

Climate variation influences flowering time overlap in a pair of hybridizing montane plants

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ABSTRACT.—Flowering time is sensitive to climatic conditions and has been a frequent focus of climate change research, yet the implications of phenological shifts for hybridization within plant communities have seldom been explored. Reproductive overlap between interfertile species is a key requirement for the production of hybrid (inter-species) offspring, and climate change may influence the opportunities for hybrid production through changes to species' flowering time, duration, and overlap with other species. To test how climate variation influences flowering overlap between hybridizing species, we analyzed 45 years of flowering phenology data on 2 common plants in the Rocky Mountains of Colorado that are known to produce hybrids (*Potentilla pulcherrima* and *Potentilla hippiana*, family Rosaceae). We estimated flowering overlap from flowering distributions in 2 ways that focus on how similar species are in terms of flowering time ("symmetric overlap") or relative floral abundance across the season ("relative overlap"). We found that the 2 species had similar phenological responses to most climate variables. Both flowered earlier in years with warm, dry growing seasons preceded by earlier snowmelt and winters with less snow, and later in cool, wet growing seasons with later snowmelt after winters with heavy snowfall. Precipitation was the best predictor of flowering time overlap. In wetter years, both species flowered later and longer, and reached peak flowering date at a more similar time in the growing season. While our results suggest that precipitation patterns influence the extent of flowering overlap between these 2 species in any given growing season, precipitation has not consistently increased or decreased in this region over the past 45 years, and therefore we do not see a consistent signature of global climate change on flowering overlap. Finally, we found that even though temperature was an important predictor of flowering phenology within each species, it was not a major driver of overlap between species, emphasizing that data on individual species responses cannot necessarily predict how climate change will affect species interactions.

RESUMEN.—El tiempo de floración depende de las condiciones climáticas y con frecuencia ha sido el enfoque de investigación sobre el cambio climático. Sin embargo, rara vez se han explorado las implicaciones de los cambios fenológicos para la hibridación dentro de las comunidades de plantas. La superposición reproductiva entre especies interfértiles es un requisito clave para la producción de descendientes híbridos (entre especies), y el cambio climático puede influir en la oportunidad de producir híbridos a través de cambios en el tiempo de floración de las especies, la duración y la superposición con otras especies. Para evaluar cómo la variación climática influye en la superposición de la floración entre las especies que hibridan, analizamos 45 años de información de fenología de floración de dos plantas comunes de las Montañas Rocosas de Colorado que se sabe que producen híbridos (*Potentilla pulcherrima* y *Potentilla hippiana*, familia Rosaceae). Estimamos la superposición de la floración a partir de las distribuciones de la floración de dos maneras, ambas se enfocan en qué tan similares son las especies en cuanto al tiempo de floración ("superposición simétrica") o abundancia floral relativa a lo largo de la temporada ("superposición relativa"). Encontramos que las dos especies presentaron respuestas fenológicas similares a la mayoría de las variables climáticas. Ambas florecieron tempranamente en años con temporadas de crecimiento cálidas y secas, precedidas por deshielo e inviernos con menos nieve, y más tarde en temporadas de crecimiento frías y húmedas con deshielo tardío después de inviernos con fuertes nevadas. La precipitación fue el mejor indicador de la superposición del tiempo de floración. En años más húmedos, ambas especies florecieron más tarde y durante más tiempo, y alcanzaron la fecha máxima de floración en un momento similar durante la temporada de crecimiento. A pesar de que, nuestros resultados sugieren que los patrones de precipitación influyen en el grado de superposición de la floración entre estas dos especies en cualquier temporada de crecimiento, la precipitación no ha aumentado o disminuido de manera constante en esta región durante los últimos 45 años, por lo tanto, no es posible percibir un patrón constante del cambio climático global en la superposición de floración. Finalmente, encontramos que, aunque la temperatura fue un indicador importante de la fenología de la floración dentro de cada especie, no fue el principal factor de superposición entre especies, enfatizando que los datos acerca de las respuestas de especies individuales no necesariamente pueden predecir cómo el cambio climático afectará las interacciones de las especies.

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Climate change has altered the phenology—the timing of key life events—for a wide array of plant and animal species (Cotton 2003, Edwards and Richardson 2004, Moyes et al. 2011, Van Asch et al. 2013, CaraDonna et al. 2014). These phenological shifts are having important ecological impacts, such as decoupling predator-prey interactions (Yang and Rudolf 2010), influencing offspring development (Richter-Boix et al. 2014), and changing survival rates and fitness (Cleland et al. 2012). In flowering plants, the timing of reproduction can have particularly important implications for reproductive success (Gezon et al. 2016). While many species are flowering earlier with warming, there is substantial variation among species in the magnitude and even direction of responses to climatic conditions, particularly in taxa that flower later in the growing season (e.g., Sherry et al. 2007, Cook et al. 2012, Wadgymar et al. 2018). This variation in species' phenological responses to changing climate will have ecological and evolutionary impacts at the community level, including the possibility of altered hybridization dynamics between closely related species (Chunco 2014).

There are several criteria for successful hybridization between co-occurring plant taxa, including genetic compatibility and shared pollinators, but a critical first step is overlap in reproductive timing, which directly shapes opportunities for pollen flow between co-occurring species (Van Oppen et al. 2002, Coyne and Orr 2004, Inskeep et al. 2021). Asynchronous flowering can promote divergence and even speciation among lineages (Savolainen et al. 2006), while flowering overlap creates opportunities for genetic exchange and the dissolution of species barriers (Miller-Rushing et al. 2007, Pascarella 2007, Chunco 2014). One of the most likely mechanisms by which climate change will influence hybridization is through its effects on the overlap of reproductive timing among taxa (Sherry et al. 2007, Thomasset et al. 2011, Walter et al. 2017). For example, climate change has been predicted to homogenize environments, removing ecological barriers between species and thus facilitating hybridization (Anderson and Stebbins 1954, Chunco 2014). Shifts in hybridization opportunities can have important effects on ecological and evolutionary dynamics of co-occurring taxa. Hybrids can

have substantial but contrasting consequences for the long-term persistence of parent lineages; for example, hybrids can compete with their parent taxa for resources or reproductive opportunities (Levin et al. 1996) or provide a reservoir of adaptive genetic variation (Lexer et al. 2003). Despite the prevalence of hybrids in nature and their potentially important ecological consequences (Mallet 2005), we know relatively little about how specific environmental conditions—and shifts in these conditions due to climate change—can mediate hybrid formation. This limits our ability to predict how climate change will affect species' barriers and community composition.

Predicting how climate change will impact overlap in flowering times between species requires understanding how species' flowering windows change with climate (e.g., Price and Waser 1998, Franks et al. 2007, Sherry et al. 2007). A study of 60 plant species found that roughly the same proportion of species pairs showed increases or decreases in flowering overlap over 43 years (CaraDonna et al. 2014), although this study did not focus on hybridizing species. Since interfertile species are typically close relatives, potentially hybridizing species could share similar phenological responses to climate (e.g., Miller-Rushing et al. 2007), such that their extent of flowering window overlap remains consistent despite climate change. Conversely, closely related species could have differing responses due to habitat differences, neutral differences in phenology, or even because selection has directly favored divergent reproductive phenologies to minimize the potential for hybrid formation if hybrids are maladaptive (Silvertown et al. 2005). Under this scenario, we may expect potentially hybridizing species to respond differently to changing climate conditions. Together, the different possible responses of species' reproductive phenology to climate change suggest a variety of possible outcomes for hybridization.

