurring earlier under warmer temperatures. Flowering peak and end were most phenologically sensitive to September mean temperature. Plant and phenological traits exhibited phylogenetic signal, although this was weak for temperature sensitivity. Apparent relationships between floral traits and temperature sensitivity were explained by shared ancestry rather than repeated evolutionary associations. Our findings demonstrate the importance of accounting for phylogeny when investigating the phenological temperature sensitivity of plants, and that

flowering phenology in this flora is highly responsive to early spring temperatures. As spring rapidly warms, alpine flowering will partially shift to be earlier, with reproductive success depending on the breeding systems and phenology of associated pollinators.

Introduction

Flowering phenology is a visible component of plant life history and an important driver of ecosystem processes, trophic interactions and reproduction. It is also a useful and widely used indicator of biotic responses to climate change (Cleland et al., 2007; Fitter & Fitter, 2002; Menzel et al., 2006; Parmesan & Yohe, 2003). In climates with cold winters, temperatures that occur in the months prior play a key role in shaping flowering times for many, but not all, species (Daru et al., 2019; Wolkovich et al., 2012), with important implications for plant fitness (Elzinga et al., 2007); biotic interactions (Elzinga et al., 2007; Wolf et al., 2017); and species persistence (Willis et al., 2008). For example, in the flora of naturalist Henry David Thoreau's Concord Woods, species whose flowering phenology was assessed as insensitive to temperature were found to have decreased in abundance over the past 150 years (Willis et al., 2008). While the authors do not attribute this decline to a single mechanism, they postulate that pollinator mismatch and increased herbivory are likely to be driving factors (Willis et al., 2008). Assessing species' phenological sensitivity to temperature is important as it allows identification of taxa that are likely to track their phenological niche under climate change, and those that may lag behind (Wolkovich & Donahue, 2021).

Phenological parameters such as event timing (e.g. onset, peak, end) and duration (end – onset) (Rathcke & Lacey, 1985) may be useful for characterising species' responsiveness to temperature (CaraDonna & Inouye, 2015). Much previous research has focused on temperature sensitivity at event onset, known as first flowering date (FFD) (Amano et al., 2010; Bucher et al., 2018; Fitter & Fitter, 2002; Gallagher et al., 2009; König et al., 2018; Mazer

et al., 2013; Suonan et al., 2019; Wadgymar et al., 2018). As with last flowering dates, first flowering dates represent the lower limit of the flowering distribution and may be subject to sampling biases (B. D. Inouye et al., 2019; Miller-Rushing et al., 2008), such as a decrease in the likelihood of observers visiting sites in adverse spring or autumn weather conditions (Daru et al., 2019). Although requiring more effort and due to more observations, peak flowering within and between species is ecologically meaningful for fitness (Preite et al., 2015; Scheepens & Stöcklin, 2013), biotic interactions (Elzinga et al., 2007), and ecosystem services (Campbell et al., 2012; Häussler et al., 2017). It is therefore important to assess phenological sensitivity to temperature, within and between species, at the onset (B. D. Inouye et al., 2019), peak (CaraDonna & Inouye, 2015; Miller-Rushing et al., 2008; Wang et al., 2015) and end of flowering (CaraDonna & Inouye, 2015; Wang et al., 2015).

Phenological responses to temperature can also show relationships with plant functional traits. Previous studies have found relationships between flowering time and seed size (Bolmgren & D. Cowan, 2008), other floral traits and plant size (Bucher et al., 2018; Cornelissen & Makoto, 2014; Dorji et al., 2013; Jia et al., 2011; König et al., 2018; Ollerton & Lack, 1998). Where such relationships exist, a trait-based approach could help to predict which species will be temperature sensitive.

Long-term observational records that capture the entirety of the flowering distribution for a large number of species are rare, but where they do exist, they allow for the characterisation of phenological sensitivity to temperature at all points within the flowering season. A synthesis of phenological responses to temperature for 1,634 plant species across four continents found that long-term observational studies were 8.5 fold better at predicting advances in flowering phenology than were experimental studies (Wolkovich et al., 2012). In the same study, early spring flowering species in observational data were found to be most

77 sensitive to temperature, a result that was not echoed in experimental studies (Wolkovich et
78 al., 2012). In addition, long-term studies have found that cold-climate species from alpine and
79 tundra environments had, on average, greater temperature sensitivity than plants growing in
80 warmer climates (Güsewell et al., 2017; Prevéy et al., 2017).
81
82 There are, however, consequences for flowering too early in cold climates. Temperature-
83 sensitive species that flower earlier in response to higher temperatures may experience
84 freezing damage to reproductive structures given the higher probability of exposure to severe
85 spring frosts (D. W. Inouye, 2000, 2008; Venn et al., 2017). Reproductive structures tend to be
86 more temperature sensitive than vegetative tissue, particularly during bolting and anthesis
87 (Ladinig et al., 2013; Sakai & Larcher, 1987). Compared to temperature-sensitive lowland
88 plants that flower earlier in response to warmer temperatures, experimental (Ladinig et al.,
89 2013) and observational (D. W. Inouye & Wielgolaski, 2013) studies indicate that alpine
90 plants may experience selection against flowering too early due to the heightened risk of
91 freezing damage. If plants are not protected by snow, then the exposed parts can be more
92 susceptible to freezing damage (Ladinig et al., 2013; Venn & Green, 2018), however in
93 extreme cases in the subnival and nival zones, frost sensitive reproductive tissues may
94 become frost damaged even when covered by snow (Ladinig et al., 2013). These various
95 freezing sensitivities across alpine landscapes can lead to changes in community composition.
96 For example, populations of *Delphinium* in the Rocky Mountains that flowered extremely early
97 in warm springs experienced population declines and local extinctions following widespread
98 freezing (D. W. Inouye & Wielgolaski, 2013). In some high-elevation regions, short- to
99 medium-term climate warming occurs independently of changes in the frequency of severe
100 frost events (≤ −8°C), which are projected to remain at levels comparable to those
101 experienced today (Woldendorp et al., 2008). Consequently, alpine plants are likely to remain
102 exposed to the risk of freezing damage despite ongoing warming.

