Historical changes in flowering phenology are governed by temperature × precipitation interactions in a widespread perennial herb in western North America

https://escholarship.org/uc/item/1rs1z375

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2015

10.1111/nph.13751

Peer reviewed
Historical changes in flowering phenology are governed by temperature × precipitation interactions in a widespread perennial herb in western North America

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Summary

- For most species, a precise understanding of how climatic parameters determine the timing of seasonal life cycle stages is constrained by limited long-term data. Further, most long-term studies of plant phenology that have examined relationships between phenological timing and climate have been local in scale or have focused on single climatic parameters. Herbarium specimens, however, can expand the temporal and spatial coverage of phenological datasets.
- Using *Trillium ovatum* specimens collected over > 100 yr across its native range, we analyzed how seasonal climatic conditions (mean minimum temperature (*T* min), mean maximum temperature and total precipitation (PPT)) affect flowering phenology. We then examined long-term changes in climatic conditions and in the timing of flowering across *T. ovatum*’s range.
- Warmer *T* min advanced flowering, whereas higher PPT delayed flowering. However, *T* min and PPT were shown to interact: the advancing effect of warmer *T* min was strongest where PPT was highest, and the delaying effect of higher PPT was strongest where *T* min was coldest. The direction of temporal change in climatic parameters and in the timing of flowering was dependent on geographic location. *T* min, for example, decreased across the observation period in coastal regions, but increased in inland areas.
- Our results highlight the complex effects of climate and geographic location on phenology.

Introduction

Phenology is the study of the timing of seasonal life cycle stages (phenophases), such as the flowering and fruiting of plants, the migration of birds and mammals, and the emergence of insect pollinators and pests. Shifts in the timing of phenophases are a well-documented response to climate change (Menzel et al., 2006; Parmesan, 2006), and these shifts can have profound and immediate effects on the interactions of species (Visser & Both, 2005; Both et al., 2006; Ozgul et al., 2010; McKinney et al., 2012), as well as longer term effects on the abundance and distribution of species (Moller et al., 2008; Chuine, 2010; Miller-Rushing et al., 2010; Willis et al., 2010; Cleland et al., 2012), and on ecosystem function and services (Richardson et al., 2010). For flowering plants, the timing of reproductive phenophases is particularly important, as it can influence the strength of mutualistic or antagonistic interactions between plants and their pollinators, seed dispersers, herbivores and seed predators (Elzinga et al., 2007; Yang & Rudolf, 2010; Forrest, 2015; Rafferty et al., 2015).

In order to identify the causes and consequences of recent or historical shifts in phenology and to predict future climate change-induced shifts, large-scale efforts to document contemporary plant and animal phenology are underway (Schwartz et al., 2012). These efforts include national-level programs, such as the USA National Phenology Network and Project BudBurst, as well as regional programs, such as the California Phenology Project (Haggerty et al., 2013; Denny et al., 2014; Mazer et al., 2015). Two primary goals of these projects are to maximize the quantity and accessibility of high-quality phenological data with respect to the frequency and duration of monitoring, the numbers of species targeted for monitoring and the variety of geographic locations monitored, and to link inter-annual and geographic variation in phenology to local climatic conditions.

Despite these efforts, our current understanding of plant phenology and its relationships with climatic parameters is constrained by a dearth of historical data against which contemporary observations can be compared. This gap can be mitigated by accessing phenological information preserved in natural history collections, and this approach has been particularly effective for the examination of patterns of plant reproductive phenology using herbarium specimens (Primack et al., 2004; Lavoie & Lachance, 2006; Miller-Rushing et al., 2006; Gallagher et al., 2009; Gaira et al., 2011; Robbirt et al., 2011; Hart et al.,...
Most of the herbarium-based phenological studies to date have examined local patterns of plant phenology and have used natural history collections to expand the temporal range of phenological observations at a given location or within a relatively small region. However, herbarium collections can also expand the spatial range of historical datasets (e.g. Park, 2012). Datasets that are geographically widespread and that represent many decades can comprise greater variation in both phenological and climatic data than datasets based on single locations or shorter term surveys. Further, with datasets representing a broad geographic range – which can be provided by herbarium specimens – larger scale relationships among geographic, climatic and temporal variables, and plant phenophases, can be identified and quantified.