Determining whether potentially hybridizing species will likely shift in tandem, or in ways that alter their reproductive overlap, hinges upon identifying phenological drivers. In temperate regions, the lengths of growing seasons have been increasing with warmer temperatures, earlier snowmelt, and delayed autumn frosts (Price and Waser 1998, Menzel et al. 2006, CaraDonna et al. 2014). Mountainous

environments have experienced particularly rapid climate change, and the rich body of botanical research in the Colorado Rocky Mountains (USA) has shown that montane plant communities are sensitive to changes in temperature, moisture, and snowpack (Harte and Shaw 1995, Panetta et al. 2018, Campbell 2019). Warm temperatures and early snowmelt have been linked to early flowering onset in mountain plant species (Price and Waser 1998, Fitter and Fitter 2002, Inouye and Wielgolaski 2013). However, early-flowering plants in the mountains may avoid late-season drought (e.g., Stinson 2004) but may also face increased risk of damage from spring frost events (Inouye 2008), especially if early snowmelt arises from low snowpack rather than warm spring conditions. Cool temperatures also slow development, such that species whose emergence tracks snowmelt may still reproduce at times similar to later-season species (Huelber et al. 2006, Inouye and Wielgolaski 2013). At the community level, climate change has led to longer flowering periods and increased flowering overlap among species in the Colorado Rocky Mountains (Price and Waser 1998). Assessing the climate responses of specific flowering stages will clarify the conditions under which each species' flowering window expands or contracts and influences opportunities for flowering overlap between parent species.

Here, we evaluated the effects of climate change on flowering overlap by analyzing the reproductive phenology of 2 common, hybridizing taxa: *Potentilla pulcherrima* and *Potentilla hippiana* (cinquefoils, in family Rosaceae). *Potentilla* is diverse and abundant across habitats in the Colorado Rocky Mountains (Weber and Wittmann 2012, Ackerfield 2015). Although hybridization has been repeatedly documented in *Potentilla* (Clausen et al. 1947, Eriksen and Töpel 2006, Weber and Wittmann 2012, Ackerfield 2015), hybrids have often been treated as a nuisance for species identification rather than an interesting context for exploring the ecological drivers of interspecific gene flow. In this study, we coupled 45 years of phenological data with climate records to test how the conditions associated with climate change—less winter snowfall, earlier snowmelt, and warmer, drier growing seasons—alter reproductive overlap between parent *Potentilla*

species through species-specific changes in flowering time and duration. We assessed (1) how flowering time responds to climatic variation over the 45-year period; (2) whether the 2 focal species, and different flowering time stages, show similar responses to environmental drivers; (3) which climatic conditions predict flowering-time overlap between *Potentilla* species, and how changes in these conditions are likely to alter overlap into the future; and (4) how phenologically relevant environmental variables, and flowering overlap, are changing over time in this region.

METHODS

Study System

The focal species, *Potentilla pulcherrima* Lehm. and *P. hippiana* (var. *hippiana* Lehm.), are well suited for evaluating the effects of climate change on flowering windows and overlap in hybridizing plant taxa. They are 2 of the most common and widespread *Potentilla* species in the Colorado Rocky Mountains, where *P. pulcherrima* occurs at higher elevations and in moist meadows, and *P. hippiana* occurs at lower elevations and on dry slopes (Ackerfield 2015). *Potentilla pulcherrima* is the taller of the two and has palmate leaves (Ackerfield 2015). *Potentilla hippiana* has pinnate leaves, which tend to have more leaflets than leaves of *P. pulcherrima*. Floral morphology of the 2 parent species is nearly identical: all *Potentilla* species have 5 petals arranged as open flowers and are visited by a wide range of insect pollinators (Alarcón et al. 2008, Burkle and Irwin 2009), including numerous bee genera, hoverflies, beetles, and butterflies (McIver and Erickson 2012). Up to 43 different pollinator species have been recorded visiting *P. pulcherrima* within a single summer (Bain et al. 2021), but the pollinators visiting *P. hippiana* plants have not been carefully surveyed. Given that these 2 *Potentilla* species broadly co-occur and have similar flowers that attract generalist pollinators, greater overlap in their flowering windows can increase opportunities for cross-pollination via any pollinators that indiscriminately visit both species. Hybrids between *P. hippiana* and *P. pulcherrima* are so common that they are identified in the taxonomic key of Colorado *Potentilla* (Ackerfield 2015). The frequency of hybrids where parents co-occur

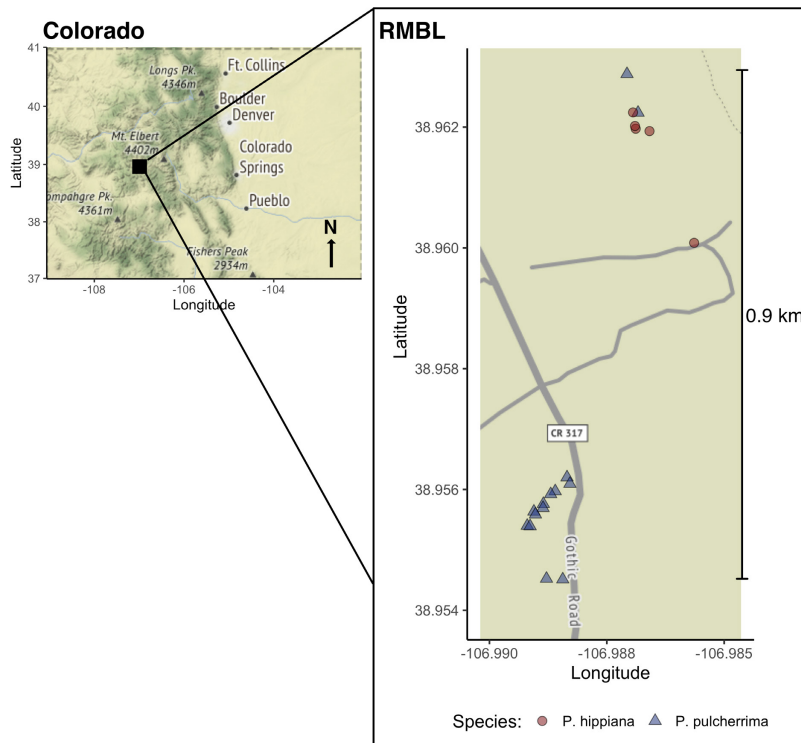


Fig. 1. Map of the study region in the West Elk Mountains of Colorado with inset showing the Rocky Mountain Biological Laboratory (RMBL) phenology plots that contain *Potentilla*. All plots are at ~2900 m (2865–2973 m) elevation and within 1 km of each other. Red circles identify plots that had flowering *P. hippiana*, whereas blue triangles identify plots that had flowering *P. pulcherrima*. Map layout created with package ‘ggmap’ (Kahle and Wickham 2013) in R.

suggests that the parent species are reasonably genetically compatible (Weber and Wittmann 2012; Carscadden personal observation). However, climate responses of species that flower late in the summer, like our focal *Potentilla*, are generally less resolved compared to early-season species (e.g., Price and Waser 1998, Rice et al. 2021). Reproductive phenology of *P. pulcherrima* shifts with snowmelt date, moisture, and temperature (Price and Waser 1998, Stinson 2004). The phenology of *P. hippiana* has been much less studied but appears from past work to be less sensitive to climate variation (CaraDonna et al. 2014).

Long-term Phenological Monitoring

We use a 45-year (1975–2019) data set on wildflower phenology collected in the West Elk Mountains (in the southern Rocky Mountains) around the Rocky Mountain Biological Laboratory (RMBL) near Gothic, Colorado (Inouye et al. 2020), to evaluate how climate variation influences flowering overlap between

P. pulcherrima and *P. hippiana*. Every other day for each growing season (snowmelt to the end of the flowering period), researchers counted the number of flowers for each of 135 species in 34 permanent plots placed in natural communities. We used data from 19 of those plots; 14 of these plots contained flowering *P. pulcherrima* and 5 contained flowering *P. hippiana* (Fig. 1). Data were not collected in 1978 and 1990. Focal plots are situated within the same drainage and all within 1 km (Fig. 1), and they span the rocky and wet meadow habitats characteristic of the focal *Potentilla*. Although hybrids were not recorded in the permanent plots, they have been identified at multiple RMBL sites (Carscadden personal observation; Carscadden 2021) and documented in herbarium specimens from the area (Gunnison County; Intermountain Region Herbarium Network 2021).