Closely related species tend to have similar life-history and phenological responses to environmental stimuli than do less closely related species (Davies et al., 2013). While many studies show that responses of flowering-time to temperature can be highly species-specific (Bucher et al., 2018; Fitter & Fitter, 2002; Menzel et al., 2006), there remains disagreement about phylogenetic conservatism of temperature responses (CaraDonna & Inouye, 2015; Willis et al., 2008). There are important implications of this question for evolution and ecosystem resilience: Willis et al. (2008) found that the phylogenetic structure of temperature responses led to non-random declines in some plant families. Conversely, in a northern hemisphere sub-alpine flora, CaraDonna and Inouye (2015) found that while there is a phylogenetic signal in first flowering dates, this did not translate to a phylogenetic signal in temperature sensitivities. Moreover, there is an important link between phylogenetic structure and prediction, because shared ancestry can also cause covariation at the species level that is not predictive (Felsenstein, 1985).

The mainland Australian alpine environment occurs as disconnected habitat islands, with no nival zone even at the highest elevations (Costin, 2000). Shared lineages exist between the Northern Hemisphere alpine flora and that of Australia (e.g. *Ranunculaceae*; *Poaceae*; *Asteraceae*) (Venn et al., 2017)**.** Community-level flowering in the Australian alpine and sub-alpine zone is highly temporarily restricted and is characterised by a short mean flowering period (Stephens et al. 2022). However, species-level phenological characteristics and phenological responsiveness to temperature of plants from the coldest places on the Australian mainland remains largely unknown (but see Gallagher et al., 2009). To address this knowledge gap, we sought to characterise the phenological temperature sensitivity of fifty-two alpine plant species using a twelve-year observational dataset of flowering in the Snowy

Mountains, Australia, and we provide the first assessment of species-specific phenological temperature sensitivities based on within- and between-year flowering observations.

Specifically, we asked:

1. How responsive to temperature are the phenological traits of flowering onset, flowering peak, and end of flowering in this restricted alpine flora?
2. Do floral traits predict phenological temperature sensitivity?
3. What is the phylogenetic structure of phenological temperature sensitivity and associated traits?

Methods

Study location

The study was located in the alpine zone of the Snowy Mountains, Australia (-36.404 S, 148.314 E). Observations of plants in flower were made along an 18-kilometre loop on the Kosciuszko Plateau starting and ending above the treeline at Charlotte Pass at elevations above 1850 m a.s.l. The route traversed all major treeless vegetation communities of the Kosciuszko Alpine Plateau, including heathland, grassland, tall open herbfield, snowpatch herbfield, feldmark, and bogs and fens (Costin, 2000; Venn et al., 2017). Of these vegetation communities, bogs and fens are listed as an Endangered ecological community under the federal EPBC Act (Australian Government of Climate Change, Energy, the Environment and Water, 2009), while snowpatch herbfield and feldmark are listed as Critically Endangered ecological communities under the NSW Biodiversity Conservation Act 2016 (NSW Threatened Species Scientific Committee, 2018), with climate change listed as a key threatening process for all three.

True alpine climate in the Snowy Mountains occurs in a narrow band of approximately 350 vertical meters, from the treeline at approximately 1850 m above sea level to the top of Australia's highest peak, Mount Kosciuszko, at 2228 m above sea level. Consistent with treeless alpine environments globally, the mean temperature of the warmest month is approximately 12 ºC (Bureau of Meteorology, 2026). Annual precipitation is between 1800 - 3000 mm, the majority of which falls as snow during the coldest quarter (Costin, 2000). Snow depths in winter are variable and highly dependent on aspect and slope, with an average depth of 1.3 metres on north-facing slopes at approximately 1900 metres elevation (Venn & Green, 2018). The average timing of snowmelt during the study period regularly occurred during late October (Snowy Hydro Ltd, n.d., unpublished data), however some communities (such as snow patch herbfields) are regularly covered by snow well into the Austral summer and snowmelt generally occurs there in January or February (Venn et al., 2011).

Flowering observations

During the Austral alpine growing season (September - April), frequent walks on the route were undertaken by K. G. to record which alpine plant species were flowering, each season from 2006/07 through 2016/17. For each survey, every plant species seen with an open flower along the route was classed as flowering, whereas the remaining species in the dataset were classed as not flowering. The 2017/18 season was not surveyed; observations resumed for the 2018/19 season, undertaken by C. K. and K. G. following the same quasi-systematic data collection approach. This yielded twelve surveyed seasons in total. Surveys commenced mid to late September on the first signs of snowpack ablation and were repeated throughout the snow-free period until mid-autumn. The repeat nature of the walks and route followed means that the data captures not only first and last observed flowering dates, but the entirety of the seasonal flowering distribution for each species.

Overall, 120 species were recorded during the study period equating to over 18,000 flowering observations. Species included in the final analysis were required to have six or more observations within a given season, and at least four years of observations. Recorded species names were standardised against the Australian Plant Census using the APCalign R package (Wenk et al., 2024), reconciling spelling variants and infraspecific name formats so that observations of the same taxon were pooled and matched consistently to the trait and phylogenetic data. After imposing these restrictions and omitting species with uncertain identification or flowering status, our final dataset included 52 species from 16 plant families, all of which are native dicotyledonous angiosperms (Table 1).