In this study, we examined the herbarium records of *Trillium ovatum* to build a dataset representing flowering dates (including both day of year (DOY) and year) and locations across the entire native range of this species. *T. ovatum* is particularly valuable for herbarium-based phenological research because the flowering status of sampled plants is unambiguous: plants typically produce a single stem per year and stems produce only one flower (older plants have been found occasionally to produce more than one stem; Jules & Rathcke, 1999; Ream, 2011). With this dataset, we ask four questions related to how flowering phenology varies across climatic, geographic and temporal gradients. (1) Which climatic variables (e.g. minimum temperature, maximum temperature and cumulative precipitation) and which seasonal time periods (three 3-month windows from January to May, before flowering) best explain the variation in the day of the year on which *T. ovatum* specimens are collected in flower? (2) Can we detect interactions between temperature and precipitation in their effects on the flowering phenology of *T. ovatum*? For example, where precipitation is not limiting, we expect that temperature will have a stronger effect than where precipitation is limiting. (3) When controlling statistically for geographic location (i.e. latitude, longitude and elevation, which affect seasonal temperatures and precipitation), can we detect long-term temporal change in the climatic variables that affect flowering phenology? (4) Finally, controlling statistically for geographic parameters, can we detect a long-term inter-annual change in the onset date of spring flowering over the past 122 yr? The application of multivariate models to historical climatic data and herbarium-derived phenological records provides a way to detect a suite of novel interactions between rainfall and temperature that affect the estimated onset of flowering, and between geographic variables and collection year that affect local climatic conditions.

### Materials and Methods

#### Study organism

*Trillium ovatum* Pursh (Western Trillium; Melianthaceae) is a long-lived perennial herb that is common in mesic coniferous and mixed coniferous–deciduous forests in western North America. Its range extends from northern California in the USA to southern British Columbia and Alberta in Canada (USDA, NRCS, 2014; Fig. 1). *Trillium ovatum* flowers in spring, with reproductive individuals producing a single flower per stem. Individual flowers last c. 22 d (Jules & Rathcke, 1999), providing a reasonable estimate of the flowering onset date given the wide range in specimen collection dates across the geographic range of the species (mean collection DOY = 122; range = 32–239).

#### Herbarium data

*Trillium ovatum* is well represented in herbaria throughout its range and produces showy flowers, making it a good candidate for study via preserved herbarium specimens. We obtained loans from five California herbaria, including Rancho Santa Ana Botanic Garden Herbarium (RSA), University of California, Riverside (UCR), Santa Barbara Botanic Garden (SBBG), and the Jepson Herbarium (JEPS) and the University Herbarium (UC) at University of California, Berkeley. Because *T. ovatum* produces a single, relatively large flower per stem, its phenological status is also simple to observe via photographs; consequently, we were able to expand the size and geographic coverage of our dataset by downloading specimen images through the Consortium of Pacific Northwest Herbaria website (http://www.pnwherbaria.org). These specimens are housed in the following herbaria: H.J. Andrews Experimental Forest (HJAEF), Stillinger Herbarium at University of Idaho (ID), Montana State (MONT), Pacific Luthern University (PLU), Reed College (REED), Rocky Mountain Herbarium at University of Wyoming (RM) and Western Washington University (WWB).

![Fig. 1 Collection locations of flowering Trillium ovatum specimens](image-url)
We examined each specimen and recorded its collection date (day, month and year), collection location (latitude, longitude and elevation) and phenological status (flowering or not). Specimens that were missing labeled information (e.g. the exact day, month and year of collection) were excluded. Many specimens did not include geographic coordinates, but provided a detailed description of the collection location (e.g. a county and road name). These specimens were geo-referenced using online tools (e.g. GEOLocate: http://www.museum.tulane.edu/geolocate/) and US Geological Survey topographic maps. We estimated the elevation for each collection location using georeferenced coordinates. Specimens for which the labels provided insufficient location information to enable the assignment of GPS coordinates or elevations were rejected. Finally, if there was more than one stem preserved on an herbarium sheet, only one datum was recorded. Our final dataset included 289 flowering specimens that met these criteria.