Using these phenological data, we characterized flowering time within each plot every year by identifying 3 flowering stages: the

TABLE 1. Landscape-scale climate variables (1975–2019) used to predict *Potentilla* flowering phenology. PC1 and PC2 indicate loadings of climate variables on major principal component axes.

Climate variable	Measurement	Source	PC1	PC2
Average growing season temperature	Averaged minimum and maximum temperatures (°C) across all days in May, June, July	PRISM	0.51	0.23
Average growing season precipitation	Averaged precipitation (mm) across all days in May, June, July	PRISM	−0.41	−0.78
Snowmelt date	Day of year the ground was snow free	RMBL weather station	−0.55	0.37
Total winter snowfall	Cumulative snowfall (cm) (e.g., for 2019, all snow in the 2018–2019 winter)	RMBL weather station	−0.52	0.45

start, peak (date with maximum flowers), and end of flowering. With this approach, we can examine changes to flowering duration for each species and overlap between species. Previous work on a broader range of species from the study site found that each flowering stage responded independently to climate (CaraDonna et al. 2014). Therefore, considering all 3 flowering stages, rather than focusing on flowering start, is necessary for predicting how climate change will alter reproductive overlap among species.

Climate Data

We used long-term climate records to test whether climate variation explains flowering phenology and phenological overlap between *P. pulcherrima* and *P. hippiana* (Fig. 1B). We obtained data on total winter snowfall and the annual timing of snowmelt from a RMBL weather station (1975–2019; Table 1; Barr 2019). This local station did not record spring and summer climate data prior to 2000, so we used data from a PRISM model interpolated to the RMBL site to characterize growing season temperature and precipitation (Table 1; PRISM Climate Group 2019). PRISM temperature estimates were highly correlated with climate records from 2 SNOTEL stations near RMBL (see Supplementary Material Fig. S1.1; Pearson's correlation $r = 0.97$, $P < 0.001$). In this region, snow melts in mid-May on average, and *Potentilla* reaches peak flower in July, so we quantified the growing season temperature and precipitation as the average of May, June, and July values for each year of the phenology data set.

We address the possibility that multiple climate variables together drive flowering time and overlap by using 2 composite multivariate

axes (principal components) that account for correlations among 4 climate variables (Supplementary Material Figs. S2.1, S2.2). The first 2 PC axes combined explained 87.49% of the total variation in the climate data (PC1 explains 68.70% and PC2 explains 18.79%; Supplementary Material Fig. S2.2). All 4 climate variables load roughly equally onto PC1 (Supplementary Material Table S2.1), such that PC1 separates cool, wet, snowy years (low PC1 values) from warm, dry, less snowy years (high PC1 values). PC2 describes how precipitation is distributed across seasons within years: a low PC2 score indicates summer precipitation (i.e., a year with wetter, cooler growing seasons preceded by winters with less snowfall and earlier snowmelt), whereas years with high PC2 scores have more of their precipitation in the winter as snow (i.e., dry, warmer growing seasons with more snowfall during winter and later snowmelt; Supplementary Material Table S2.1, Fig. S2.2). All analyses of climate data were conducted in R (version 4.0.3; R Core Team 2020).

Analyses

We tested for relationships between flowering phenology and each individual climate variable to determine (1) whether climate variables (individual or composite PC axes) significantly predict the timing of the 3 flowering stages and (2) whether the relationships between climate variables and flowering phenology differ between the 2 focal species. With flowering time (day of year) as our response variable, we fit a separate global linear mixed effects model for each climate predictor. Each global model included fixed effects of climate, species, and flowering stage (a factor indicating flowering start, peak, or

end), as well as their 2- and 3-way interactions, a random intercept to account for plot structure, and a year random intercept to account for annual environmental effects unrelated to climate (using *lme4* in R; Bates et al. 2015). All climate variables were Z-scored (standardized to a mean of 0 and a standard deviation of 1) to facilitate comparisons across variables and improve model convergence. A significant climate $\times$ stage interaction could indicate that flowering windows are either expanding or contracting with climate change if flowering start and end have contrasting climate responses; therefore, when significant climate $\times$ stage interactions were detected (using *F* tests in *lmerTest*; Kuznetsova et al. 2017), we evaluated the climate responses of each stage separately using post hoc contrasts and Tukey's *P*-value adjustment for multiple comparisons. Because testing these interactions is central to addressing our questions, we limited each model to one climate variable (and its interactions with stage and species) for interpretability. We present each model result to show how each climate predictor influences flowering, and we gauge the relative importance of climate predictors (i.e., compare global models for each climate variable) using model AICc. To characterize overall differences in flowering time between *P. hippiana* and *P. pulcherrima*, we fit a model omitting climate variables (i.e., including species, stage, and their interaction as fixed effects, and plot and year as random effects).

We quantified the extent of overlap in flowering between *P. pulcherrima* and *P. hippiana* across the study region for each of the 45 years. We estimated flowering overlap in 2 complementary ways: symmetric and relative overlap. Symmetric overlap compares the empirical probability density functions for flowering times between species, which standardize across differences in the total number of flowers produced by each species. In contrast, relative overlap is calculated for each species and incorporates differences in the magnitude of floral production between species. With this approach, a large asymmetry in the number of flowers produced by each species leads to a higher overlap value for the species with fewer flowers, and a smaller overlap value for the species with more flowers. If pollen flow was purely random, the species with fewer flowers would be more

likely to receive interspecific pollen than the other co-flowering species. So, although both measures of overlap are based on comparisons of flowering time distributions, the symmetric measure focuses solely on flowering time density functions (i.e., at each point over the growing season, do the 2 species have a similar proportion of their total flowers in bloom?), while the relative measure reveals whether one species may experience swamping of conspecific pollination as a result of asymmetries in abundance or floral production between species.

To first estimate symmetric overlap, we obtained separate kernel density estimates of flowering time for each species, for each year (pooled across plots). Kernel densities are by definition scaled to unit area for each species, which eliminates differences in overall floral output by each species. We then calculated a symmetric overlap value for each year as the extent of overlap between *P. hippiana* and *P. pulcherrima* flowering kernel densities (*overlap*; Ridout and Linkie 2009). Second, relative overlap was estimated by integrating the area under a *flower_count* $\sim$ *time* curve (for each year, pooled across plots) for each species, calculating the shared area under the curves, and then dividing the shared area by the area of each species' curve. Specifically, we approximated each area using Riemann summation:

$$\sum_{i=0}^{n-1} \Delta x \cdot f(x_i),$$

where n is the number of intervals, Δx is the interval width (here, 1 day), and $f(x_i)$ is the number of flowers present on day i . With this approach, each species gets a separate estimate of relative overlap each year, and a species whose flowering window is fully engulfed in the flowering window of another species would have a relative overlap of 1 (Supplementary Material Fig. S3.1).

We tested whether annual flowering overlap values could be predicted by climate conditions by fitting separate linear models for each overlap measure and climate predictor. We used beta regression to bound predictions of overlap between 0 and 1 (package *betareg*; Grün et al. 2012), with the overlap measure as the response variable and each climate variable as a predictor variable (e.g., *overlap* $\sim$ *temperature*). Choice of link function did not

substantially influence model performance (AICc, not shown), so we used the default logit link for the mean and log link for the precision parameter (ϕ). When heteroskedasticity was detected, we modeled ϕ as a function of the predictor, which allows variability to scale with the predictor. Relative overlap estimates included values of 1, so we transformed relative overlap values to work within the (0, 1) support of the beta distribution (Grün et al. 2012):

$$\text{transformed_overlap} = \frac{\text{relative_overlap} \times [n_{\text{obs}} - 1] + 0.5}{n_{\text{obs}}},$$

where n_{obs} is the number of observations (45 years, here). Predicted values of relative overlap were back-transformed for plotting.