Climate and snow data

Temperatures that occur one to three months prior to flowering are important for phenological events across taxa (Fitter & Fitter, 2002; Miller-Rushing et al., 2008). To characterise phenological temperature sensitivity, we used mean monthly temperature for the months of August, September, October, November, and December. Temperature data were obtained from the Thredbo Automated Weather Station which is sited at 1957 metres above sea level and located approximately 8 km from the observational route (Bureau of Meteorology, 2026). Most plants in this region do not commence flowering until the surrounding snowpack has melted. Therefore, we used snow records from Spencer's Creek snow course (1830 m a.s.l.) to calculate the first snow free day for each year of the study as 'days since 1 July' (Snowy Hydro Ltd, n.d., unpublished data).

Plant traits

We accessed data of growth and dispersal traits for every native alpine plant species (n = 212) distributed on the Kosciuszko Alpine Plateau (Morgan & Venn, 2017). Plant traits from the database that we used were growth form ('herb', 'shrub'); dispersal syndrome ('animal', 'gravity', and 'wind'); and seed release height (Morgan & Venn, 2017). We compiled data on

the following traits not present in the database from the literature, expert opinion, and the National Herbarium of New South Wales' PlantNet (PlantNET, 2026): corolla colour ('white', 'yellow', 'pink', 'purple'); floral display size ('large', 'small'); flower orientation ('vertical', 'horizontal'); reproductive morphology ('unisexual', 'bisexual', 'polygamous'); and habitat ('wet', 'dry' or 'wetdry'). There are just two annual plant species present in this system, neither of which were present in the final dataset after applying data quality filters.

Seed mass, maximum vegetative plant height, and leaf mass per area (LMA) were sourced from AusTraits (Falster et al., 2021), version 7.0.0, accessed via the `austraits` R package. For each species and trait, we took the median across all matching AusTraits records (which pool multiple studies and individuals per taxon, with mixed value types such as mean, minimum, and maximum). Four species required name reconciliation against AusTraits' accepted taxonomy: *Senecio pectinatus* (recorded as *Scapisenecio pectinatus*), *Neopaxia australasica* (*Montia australasica*), and *Euphrasia collina* subsp. *glacialis* (matched at the subspecies level). *Richea continentis* has no AusTraits records at any taxonomic level; its seed mass value is retained from the original database (Morgan & Venn, 2017), and it has no plant-height or LMA value. AusTraits coverage was 51 of 52 species for seed mass, 47 of 52 for plant height, and 46 of 52 for LMA.

We also considered sourcing flower shape (cup, dome, irregular, radial, tubular) from AusTraits, but no equivalent categorical trait has adequate coverage for these species (the closest, flower perianth symmetry, covers only 6 of 52 species), so flower shape remains excluded from the trait analysis pending a manual check of its original source.

Analysis of phenological temperature sensitivity and phylogenetic data

Observation dates of flowering were converted to 'days since 1 July', taking a value between 1-365 for flowering onset, peak, and end, for each species in each year. To account for observational infrequency in our dataset, we fit flexible Weibull distributions to date-corrected observation values for each species using the PHEST package in the R computing environment (Pearse et al., 2017). Weibull distributions are typically used to estimate time to extinction and have recently been applied to phenological research to estimate the time to a phenological event (Pearse et al., 2017; Taylor, 2019). We estimated flowering onset and flowering end as the lower and upper limits of the flowering distribution, respectively, each weighted by the Weibull distribution; flowering peak was taken as the midpoint between the estimated onset and end. Within and between season observations were used to obtain a Weibull fit for the onset and end of flowering for each species, providing a more robust estimation of true event timing than raw first and last values (Pearse et al., 2017). We then modelled Weibull fit as a function of mean monthly temperature for each species to derive a temperature sensitivity coefficient.

To investigate the phenological characteristics of the study species, we derived the average flowering onset for all species across all years as days since 1 July. We then classified each species as either 'early' or 'late' depending on whether their mean onset value was higher or lower than the total mean value of 136.16. We similarly obtained mean flowering duration as the total number of days between flowering onset and flowering end for each species in each year. The mean flowering duration value of 128.20 days across all species was then used to categorise species as 'short' or 'long' flowering. We further assigned each species to a phenological response group from the signs of its onset and end temperature-sensitivity coefficients: species whose onset did not advance with warming (onset slope >= 0) were classed as showing no response; the remainder were classed by the change in flowering

duration with temperature (the difference between the end and onset coefficients, within a +/-2 days per degree C band for 'similar duration') as broadening, contracting, or shifting earlier or later at similar duration.

We used linear models to determine the month(s) that explained the majority of flowering times in this system. We modelled phenological traits (onset; peak; end) with monthly mean temperature as a fixed factor and species as a fixed factor. Model performance was assessed using AIC values and ANOVA was used to obtain p values for all models. As September and October mean temperature were the strongest predictors of flowering in temperature sensitive species, we then used modelled September and October mean temperature sensitivity coefficients for each species against the plant traits listed above. R version 4.5.3 was used for all analyses (R Core Team, 2026).

To quantify the phylogenetic signal of phenological sensitivity, we used a phylogenetic tree pruned from Smith and Brown (2018), with the matching algorithm phyndr (Pennell et al., 2016). With these tools we were able to include all 52 species in this analysis. We repeated the linear models described above including phylogeny following (Ho et al., 2018) as well as the estimated phylo-signal following (Keck et al., 2016).

Results

Phenological temperature sensitivity

Between 2000 and 2017, October mean temperature in the alpine zone of the Snowy Mountains increased on average by approximately 2.4°C, from a fitted value of ~3.0°C in 2000 to ~5.4°C in 2017. This average warming occurred against a backdrop of substantial year-to-

year variability — yearly October means ranged from 1.2°C to 8.5°C (SD = 1.9°C) over this period.

Overall, 94.2% of species in our study (49 of 52) advanced their flowering onset in warmer Octobers; the remaining 3 species (*Cardamine lilacina*, *Epacris paludosa*, and *Neopaxia australasica*) showed no onset response to temperature.