Climatic data

The link between temperature and plant phenology is well documented (Menzel et al., 2006; Parmesan, 2006; Gallagher et al., 2009; and references therein), but fewer studies have examined the degree to which precipitation drives phenological variation and how temperature and precipitation may interact to influence phenology (but see Crimmins et al., 2011 and Mazer et al., 2015). Because our study area covers a large geographic range and climate stations are available at few of our sample locations, we accessed climatic data for our study area from the PRISM dataset (PRISM Climate Group, 2013). The PRISM dataset includes 4 km gridded data for the conterminous USA, interpolated from point station data; PRISM data are readily available online and have been used frequently in phenological research (Crimmins et al., 2011; Park, 2014; Mazer et al., 2015). For the georeferenced location of each specimen, we downloaded monthly climatic data for the year of collection. For each collection event (a combination of the collection location and date), we obtained monthly mean maximum temperature ($T_{\text{max}}$), mean minimum temperature ($T_{\text{min}}$) and total precipitation (PPT) (the three climatic variables provided by the PRISM dataset). We then generated composite seasonal climatic parameters representing the $T_{\text{max}}$, $T_{\text{min}}$ and PPT during three 3-month windows preceding the collection date of *T. ovatum* specimens: JFM (January, February and March), FMA (February, March and April) and MAM (March, April and May).

Statistical analysis

**Effects of temperature and rainfall on flowering date** We constructed multiple linear regression models to detect the effect of each site- and year-specific climatic variable on the flowering DOY. For each specimen, we calculated the flowering DOY as the number of days after 1st January (e.g. 1st April is day 90) on which it was collected. We first constructed saturated models, which included (for each specimen’s georeferenced location) the three seasonal climatic parameters ($T_{\text{min}}$, $T_{\text{max}}$ and PPT) and their interactions during each of the 3-month windows (JFM, FMA or MAM); in these models, DOY was the response variable, and $T_{\text{min}}$, $T_{\text{max}}$, PPT and the interactions among them were the independent variables. Each seasonal window (JFM, FMA and MAM) was analyzed separately. Because the first year represented in the PRISM dataset is 1895, collection events before 1895 were not used in any analysis that included climatic data ($n = 282$) for analyses that included climate data. Precipitation values were log transformed to achieve normality. We identified a minimal adequate model through backward elimination, in which non-significant predictors ($P > 0.05$) were removed in successive steps (Crawley, 2007). A stepwise approach to multiple regression analysis is frequently used in phenological research studies (Keatley et al., 2002; Moller et al., 2008; Hulme, 2011; Mazer et al., 2015), and has the benefit of identifying the independent variables that have the strongest influence on phenology (Roberts, 2009). The statistically significant regression coefficients associated with the independent variables were examined to determine whether DOY was advanced or delayed in response to higher temperatures and/or precipitation. The relative sensitivity of DOY to each of the three seasonal windows was also examined to determine whether flowering DOY was more sensitive to winter or to spring conditions.

Temporally significant two-way interaction terms were examined graphically to reveal how the effect of one factor (e.g. $T_{\text{min}}$) on DOY was dependent on the value of a second (i.e. interacting) factor (e.g. PPT). We used the equation estimated by the linear model to generate three lines, each of which plotted the predicted DOY against a range of values for the first climatic variable in the interaction term whilst using one of three values of the second climatic variable in the interaction term: the minimum value, mean value and maximum value. All other significant predictors were included in the equation at their mean value. For example, we used the equation of the linear model to illustrate the effects of $T_{\text{min}}$ on DOY using the minimum, mean and maximum values of PPT (see Fig. 2a). We similarly created three lines in which the predicted DOY was plotted against a range of values for the second climatic variable in the significant interaction term, where each line used one of three values of the first climatic variable in the interaction (again, the minimum, mean and maximum values; see Fig. 2b).