Lastly, to assess whether phenologically relevant climate variables and flowering overlap have changed directionally through time, we fit separate models (e.g., linear model of *temperature* ~ *year* or beta regression of *overlap* ~ *year*). We only investigated climate predictors that were found to explain significant levels of variation in flowering phenology in the analyses described above.

All analyses were conducted in R (version 4.0.3; R Core Team 2020), and we confirmed that model assumptions were met for each analysis using visual diagnostics.

RESULTS

All climate variables except PC2 were significant predictors of flowering phenology (Fig. 2, Table 2). PC1, which distinguishes wet, cool years from warm, dry years, was the best climate predictor of flowering time, followed by temperature alone (see AICc, Table 2). Flowering windows were significantly earlier in growing seasons that followed winters with low snowfall, experienced earlier snowmelt, and consisted of relatively warm and dry conditions (Fig. 2). As expected, flowering stage (i.e., the differences in timing among start, peak, and end flowering stages) explained the most variation in flowering time of all predictors in all models (>90% of the variation explained by fixed effects). Significant main effects of climate explained 16% to 77% of the remaining variation in flowering time (i.e., after accounting for the main effect of stage).

Random effects of year and plot both explained similar amounts of variation, though their relative importance varied across models. For example, differences among years explained more variation than plot in temperature, snowfall, precipitation, and PC2 models (Table 2), possibly because these climate variables are unlikely to vary much across plots (which all occur within the same region; see Fig. 1). In contrast, among-plot differences explain more variation than year in the snowmelt model (Table 2), which could reflect deviations of plots from an average snowmelt date due to microhabitat characteristics like aspect and shading.

We detected differences between *P. hippiana* and *P. pulcherrima* in the timing of different flowering stages (see species × stage interactions; Table 2) and their responses to climate variation (see climate × species interactions; Table 2). On average, *P. hippiana* has a shorter flowering window, with the start of flowering 5 days later and the end of flowering 2 days earlier than *P. pulcherrima* (Supplementary Material Fig. S4.1). The longer flowering window of *P. pulcherrima* may reflect its more mesic habitat or its occurrence across more plots (increasing the variation in flowering time across individuals and microhabitats). *Potentilla pulcherrima* was consistently more responsive to climate variation than *P. hippiana* (i.e., *P. pulcherrima* had steeper slopes for all significant climate predictors and all flowering stages; Supplementary Material Table S4.1). Each species' flowering window shifted in response to variation in snowmelt and snowfall (i.e., climate effect; Table 2) but did not substantially expand or contract (i.e., no climate × stage interactions; Table 2). However, more complex responses were observed in response to temperature, precipitation, and the PC1 climate axis (i.e., significant climate × stage interactions; Table 2). For *P. pulcherrima*, flowering end and peak were more responsive than flowering start to each of these 3 climate variables (Table 3). These findings suggest that warmer and/or drier growing seasons will lead to earlier and compressed windows for *P. pulcherrima* flowering: both the start and end of the flowering period shifted earlier, but the end by a greater amount than the beginning. Similarly, in *P. hippiana*, the end of the flowering period was more sensitive to precipitation than the

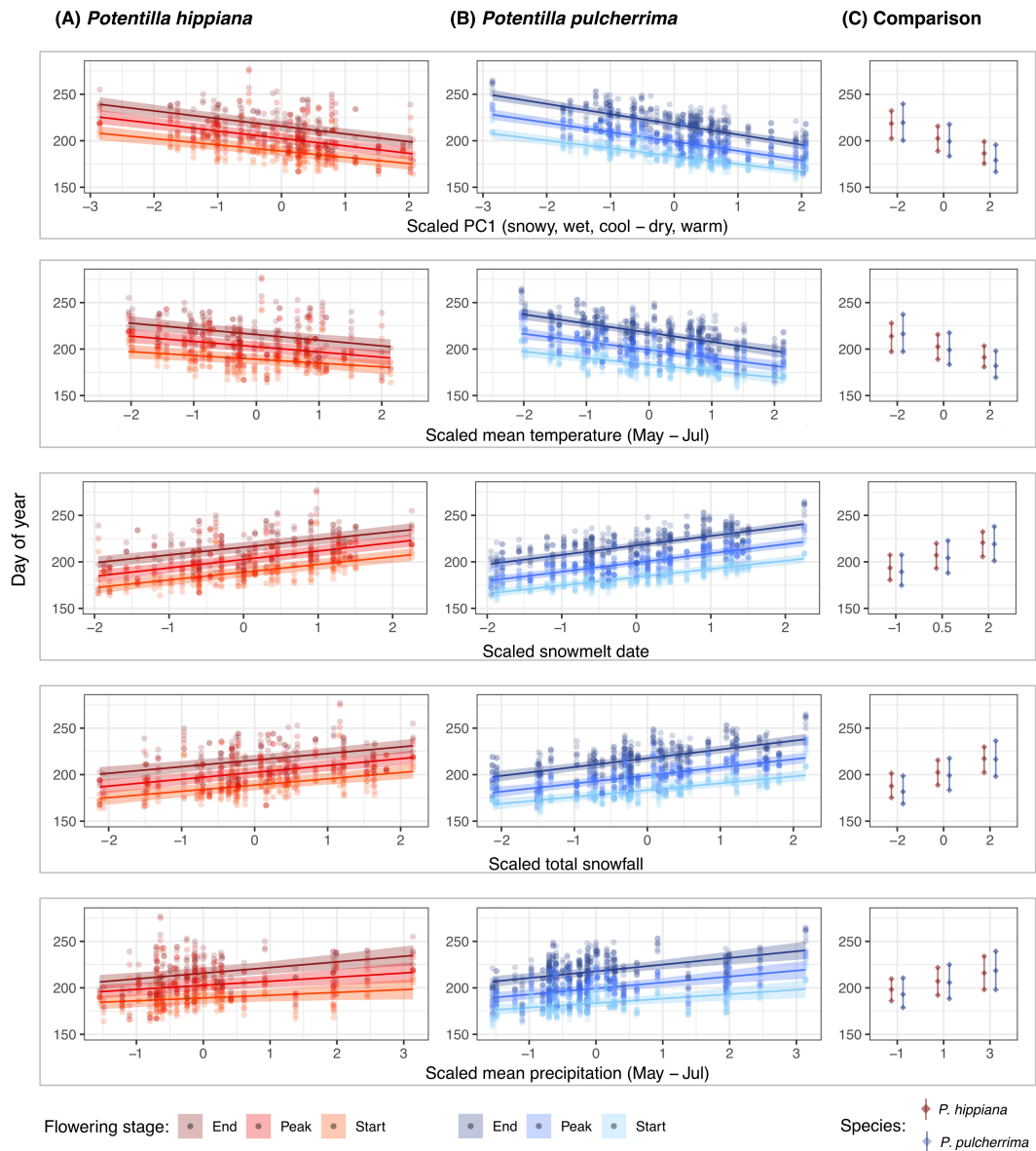


Fig. 2. Effects of climate, species, and flowering stage on flowering phenology for (A) *Potentilla hippiana* and (B) *Potentilla pulcherrima*. All the climate predictors that are shown are significant in a linear mixed model ($climate \times species \times stage + (1|plot) + (1|year)$). Points are years, and ribbons are 95% confidence intervals. (C) Comparisons of *Potentilla* flowering windows across example low, mid, and high scaled climate values. Points are predicted times for flowering start, peak, and end. Model fits were generated with package ‘*ggeffects*’ (Lüdtke 2018) in R.

beginning, shortening the flowering window in dry growing seasons (Table 3). In contrast to *P. pulcherrima*, we found no evidence that the length of the flowering window of *P. hippiana* changes predictably with temperature or PC1 (i.e., shifts in timing in response to each variable were similar across flowering stages;

Table 3). Three-way interactions between climate, species, and stage were never significant (Table 2).