Of the 52 species in our study, 40.4% (21 species) are early flowering (mean onset prior to the across-species mean onset date, ~14 November), and the remaining 59.6% (31 species) are late flowering. Mean within-season flowering duration across the study period was 128.2 days, with 36.5% (19 species) classed as long flowering and 63.5% (33 species) as short flowering. Community-level peak flowering occurred on average around 17 January. Species fell into four phenological response groups based on how their flowering duration changed with warming (Table 1, Figure 1): most species (60%) showed a broadening of flowering duration, 19% shifted earlier with a similar duration, 15% contracted, and 6% showed no response; no species shifted later at a similar duration.

October mean temperature was the strongest predictor of flowering onset (Figure 2); September mean temperature was the strongest predictor of peak flowering and flowering end. August, November, and December mean temperatures did not predict onset, peak, or end at any point (Table 2).

Table 1. The 52 study species, their phenological response group, and their onset (early/late) and duration (short/long) classes.

Species	Family	Response group	Onset	Duration

Aciphylla glacialis	*Apiaceae*	Broadening	late	short
Asperula pusilla	*Rubiaceae*	Broadening	late	short
Brachyscome nivalis	*Asteraceae*	Broadening	early	long
Brachyscome scapigera	*Asteraceae*	Broadening	late	short
Brachyscome spathulata	*Asteraceae*	Broadening	late	long
Brachyscome stolonifera	*Asteraceae*	Broadening	late	long
Celmisia costiniana	*Asteraceae*	Broadening	early	long
Coronidium scorpioides	*Asteraceae*	Broadening	late	short
Craspedia adenophora	*Asteraceae*	Broadening	late	long
Craspedia costiniana	*Asteraceae*	Broadening	late	long
Craspedia lamicola	*Asteraceae*	Broadening	late	long
Dichosciadium ranunculaceum	*Apiaceae*	Broadening	early	short
Epacris microphylla	*Ericaceae*	Broadening	early	short
Epilobium gunnianum	*Onagraceae*	Broadening	late	short
Euphrasia collina glacialis	*Orobanchaceae*	Broadening	early	long
Gentianella muelleriana	*Gentianaceae*	Broadening	late	long
Grevillea australis	*Proteaceae*	Broadening	early	short
Leptorhynchos squamatus	*Asteraceae*	Broadening	late	short
Oreomyrrhis eriopoda	*Apiaceae*	Broadening	early	short
Oreomyrrhis pulvinifica	*Apiaceae*	Broadening	early	long
Pimelea alpina	*Thymelaeaceae*	Broadening	early	short
Ranunculus anemoneus	*Ranunculaceae*	Broadening	early	long
Ranunculus graniticola	*Ranunculaceae*	Broadening	early	long
Ranunculus gunnianus	*Ranunculaceae*	Broadening	early	long
Ranunculus millanii	*Ranunculaceae*	Broadening	early	short
Ranunculus niphophilus	*Ranunculaceae*	Broadening	early	long

Senecio pinnatifolius	*Asteraceae*	Broadening	late	short
Stackhousia pulvinaris	*Stackhousiaceae*	Broadening	late	short
Stylidium montanum	*Stylidiaceae*	Broadening	late	short
Viola betonicifolia	*Violaceae*	Broadening	late	short
Wahlenbergia ceracea	*Campanulaceae*	Broadening	late	short
Epacris glacialis	*Ericaceae*	Contraction	early	short
Epacris petrophila	*Ericaceae*	Contraction	early	short
Leucochrysum alpinum	*Asteraceae*	Contraction	late	short
Microseris lanceolata	*Asteraceae*	Contraction	late	short
Prostanthera cuneata	*Lamiaceae*	Contraction	late	long
Psychrophila introloba	*Ranunculaceae*	Contraction	early	long
Richea continentis	*Ericaceae*	Contraction	late	short
Senecio gunnii	*Asteraceae*	Contraction	late	short
Acrothamnus montanus	*Ericaceae*	Earlier, similar duration	early	long
Baeckea gunniana	*Myrtaceae*	Earlier, similar duration	late	short
Brachyscome obovata	*Asteraceae*	Earlier, similar duration	late	short
Craspedia maxgrayi	*Asteraceae*	Earlier, similar duration	late	short
Ewartia nubigena	*Asteraceae*	Earlier, similar duration	late	short
Kunzea muelleri	*Myrtaceae*	Earlier, similar duration	late	short
Nematolepis ovatifolia	*Rutaceae*	Earlier, similar duration	early	short
Olearia phlogopappa	*Asteraceae*	Earlier, similar duration	late	short
Ranunculus muelleri	*Ranunculaceae*	Earlier, similar duration	early	long
Senecio pectinatus	*Asteraceae*	Earlier, similar duration	late	short
Cardamine lilacina	*Brassicaceae*	No response	late	short
Epacris paludosa	*Ericaceae*	No response	early	short
Neopaxia australasica	*Portulacaceae*	No response	late	long

Table 2. Contribution of monthly mean temperatures to flowering onset, peak, and end. Significant p-values (p = <0.05) are highlighted in bold.