**Temporal changes in temperature and rainfall** We analyzed data comprising each specimen’s latitude, longitude, elevation, year of collection and climatic parameters to quantify the relationship between the seasonal climatic parameters that were identified as significant predictors of flowering phenology in the previous analysis (as the dependent variables) and the collection year, controlling for variation in climate that is associated with latitude, longitude and elevation. We used an analytical approach similar to the previous analysis of flowering dates and climatic variables. We built multiple linear regression models, using a seasonal climatic parameter (e.g. mean $T_{\text{min}}$ in JFM) as the response variable, and collection year (treated as a continuous variable), geographic parameters (latitude, longitude and elevation) and their interactions as independent variables. In this model,
significant effects of collection year on the response variable were interpreted as a significant long-term temporal trend, and the values of the statistically significant regression coefficients associated with year, latitude, longitude and elevation were examined to determine whether each of the climatic variables increased (or decreased) over time (independent of geographic location) or in association with geographic location (independent of temporal effects).

Where significant interactions between two variables were detected, we again used a graphical approach to visualize how the effects of one factor were dependent on the value of a second factor. We graphed the predicted values of the seasonal climatic parameters against a range of values for the first variable contributing to the interaction term and, for each of three separate lines, one of three levels of the second variable contributing to the interaction term (the minimum value, mean value and maximum value of the second variable). For example, the interacting effects on FMA $T_{\text{min}}$ of collection year and longitude were examined by graphing predicted FMA $T_{\text{min}}$ against collection year using each of three longitude values (the westernmost, mean and easternmost longitude values represented by the specimens; see Fig. 3a).

**Long-term temporal changes in flowering date** We used multiple linear regression to quantify the relationship between flowering phenology (DOY) and collection year. To control for environmental effects on DOY associated with geographic location rather than temporal changes in climate, we created a regression model with flowering DOY as the response variable and collection year, geographic variables (latitude, longitude and elevation) and their interactions as independent variables. The sign of the regression coefficient associated with collection year was examined to determine whether the DOY was significantly delayed or advanced (earlier) over time, controlling for environmental variation (climatic or biotic) associated with geographic location that may have also influenced DOY. In addition, the regression coefficients associated with latitude, longitude and elevation were examined to corroborate the prediction that DOY would be delayed at higher latitudes and elevations and to detect, if present, an association between flowering DOY and longitude.

All statistical analyses were performed in R (R Development Core Team, 2013).

**Results**

Our dataset spanned a 122-yr period from 1888 to 2009. The mean collection DOY was 122 (3rd May) ± 40.29 (range = 32–239; SE = ± 2.37; Fig. 4).

**Effects of seasonal temperature and rainfall on flowering date**

Temperature and precipitation in both winter and spring influenced flowering DOY. For each of the three seasonal windows, there were significant effects of mean $T_{\text{min}}$, PPT or their interaction on flowering DOY (Table 1). In none of the models did mean $T_{\text{max}}$ have a significant effect on DOY. The climate models account for 34–36% of the variation in flowering DOY.

Flowering DOY was advanced (earlier) where January–March mean $T_{\text{min}}$ was warmer, and delayed (later) where January–March PPT was higher. For the February–April and March–May climate windows, the main effects of $T_{\text{min}}$ and precipitation were similar, but there was also a significant interaction between mean $T_{\text{min}}$ and PPT. The advancing effect of warmer mean $T_{\text{min}}$ was stronger where PPT was higher (Fig. 2a shows this interaction for the FMA window), and the
The delaying effect of increased precipitation was stronger where mean $T_{\text{min}}$ values were lower (Fig. 2b shows this interaction for the FMA window).

Temporal changes in temperature and rainfall

We detected long-term temporal changes in mean $T_{\text{min}}$ and PPT, independent of variation associated with geographic location. Across all three seasonal windows, there were significant independent effects of year, elevation, latitude, longitude and their interactions on mean $T_{\text{min}}$ and PPT (Tables 2, 3). The models account for 74–81% of the variation in $T_{\text{min}}$ and 41–52% of the variation in precipitation.