Symmetric overlap in flowering between *P. pulcherrima* and *P. hippiana* significantly increased with growing season precipitation, as did model precision (i.e., symmetric overlap

TABLE 2. Model predictions for flowering time (see Fig. 2 for model visualizations). Percent variance (%Var) is calculated based on sums of squares within fixed or random effects. Degrees of freedom are shown for the numerator and denominator (ndf, ddf), estimated with Satterthwaite's approximation. *F* statistics and *P* values are shown, with significant ($\alpha = 0.05$) scaled predictors indicated in bold text. Pseudo R^2 values are estimated using the delta method in package 'MuMIn' in R (Nakagawa and Schielzeth 2013, Barto 2020). Within the tables below, the marginal R^2 for fixed effects is in the first row, while the conditional R^2 (which includes fixed and random effects) is listed below. Models are ordered by AICc, and AICc difference from the best model (AICc) is reported. Table constructed with *kableExtra* (Zhu 2020).

PC1 Model						Temperature Model					
	%Var	df	<i>F</i>	<i>P</i>	R^2		%Var	df	<i>F</i>	<i>P</i>	R^2
PC1 model–fixed effects						Temperature model–fixed effects					
pc1	5.20	1, 43	157.27	<0.001	0.64	temp	1.31	1, 42	38.87	<0.001	0.57
species	0.02	1, 16	0.52	0.48		species	0.02	1, 16	0.59	0.45	
stage	92.15	2, 1810	1393.94	<0.001		stage	94.99	2, 1810	1409.33	<0.001	
pc1:species	0.68	1, 1823	20.60	<0.001		temp:species	1.46	1, 1817	43.27	<0.001	
pc1:stage	0.45	2, 1810	6.77	<0.01		temp:stage	0.63	2, 1810	9.31	<0.001	
species:stage	1.48	2, 1810	22.39	<0.001		species:stage	1.57	2, 1810	23.29	<0.001	
pc1:species:stage	0.03	2, 1810	0.40	0.67		temp:species:stage	0.02	2, 1810	0.34	0.71	
PC1 model–random effects						Temperature model–random effects					
year	13.67				0.78	year	29.88				0.78
plot	23.86					plot	19.36				
residual	62.48					residual	50.77				
Snowmelt Model						Snowfall Model					
	%Var	df	<i>F</i>	<i>P</i>	R^2		%Var	df	<i>F</i>	<i>P</i>	R^2
Snowmelt model–fixed effects						Snowfall model–fixed effects					
melt	5.80	1, 42	173.11	<0.001	0.64	snow	2.09	1, 42	60.34	<0.001	0.59
species	0.02	1, 16	0.53	0.48		species	0.02	1, 16	0.52	0.48	
stage	92.48	2, 1810	1379.41	<0.001		stage	95.87	2, 1810	1385.09	<0.001	
melt:species	0.16	1, 1819	4.76	<0.05		snow:species	0.30	1, 1816	8.64	<0.01	
melt:stage	0.09	2, 1810	1.27	0.28		snow:stage	0.17	2, 1810	2.45	0.09	
species:stage	1.41	2, 1810	20.99	<0.001		species:stage	1.48	2, 1810	21.39	<0.001	
melt:species:stage	0.05	2, 1810	0.71	0.49		snow:species:stage	0.08	2, 1810	1.11	0.33	
Snowmelt model–random effects						Snowfall model–random effects					
year	12.92				0.77	year	25.11				0.78
plot	23.98					plot	20.78				
residual	63.10					residual	54.10				
Precipitation Model						PC2 Model					
	%Var	df	<i>F</i>	<i>P</i>	R^2		%Var	df	<i>F</i>	<i>P</i>	R^2
Precipitation model–fixed effects						PC2 model–fixed effects					
prec	0.54	1, 41	15.62	<0.001	0.50	pc2	0.02	1, 41	0.54	0.47	0.42
species	0.02	1, 16	0.53	0.48		species	0.02	1, 16	0.52	0.48	
stage	96.61	2, 1811	1389.44	<0.001		stage	97.61	2, 1811	1382.78	<0.001	
prec:species	0.42	1, 1814	12.01	<0.001		pc2:species	0.19	1, 1812	5.34	<0.05	
prec:stage	0.80	2, 1811	11.49	<0.001		pc2:stage	0.51	2, 1811	7.24	<0.001	
species:stage	1.59	2, 1811	22.80	<0.001		species:stage	1.54	2, 1811	21.79	<0.001	
prec:species:stage	0.02	2, 1811	0.32	0.72		pc2:species:stage	0.11	2, 1811	1.58	0.21	
Precipitation model–random effects						PC2 model–random effects					
year	38.58				0.78	year	46.99				0.78
plot	17.32					plot	14.87				
residual	44.09					residual	38.14				

was more variable in drier years) (Fig. 3A, Supplementary Material Table S5.1). The probability of overlap varied by 33% (from 0.63 to 0.84) over the range of precipitation investigated (21–135 mm). The precipitation model explained 7% of the variation in flowering

overlap overall, and the relationship was most obvious in a few extreme wet years when overlap was consistently high (Fig. 3A). When the 5 wettest years were removed from the analysis (bolded points in Fig. 3A), the relationship between symmetric overlap and precipitation

TABLE 3. Contrasts for models with significant climate effects and climate $\times$ stage interactions. Contrasts test for differences in the slopes of the relationships between each climate variable and the timing of flowering stages (flowering start = fstart, peak flowering = fpeak, and flowering end = fend). Degrees of freedom are estimated using Satterthwaite's approximation. Probability (P) values are adjusted for multiple comparisons (i.e., between the 3 flowering stages) using Tukey's adjustment, and significant results ($\alpha = 0.05$) are indicated in bold text. Table constructed with *kableExtra* (Zhu 2020). Slopes of flowering time versus PC1 or temperature are negative, so negative slopes in the contrasts below for those 2 climate variables indicate that *P. pulcherrima* flowering end and peak have larger climate responses than flowering start.

PC1 Model—contrasts

Stage	Slope	SE	df	Lower CL	Upper CL	t ratio	P
<i>Potentilla hippiana</i>							
fend–fpeak	–0.24	0.97	1810.24	–2.51	2.03	–0.25	0.97
fend–fstart	–1.55	0.97	1810.24	–3.82	0.71	–1.61	0.24
fpeak–fstart	–1.32	0.97	1810.24	–3.58	0.95	–1.36	0.36
<i>Potentilla pulcherrima</i>							
fend–fpeak	–0.89	0.64	1810.24	–2.40	0.62	–1.38	0.35
fend–fstart	–2.58	0.64	1810.24	–4.09	–1.07	–4.01	<0.001
fpeak–fstart	–1.69	0.64	1810.24	–3.20	–0.18	–2.63	<0.05

Temperature Model—contrasts

Stage	Slope	SE	df	Lower CL	Upper CL	t ratio	P
<i>Potentilla hippiana</i>							
fend–fpeak	–0.43	0.96	1810.39	–2.69	1.83	–0.45	0.90
fend–fstart	–2.03	0.96	1810.39	–4.29	0.23	–2.10	0.09
fpeak–fstart	–1.60	0.96	1810.39	–3.86	0.66	–1.66	0.22
<i>Potentilla pulcherrima</i>							
fend–fpeak	–1.23	0.64	1810.39	–2.73	0.26	–1.93	0.13
fend–fstart	–2.88	0.64	1810.39	–4.37	–1.38	–4.51	<0.001
fpeak–fstart	–1.64	0.64	1810.39	–3.14	–0.15	–2.58	<0.05