	Onset		Peak		End	
Month	**F**	**p**	**F**	**p**	**F**	**p**
August	0.91	0.342	1.02	0.312	0.70	0.402
September	10.30	**0.001**	9.76	**0.002**	19.08	**0.000**
October	68.86	**0.000**	1.67	0.197	0.95	0.329
November	0.18	0.673	0.14	0.709	0.08	0.773
December	0.11	0.743	0.09	0.764	0.06	0.814

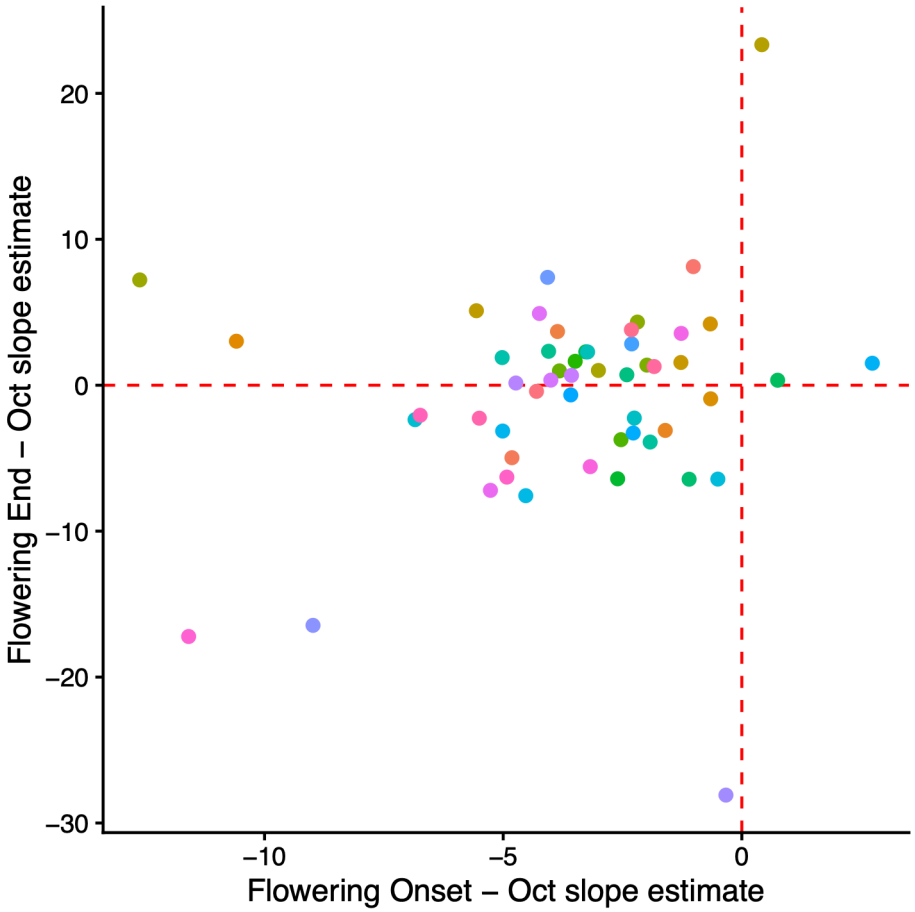
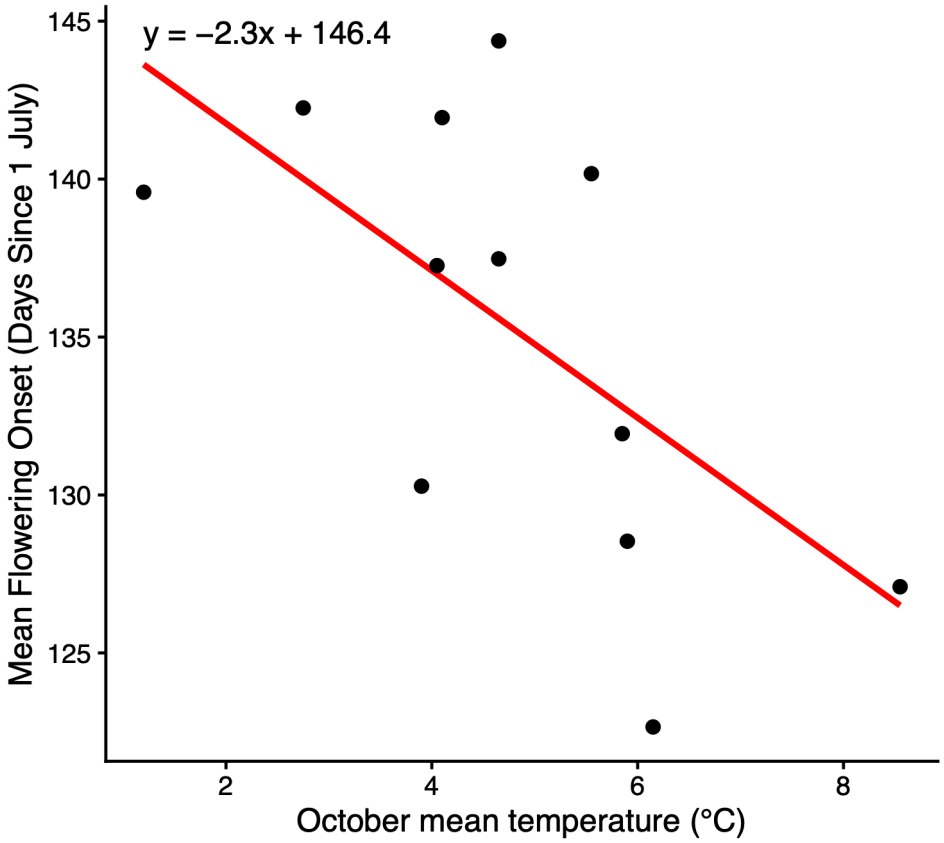


Figure 1. Per-species October flowering-end slope vs. October flowering-onset slope (days/°C). Both axes use the same October coefficients as the response-group classification in Table 1, so each species' position corresponds directly to its assigned group.



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306 Figure 2. Yearly mean flowering onset (days since 1 July) against October mean temperature,

307 with the linear fit. Points represent mean values for a single year (n = 12).

308 **Phylogeny**

309 Phylogenetic signal was weak for temperature sensitivity at every phase. Pagel's lambda,

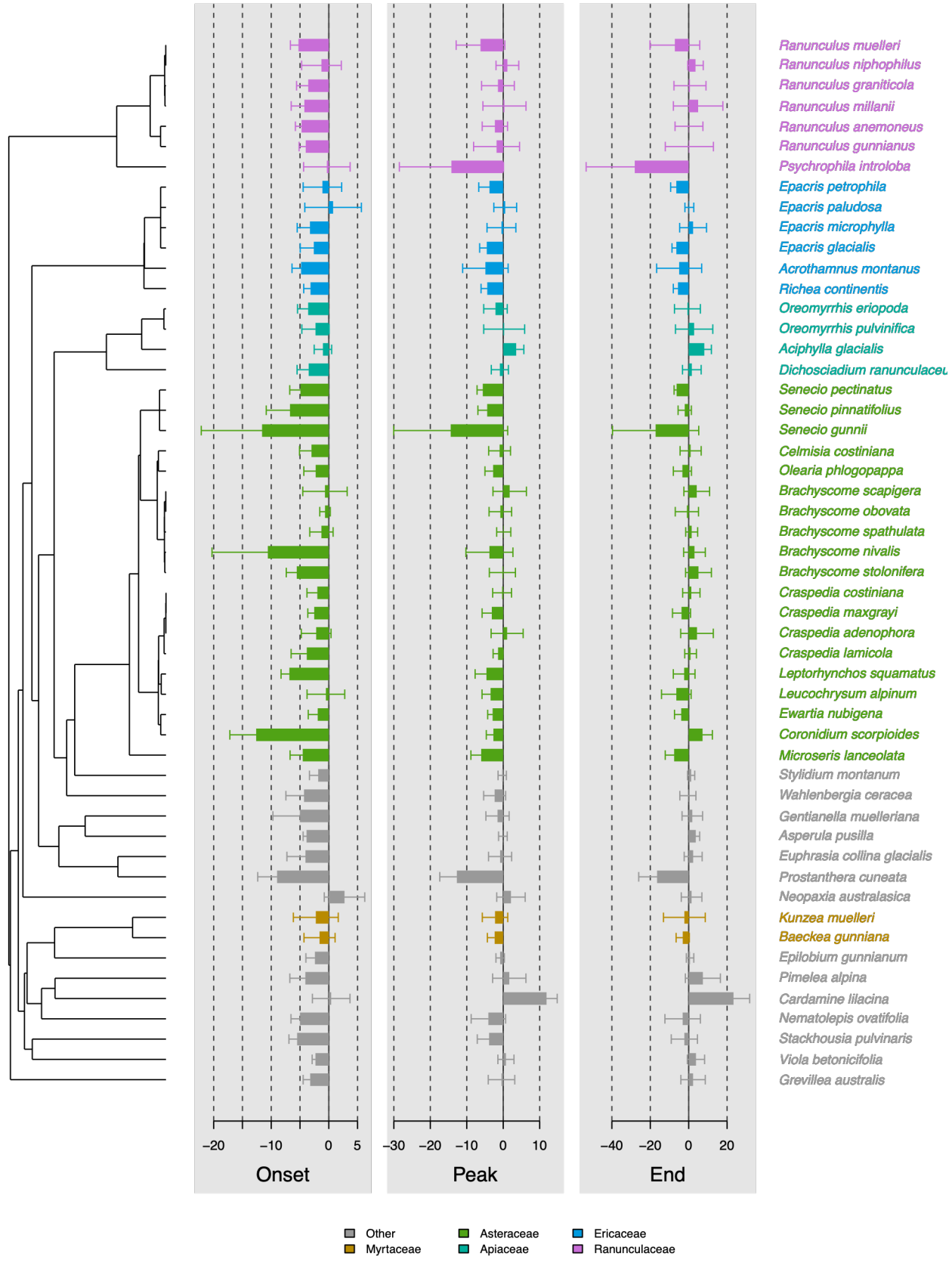
310 Blomberg's K and K*, Moran's I, and Cmean were all non-significant at onset, peak, and end

311 (Table 3, Figure 3).

312

313 Table 3. Phylogenetic signal of temperature sensitivity, by flowering phase.

Statistic	Value	P
Onset		
Cmean	0.075	0.149
Moran's I	0.016	0.209
Blomberg's K	0.023	0.060
Blomberg's K*	0.025	0.071
Pagel's lambda	<0.001	1.000
Peak		
Cmean	0.063	0.191
Moran's I	-0.009	0.402
Blomberg's K	0.004	0.479
Blomberg's K*	0.005	0.493
Pagel's lambda	0.759	0.263
End		
Cmean	0.042	0.226
Moran's I	-0.017	0.491
Blomberg's K	0.004	0.499
Blomberg's K*	0.005	0.509
Pagel's lambda	0.777	0.330



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315 Figure 3. Phylogeny of each species in the study and their phenological responsiveness to

316 October mean temperature at flowering onset, peak and end.

Plant traits

We tested six categorical and four continuous traits against temperature sensitivity at each phase, using an omnibus test for each trait-phase combination: an ANOVA F-test for categorical traits, and the trait's own slope for continuous traits (Table 4). Given the weak phylogenetic signal above, we also fit each model under a phylogenetic correction (`model = "lambda"`); the two rarely disagreed.

Habitat type was associated with onset sensitivity (P = 0.022): drier-habitat species advanced flowering about twice as fast as wetter-habitat species (Table 5). This weakened to a marginal effect at peak (P = 0.071) and was absent at end (P = 0.172).

Corolla colour was not associated with onset sensitivity (P = 0.232), but was with peak (P = 0.033): yellow- and white-flowered species advanced peak flowering more than pink- or purple-flowered species. The effect was marginal at end (P = 0.050), where pink-flowered species tended to delay rather than advance.

Seed release height was not associated with onset sensitivity (P = 0.450), but taller release heights predicted a stronger advance at both peak (P = 0.027) and end (P = 0.026).

Dispersal syndrome, growth form, reproductive morphology, and flower orientation were not associated with sensitivity at any phase (lowest P = 0.058, for growth form at end; Table 4), nor were seed mass, plant height, or leaf mass per area — three continuous traits newly sourced from AusTraits (lowest P = 0.210, for leaf mass per area at peak; see Methods). Phylogenetic correction did not change any of these results. Flower shape was not included in the trait analysis (see Methods).