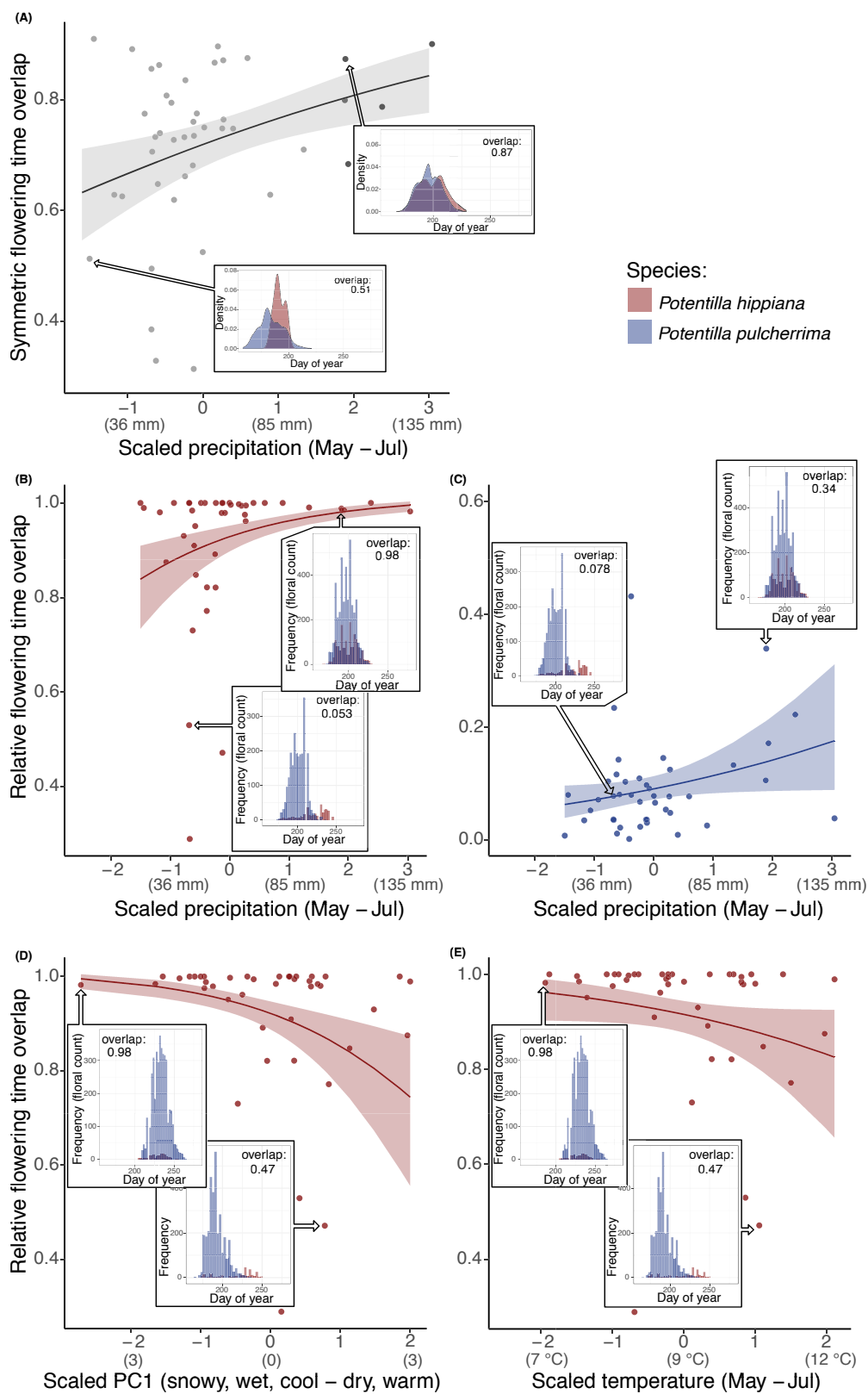
Precipitation Model—contrasts

Stage	Slope	SE	df	Lower CL	Upper CL	t ratio	P
<i>Potentilla hippiana</i>							
fend–fpeak	1.65	0.93	1810.66	–0.54	3.84	1.77	0.18
fend–fstart	3.08	0.93	1810.66	0.89	5.27	3.30	<0.01
fpeak–fstart	1.43	0.93	1810.66	–0.76	3.62	1.53	0.28
<i>Potentilla pulcherrima</i>							
fend–fpeak	0.79	0.65	1810.66	–0.75	2.32	1.20	0.45
fend–fstart	2.38	0.65	1810.66	0.84	3.91	3.64	<0.001
fpeak–fstart	1.59	0.65	1810.66	0.06	3.13	2.43	<0.05

was no longer significant, confirming that flowering overlap is most heavily affected by extreme wet conditions. None of the other climate variables (temperature, snowfall, snowmelt date, PC1, PC2) predicted variation in symmetric overlap in flowering between the 2 species (Supplementary Material Table S5.1).

Several climate variables were statistically significant predictors of relative overlap in flowering time (Fig. 3, Supplementary Material Table S6.1). Relative overlap of both species increased by similar amounts with precipitation (Fig. 3B, C), but the proportional increase in overlap was greater for *P. pulcherrima*

than *P. hippiana*. Specifically, as precipitation increased from 24 to 135 mm, relative overlap of *P. hippiana* increased by 19% (from 0.84 to 1.00; pseudo $R^2 = 0.06$, $P < 0.001$; Fig. 3B), while relative overlap of *P. pulcherrima* increased 200% (from 0.06 to 0.18; pseudo $R^2 = 0.08$, $P < 0.05$; Fig. 3C, Supplementary Material Table S6.1). Although no other climate variable predicted relative overlap of *P. pulcherrima*, relative overlap of *P. hippiana* changed along PC1 (pseudo $R^2 = 0.06$, $P < 0.001$; Fig. 3D). That is, relative overlap of *P. hippiana* was reduced in warm, dry summers preceded by low snowfall and early snowmelt,



consistent with trends seen with each climate variable (Fig. 3E, Supplementary Material Table S6.1). Although temperature, snowfall, and snowmelt had only little to weak individual relationships with relative overlap of *P. hippiana*, the collective effects of multiple climate variables likely drove the significant relationship with PC1. Taking all models of relative overlap together, relative overlap tended to be more variable in years with little winter snow, early melt, and/or warm, dry growing seasons (see Precision Models in Supplementary Material Table S6.1).

The analyses of climate variation over time indicated that growing season temperatures have increased at a rate of approximately 0.6 °C per decade in the study region between 1975 and 2019 (Fig. 4A, Supplementary Material Table S7.1), but growing season precipitation, snowmelt, and total amount of winter snowfall showed no directional change (Supplementary Material Fig. S7.1, Table S7.1). As a result of the discordant changes in different climate variables, PC1 (which represents a fairly even combination of all 4 individual climate variables) has increased over time, but with more variation around that trend than temperature alone.

We found no evidence that symmetric flowering overlap has increased or decreased

over time between 1975 and 2019 (Fig. 5A, Supplementary Material Table S8.1), though there has been substantial interannual variation (from 0.31 to 0.91; see Supplementary Material Fig. S8.1 for flowering distributions for each year in the data set). Relative overlap for each species has also varied but shown no significant temporal trend (Fig. 5B, Supplementary Material Table S8.1). Flowers of *P. pulcherrima* remained numerically dominant throughout the study period, which contributed to the consistently high relative overlap observed for *P. hippiana* (i.e., *P. hippiana* only dipped below 50% overlap in 1976 and 2013).