342 Table 4. Omnibus test of whether each trait explains variation in October temperature sensitivity, without (p) and with (+phy p) phylogeny.

		Onset			Peak			End		
Trait	**df**	**Onset est.**	**Onset p**	**Onset +phy p**	**Peak est.**	**Peak p**	**Peak +phy p**	**End est.**	**End p**	**End +phy p**
Habitat type	2	NA	**0.022**	**0.018**	NA	0.071	0.119	NA	0.172	0.284
Corolla colour	3	NA	0.232	0.204	NA	**0.033**	**0.044**	NA	0.050	0.059
Dispersal syndrome	2	NA	0.393	0.372	NA	0.888	0.715	NA	0.988	0.363
Growth form	1	NA	0.533	0.522	NA	0.310	0.134	NA	0.156	0.058
Reproductive morphology	2	NA	0.859	0.851	NA	0.248	0.190	NA	0.206	0.190
Flower orientation	1	NA	0.510	0.499	NA	0.428	0.456	NA	0.522	0.564
Seed release height	1	-1.05	0.450	0.450	-4.27	**0.027**	**0.024**	-7.49	**0.026**	**0.033**
Seed mass	1	-0.03	0.868	0.868	0.06	0.814	0.760	0.16	0.737	0.899
Plant height	1	-0.07	0.951	0.951	-0.91	0.560	0.588	-1.76	0.521	0.562
Leaf mass per area	1	-0.01	0.319	0.319	-0.01	0.324	0.210	-0.02	0.467	0.822

343

344 Table 5. Per-category October temperature-sensitivity estimates (days/°C; negative = earlier
345 with warming), for direction and magnitude only.

Level	Onset	Peak	End
Habitat type			
Dry	-4.97	-4.06	-3.15
Wet	-2.12	-1.63	-1.14
Wet-dry	-3.38	-1.06	1.25
Corolla colour			
Pink	-2.35	2.46	7.28
Purple	-2.63	-0.49	1.65
White	-3.10	-2.39	-1.68
Yellow	-4.63	-3.33	-2.03
Dispersal syndrome			
Animal	-3.99	-2.17	-0.36
Gravity	-3.04	-1.91	-0.78
Wind	-4.22	-2.54	-0.87
Growth form			
Herb	-3.68	-1.78	0.11
Shrub	-3.11	-3.10	-3.09
Reproductive morphology			
Bisexual	-3.55	-2.48	-1.41
Polygamous	-3.75	-0.58	2.59
Unisexual	-2.44	1.73	5.90
Flower orientation			
Horizontal	-4.35	-3.54	-2.73
Vertical	-3.44	-1.99	-0.54

Discussion

Three results stand out from this study of the largely endemic, spatially restricted flora of the Australian Alps. First, flowering phenology here is overwhelmingly temperature-sensitive; 94% of species (49 of 52) advanced their onset of flowering with warmer springs, and only three failed to respond at all. Second, the dominant response was not a simple shift but an expansion of the flowering season; most species (60%, 31 of 52) began flowering earlier and continued for longer. Third, identifying which species had this sensitivity was largely unpredictable; it carried little phylogenetic signal, and of ten functional traits tested, only habitat type and corolla colour were associated with it. Together these results suggest that spring warming will lengthen and reshape the flowering season for most of this alpine flora while only leaving a few behind, with consequences for how these plants overlap with their pollinators. Neither ancestry nor the traits routinely measured by researchers will identify those few in advance.

We classified each species into one of five possible response groups, defined by how flowering duration changes with warming: (1) expansion of the temporal niche (broadening), (2) an earlier shift at similar duration, (3) a later shift at similar duration, (4) contraction of the temporal niche, and (5) no response. Of these, four were observed in this study: 60% of species (31 of 52) showed a broadening response, 19% (10) shifted earlier at a similar duration, 15% (8) contracted, and 6% (3) showed no response. No species shifted later at a similar duration (Group 3, 0 species).

The prevalence of broadening has clear implications for plant–pollinator interactions. A phenological niche expansion of this kind may improve temporal overlap with pollinators, buffering these species against mismatch whether their pollinators are themselves temperature-sensitive or not. The temperature-insensitive species (Group 5) are the more

concerning case. As their pollinators advance with warming, these plants may be left flowering out of phase, warranting closer phenological study and, potentially, additional conservation attention. An important next step is to determine whether a potential pollination mismatch translates to demographic outcomes such as reduced output of viable seed and population decline. Evidence for such impacts should precede manipulative actions such as supplementary cross-pollination or ex- situ collections and propagation.

Temperature sensitivity and flowering phenology

The majority of long-term observational data are from well-studied Northern Hemisphere systems, creating a global bias in known phenological responses to temperature (Prevéy et al., 2019). While there are many shared genera between Southern and Northern Hemisphere alpine floras (e.g. fleabanes, *Erigeron*; eyebrights, *Euphrasia*; buttercups, *Ranunculus*) (Venn et al., 2017), extrapolation to unstudied taxa can be problematic (Lord, 2008).

Our results clearly show that ambient temperatures in early spring are important for flowering phenology in Australian alpine plants. October mean temperature was the strongest predictor of flowering onset, and September mean temperature was the strongest predictor of peak flowering and flowering end (Table 2). The relative importance of mean temperatures two to three months prior to event timing (Austral September and October) agrees with previous studies of phenological temperature sensitivity in high elevation plants elsewhere (D. W. Inouye, 2008; D. W. Inouye & Wielgolaski, 2013; Vorkauf et al., 2021). For example, the timing of flowering in several species in a sub-alpine meadow in the Rocky Mountains, Colorado, was strongly affected by snowmelt date and accumulated temperature since then (D. W. Inouye, 2008). In our study area, October temperature is likely to be more strongly linked to flowering onset than September temperature due to the "zero-curtain" effect, whereby latent heat maintains soil temperatures near 0°C during snow and soil thaw (Outcalt

et al., 1990). As ice in the soil melts, energy is absorbed by the phase change rather than warming the soil, keeping the ground and plant microenvironment close to 0°C even after visible snow has disappeared. In the Australian Snowy Mountains, September snow cover may therefore decouple air and soil temperatures until all snow and frozen soil have thawed, potentially explaining why October air temperatures better predict flowering than September temperatures. This reinforces the interaction between early spring temperature, snowmelt timing, and phenological events in alpine ecosystems. Flower onset may also be impacted by temperatures in March, April or May: some plants pre-form their flower buds late in the growing season to prime them to flower early in the next snow-free season (Körner, 2021). Favourable conditions allow plants to enter the winter with nearly fully formed buds (Körner, 2021), however, cooler temperatures later in the growing season may inhibit complete bud formation. This could lead to a lag in flowering onset the following growing season, as plants need to complete bud formation after snowmelt.

A widening of the community-level phenological season appears to be evident in our finding that most temperature-sensitive species start flowering earlier and finish flowering later under warmer spring temperatures. Expansion of the flowering season has been reported in subalpine environments of the Colorado Rocky Mountains (CaraDonna et al., 2014). However, this is contrary to global trends of tundra flowering phenology with climate warming, where a contraction of the phenological season is more frequently detected (Prevéy et al., 2019), with the advancing phenology of late-flowering species driving this seasonal contraction, while early-flowering species are largely constrained by late-season freezing events and snowpack (Prevéy et al., 2019). While some species may indeed have the capacity to phenologically track warmer spring temperatures, alpine plants may experience strong selection against flowering too early due to the heightened risk of frost damage (D. W. Inouye, 2008; Ladinig et al., 2013; Prevéy et al., 2019). This is a potential biogeographical explanation for our contrasting results.

423 Among species that advance their onset with warming (49 of 52), the magnitude of advance
424 ranges from approximately 0.3 to 12.6 days per degree (median ~3.5 days/°C), and thus at
425 least some plants of the Australian Alps appear to be capable of occupying a marginally earlier
426 phenological niche.

427 **Flowering-time temperature sensitivity and phylogeny**

428 Our finding that flowering onset in the majority of species closely tracks spring temperature is
429 indicative of phenological plasticity. Species which phenologically track seasonal
430 temperatures may be more likely to persist in-situ under warming than those that are
431 phenologically non-responsive (Willis et al., 2008). Repeat surveys of historical floristic
432 records in a temperate climate have shown that flowering-time temperature responses were
433 strongly correlated with changes in species abundance over a period of approximately 150
434 years; a decrease in abundance in the flora observed in the study was most pronounced in
435 species with weak flowering-time temperature responses, with closely related species more
436 likely to respond similarly to temperature than are less closely related species.
437 For the most part, phenology is not related to ancestry. Phylogenetic signal of phenological
438 temperature sensitivity itself was weak in our data (Table 3). Trait associations with
439 sensitivity were similarly mostly independent of phylogeny: of the ten traits tested, only
440 habitat type (at flowering onset) and corolla colour (at peak) were associated with
441 temperature sensitivity, and both relationships were essentially unchanged by a phylogenetic
442 correction (Table 4). Drier-habitat and yellow/white-flowered species are evidently more
443 sensitive to temperature, not merely sharing that sensitivity by common descent. Dispersal
444 syndrome, growth form, reproductive morphology, flower orientation, seed mass, plant height
445 and leaf mass per area were not associated with sensitivity at any phase. That so few of the
446 standard functional traits predict phenological sensitivity is itself informative: it suggests that

sensitivity cannot be readily extrapolated to unmeasured species from the trait data most commonly available for them, and that direct phenological monitoring remains necessary.

Because that inference depends on how our species were sampled, the phylogenetic structure of the dataset warrants comment. As with all site-based, rather than clade-based, datasets, family representation in our dataset is uneven, and the distribution of species and families closely reflects the actual dicot flora of the study system (Figure 3). Speciose families in our dataset mirror speciose families in the environment (e.g. *Apiaceae*, *Asteraceae*, *Ranunculaceae*), which is also characterised by a high proportion of families with just a single or few representative species (e.g. *Brassicaceae*, *Portulacaceae*). Our sampling is therefore phylogenetically representative of the flora it describes, even though it is not phylogenetically balanced. The weak phylogenetic signal we report is thus better read as a property of this alpine flora than as an artefact of a skewed sample of it.

Our study suggests that much of the alpine flora of Australia may have the capacity to phenologically adjust in-situ to climate warming. However, ongoing reductions in snow cover and associated exposure to light and diurnal fluctuations in soil temperature in winter and early spring, coupled with more frequent and intense summer droughts (Fiddes et al., 2015; Pepler et al., 2015; Sánchez-Bayo & Green, 2013), may complicate the shifts shown here. These data suggest that flowering duration in these species will likely lengthen with climate warming in the future. In the 1979 edition of *Kosciusko Alpine Flora*, Costin et al. (1979) comment that "many species have their peak of flowering in late January and early February (e.g. *Celmisia*, *Craspedia*, *Euphrasia*)." Our findings indicate that peak flowering in these herbfield genera now spans early January to mid-February.

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Declaration of generative AI use

The authors confirm that the originality and accuracy of the manuscript have been reviewed and verified. Claude (Anthropic; Claude Code v2.1.218 running Claude Opus 4.8 with high effort) was used to refine writing clarity, assist with coding, identify and resolve bugs in code used for data analysis and figure generation, and to improve the ability for others to replicate the analysis. The authors have reviewed Claude's terms of use and confirm that its use complies with the journal's publication requirements. The authors take full responsibility for the integrity and accuracy of the whole content, including references.

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