DISCUSSION

We evaluated how climate variation influences opportunities for hybridization by changing flowering phenology in 2 potentially hybridizing *Potentilla* species over 45 years. We found that *Potentilla* flowering windows varied in timing and duration with multiple climate variables. Of the 6 climate variables that we investigated, growing season precipitation, PC1, and temperature altered the timing and duration of flowering for one or both species (Fig. 2, Table 3). The 2 species showed fairly parallel responses to other climate variables. Precipitation was the strongest predictor of flowering time overlap for both species and all measures of overlap (Fig. 3). Precipitation in this region has not changed directionally over time, and so neither has the amount of overlap in these species' flowering windows (Fig. 5). In this region, *P. hippiana* flowers are substantially less abundant than those of *P. pulcherrima*. Therefore, *P. hippiana* should be much more affected by flowering overlap than *P. pulcherrima* across the climatic conditions explored (Fig. 5B, see also Supplementary Material Fig. S9.1), in line with other studies showing that species with low relative abundance experience greater rates of hybridization and introgression (Lepais et al. 2009, de Lafontaine and Bousquet 2017).

Flowering time in *P. hippiana* and *P. pulcherrima* showed similar shifts in response to each climate variable investigated: both species flowered earlier in years with warm, dry growing seasons preceded by earlier snowmelt and winters with less snow, and later in cool, wet growing seasons with later snowmelt

Fig. 3 (facing page, p. 138). Flowering overlap shifts with climate. Results are from beta regression models with pseudo $R^2 > 0.05$. Points are years, and ribbons are 95% confidence intervals. Values in parentheses on the x-axes are rounded reference points for the original, unscaled climate variables. (A) Symmetric overlap in flowering between *P. hippiana* and *P. pulcherrima* increases with scaled growing season precipitation. Overlap was quantified using kernel density estimates from flowering across the growing season. Insets show flowering distributions from example dry (2002) and wet (2015) summers. The relationship is no longer statistically significant when 5 extreme wet years (bolded points) are removed. Panels B–E show trends in relative overlap of either species. Relative overlap incorporates differences in total floral production between focal species. Relative overlap of *P. hippiana* flowering (by *P. pulcherrima*) increases with scaled precipitation (B), as does relative overlap of *P. pulcherrima* (by *P. hippiana*) (C). Insets show flowering distributions from example dry (2017) and wet (2015) summers that illustrate the observed trend in overlap. Relative overlap of *P. hippiana* decreases with increasing PC1 (D) and shows a marginally significant decrease ($P < 0.1$) as scaled growing season temperature increases (E). Insets show overlap in example cool (1995) and warm (2013) summers. Model fits were generated with package 'ggeffects' (Lüdtke 2018) in R.

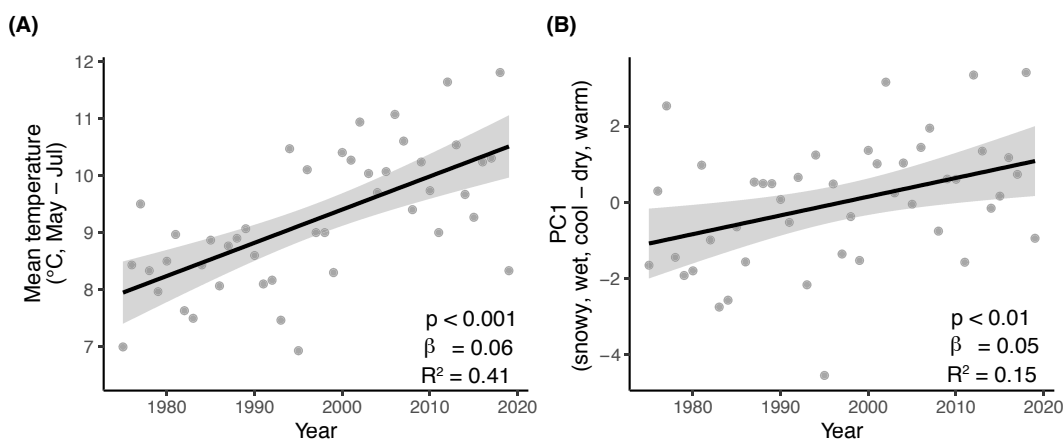


Fig. 4. Mean growing season temperature (A) and PC1 (B) increase over time (1975–2019). Points are years, and ribbons are 95% confidence intervals. Increased PC1 corresponds to years with warm, dry growing seasons with earlier snowmelt and less winter snow. Only significant linear models of climate change are shown (see Supplementary Material Fig. S7.1 for other climate variables).

after heavy-snowfall winters (Fig. 2). The similar phenological responses to climate variation of these 2 *Potentilla* species suggest that selection has not favored divergent flowering times to minimize hybridization between the species. These results indicate that if there is selection against hybrids, it is operating on other traits (e.g., pollen incompatibility, microhabitat differences; Brennan et al. 2009, Mizuta et al. 2010, Melo et al. 2014, Guerrero et al. 2017) and likely does not play a big role in the flowering time and climate responses of *Potentilla* in the subalpine zone of the southwestern Colorado Rockies.

The parallel phenological responses of our focal *Potentilla* species are consistent with many previous studies that show that plant phenology advances with warming, drought, and earlier snowmelt (Price and Waser 1998, Fitter and Fitter 2002, Parmesan and Yohe 2003, Franks et al. 2007, Wadgyr et al. 2018). Of the 3 flowering stages we investigated, flowering start was the least sensitive to climate variation (Table 3, Supplementary Material Table S4.1). Flowering end and peak had stronger climate responses than flowering start (Table 3, Supplementary Material Table S4.1), perhaps because drought intensifies across the growing season, curtailing late-season flowering in warm, dry years (Theobald et al. 2017). These flowering stage responses contrast with the substantial shifts in flowering start seen in other systems and regions

(e.g., Menzel et al. 2006) and the general trend for 60 species from the broader RMBL phenology study, which reported that shifts in the onset of flowering were more common and larger on average than shifts in flowering peak or end (CaraDonna et al. 2014). Furthermore, some other studies in temperate regions have suggested that later-season flowering species, which would include *Potentilla*, begin flowering later with increased warming (Sherry et al. 2007, Cook et al. 2012). However, at RMBL, warm years with early snowmelt experience more intense early summer drought that limits plant productivity (Wainwright et al. 2020). Therefore, drought associated with warmer temperatures may limit late-season flowering plants like *Potentilla* from delaying or extending their flowering, as shown in another temperate montane system (Theobald et al. 2017).

Despite the phenological similarities of the focal *Potentilla* species, some key differences in their flowering durations and the strengths of their climate responses nonetheless led to variation in flowering overlap between species. Growing season precipitation was a poor predictor of flowering time variation (Fig. 2, Table 2), but it was the best predictor of all measures of flowering time overlap. The effect of precipitation on all overlap measures is likely due to notable species-specific differences in the magnitude of their responses to precipitation (Table 2). In dry years, *P.*

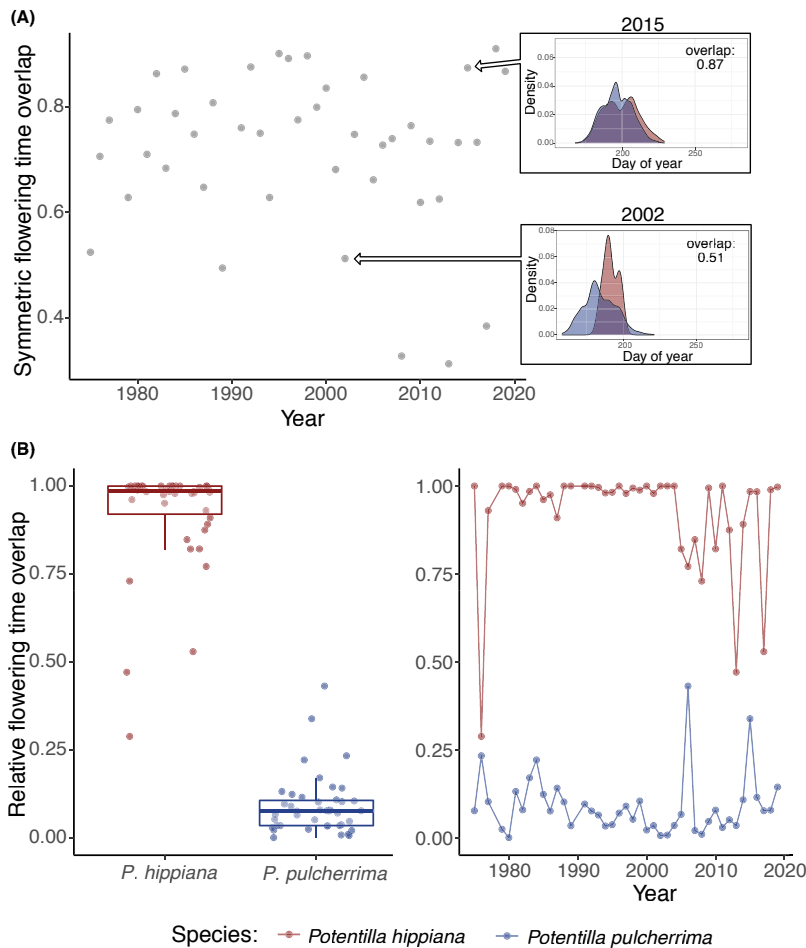


Fig. 5. Variation in flowering overlap between 1975 and 2019 (flowering data not recorded in 1978 and 1990). Neither symmetric nor relative overlap changed directionally over time; beta regressions with scaled year as the predictor were not significant ($P > 0.05$). Points are years. (A) Symmetric flowering time overlap between *Potentilla hippiana* and *P. pulcherrima*, as quantified using kernel density estimates from flowering across the growing season. Insets show flowering distributions from example years with high (2015) and low (2002) overlap between species. (B) Relative flowering time overlap of *P. hippiana* by *P. pulcherrima* fluctuated but was higher (on average and in each year) than overlap of *P. pulcherrima* by *P. hippiana*. Relative overlap estimates account for differences in floral abundance between the focal species. That is, *P. pulcherrima* flowers are much more abundant in the study region, leading to higher relative overlap of *P. hippiana* flowering than *P. pulcherrima*.

pulcherrima began flowering earlier than *P. hippiana* (see inset Fig. 3A, Fig 2C). When precipitation increased, both species shifted later and flowered longer due to later flowering ends, increasing the symmetric overlap in flowering. Relative flowering overlap for each species also increased slightly but significantly in wet years because of shifts in the distribution of flowers within these flowering windows (e.g., see peak in Fig. 2C). That is, although the flowering window of *P. hippiana* appears nested within that of *P. pulcherrima*

in dry years, *P. pulcherrima* started and reached peak flowering before *P. hippiana* in dry years, reducing the relative overlap experienced by *P. hippiana* (see inset Fig. 3A). Supplemental analyses indicate that the observed changes in relative flowering overlap were not due to the effects of precipitation on overall floral production (see Supplementary Material Fig. S9.1). Rather, changes in the distribution of flowers within each species' flowering window drove shifts in relative and symmetric flowering overlap. Since precipitation has shown

no directional change over time (Fig. 4), neither symmetric nor relative flowering overlap has shifted consistently between 1975 and 2019 (Fig. 5). Instead, extreme wet years may increase opportunities for hybridization through increased symmetric and relative overlap of flowering time. In a warming experiment, 2 fall-flowering species (in different genera) that typically flower concurrently bloomed earlier with warming but showed such contrasting responses to dry conditions that flowering onset of the 2 species was more than a month apart (Rice et al. 2021). Consistent with our results, this study suggests that late-flowering species will have greater flowering overlap in wetter years and highlights conflicting responses of overlap to different climate drivers.

The multivariate climate axis PC1 (which separates cool, wet years from warm, dry years) was the best predictor of phenology (Table 2) but was a less important predictor of overlap. With increasing values of PC1, each flowering stage occurred earlier for *P. pulcherrima* than *P. hippiana* (Fig. 2C). As a result, relative overlap of *P. hippiana* flowering decreased (but was highly variable) in warm, dry years (Fig. 3D, Supplementary Material Table S6.1). Importantly, relative overlap for *P. hippiana* remained high (>50%) in all years because there were always many more *P. pulcherrima* flowers in the study region than *P. hippiana* flowers (Fig. 5B). PC1 incorporates variation in precipitation, temperature, snowmelt date, and snowfall. An analysis of just snowmelt, snowfall, or temperature alone would have missed the collective effects on *P. hippiana* relative overlap that were captured by PC1.

Both species showed similar phenological shifts with temperature as with PC1 (Fig. 2). In hot summers, the flowering window of *P. pulcherrima* was compressed, starting and peaking before *P. hippiana*'s window, and therefore producing a marginally significant reduction in the overlap of *P. hippiana* by *P. pulcherrima* (Supplementary Material Table S6.1). In line with these results, one survey of British plant species reported that climate warming widened the offset in flowering start times between 2 pairs of potentially hybridizing species (although 4 other pairs showed the reverse pattern: a narrower gap in flowering start times between species; Fitter and Fitter

2002). We saw no change in relative overlap of *P. pulcherrima* with temperature, because the abbreviation and shift of its flowering window with warming appear to have cancelled out each other's effects on its relative overlap by *P. hippiana*. Symmetric overlap did not vary predictably with temperature (Supplementary Material Table S5.1). Previous experimental work in *P. pulcherrima* at RMBL found that populations from different elevations showed similar reproductive timing and plasticity in a common garden (Stinson 2004), suggesting that *Potentilla* populations beyond our study area may share similar reproductive responses to changing climates.

Our results provide new insights into the implications of phenological shifts for flowering overlap, which in turn influences the opportunity for interbreeding between 2 potentially hybridizing taxa. Our study emphasizes the need to study the phenological responses to climate of multiple interacting species. In particular, responses of related species can alter gene flow and species boundaries, thereby impacting not only their own population dynamics but also genetic and phenotypic diversity in a region through hybridization. Relatively few studies have quantified changes in phenological overlap among species due to climate, and most of these have focused on plant-pollinator, insect-host, or other trophic interactions (e.g., Visser and Both 2005, Memmott et al. 2007), rather than hybridization. Additionally, our study highlights the need to examine changes in hybridization as a consequence of variation along multiple climate axes. Direct tests of hybridization rates would provide a valuable complement to phenological studies such as ours and further clarify how climate change is shaping montane plant communities.

SUPPLEMENTARY MATERIAL

One online-only supplementary file accompanies this article (<https://scholarsarchive.byu.edu/wnan/vol82/iss1/12>). The supplementary material is divided into numbered subsections (S1 through S9) that contain explanatory text, figures, and tables:

S1. Correlation between PRISM and SNOTEL climate data sets (explanatory text, Fig. S1.1).

S2. Construction of multivariate climate axes (Fig. S2.1, Fig. S2.2, and Table S2.1).

S3. Illustration of two measures of flowering overlap (Fig. S3.1).

S4. Output tables from flowering time models (Fig. S4.1 and Table S4.1).

S5. Supplementary analyses and output tables from symmetric overlap models (Table S5.1).

S6. Output tables from relative overlap models (Table S6.1).

S7. Climate patterns across years (Fig. S7.1 and Table S7.1).

S8. Symmetric overlap across time (Fig. S8.1 and Table S8.1).

S9. Climate effects on peak floral production (explanatory text and Fig. S9.1).

Literature cited containing 6 references.

AUTHOR CONTRIBUTIONS

KAC devised the study, analyzed the data, and wrote the manuscript, all with advice and edits from DFD and NCE.

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