The model of January–March mean $T_{\text{min}}$ as influenced by the geographic variables detected significant interactions between each pair of geographic parameters (e.g. elevation × latitude; elevation × longitude; latitude × longitude; Table 2a), indicating complex effects of geography on winter minimum temperatures. The effects of elevation on mean $T_{\text{min}}$, for example, were dependent on latitude and longitude. By contrast, the effect of geographic parameters on mean $T_{\text{min}}$ in the FMA and MAM windows was primarily attributed to the main effects, with lower $T_{\text{min}}$ values associated with higher latitudes (more northern sites), higher elevations and...
more easterly (inland) sites (Table 2b,c). In all three seasonal windows, there was a significant interaction between year and longitude: $T_{\min}$ increased over time at inland (eastern) sites, whereas $T_{\min}$ decreased at coastal (western) sites (Fig. 3a illustrates this relationship for the FMA seasonal window).

The sign and statistical significance of the regression coefficients in the models of precipitation as influenced by geographic parameters differed among the 3-month focal windows (Table 3). The negative coefficients associated with longitude, however, indicate that precipitation consistently declined from western to eastern collection localities. The models detected at least one main effect detected was that of elevation on DOY, with flowering DOY was dependent on elevation. The only significant main effect detected was that of elevation on DOY, with flowering DOY increasing with increasing temperature or precipitation. Interaction terms are discussed in the text.

Long-term temporal changes in flowering date

Collection year and geographic variables explained 48% of the variation in flowering DOY. The effect of year on flowering date, however, was dependent on geographic location. The model detected two significant three-way interaction terms that included year and geographic parameters (year × elevation × latitude and year × elevation × longitude) and several two-way interaction terms between year and geographic parameters (Table 4). For example, a significant two-way interaction between year and elevation indicated that the long-term direction of the change in flowering DOY was dependent on elevation. The only significant main effect detected was that of elevation on DOY, with advanced flowering dates associated with high elevations.

Discussion

Effects of temperature and rainfall on flowering date

Flowering DOY is associated with winter and spring mean $T_{\min}$ and PPT. Higher spring $T_{\min}$ is associated with earlier flowering phenology, and greater spring precipitation is associated with delayed flowering. Advanced flowering phenology as at western (coastal) sites (Fig. 3c). The FMA window was the only season in which there was no temporal trend in precipitation (Table 3b).
Table 2 Summary of multiple linear models conducted to detect effects of year, elevation, latitude, longitude and their interactions on mean minimum temperature ($T_{\text{min}}$) during three 3-month windows (January–March, February–April and March–May) preceding the collection date of each sampled *Trillium ovatum* specimen

<table>
<thead>
<tr>
<th>(a) Response variable: mean $T_{\text{min}}$ (January–March) Analysis of variance Source</th>
<th>df</th>
<th>Sum of squares</th>
<th>F ratio</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
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<td>94.38</td>
<td>20.92</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Elevation</td>
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<td>805.30</td>
<td>178.54</td>
<td>&lt; 0.001</td>
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<tr>
<td>Latitude</td>
<td>1</td>
<td>272.23</td>
<td>60.35</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Longitude</td>
<td>1</td>
<td>349.78</td>
<td>77.55</td>
<td>&lt; 0.001</td>
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<tr>
<td>Interaction × Latitude</td>
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<td>1.30</td>
<td>0.22</td>
<td>0.63</td>
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<tr>
<td>Interaction × Longitude</td>
<td>1</td>
<td>60.46</td>
<td>13.40</td>
<td>&lt; 0.001</td>
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<tr>
<td>Interaction × Latitude × Longitude</td>
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<td>8.01</td>
<td>1.88</td>
<td>0.18</td>
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<td>Error</td>
<td>272</td>
<td>1226.87</td>
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<td></td>
</tr>
<tr>
<td>$R^2$</td>
<td></td>
<td></td>
<td></td>
<td>0.81</td>
</tr>
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Parameter estimates

| Term | Estimate | SE | t ratio | Prob > |t
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
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<td>405.00</td>
<td>−2.859</td>
<td>0.004</td>
</tr>
<tr>
<td>Year</td>
<td>0.70</td>
<td>0.19</td>
<td>3.634</td>
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<tr>
<td>Elevation</td>
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<td>2.179</td>
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<td>5.65</td>
<td>−0.96</td>
<td>0.34</td>
</tr>
<tr>
<td>Longitude</td>
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<td>−2.826</td>
<td>0.005</td>
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<td>0.01</td>
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<td>0.03</td>
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<tr>
<td>Interaction × Longitude</td>
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<td>0.001</td>
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<tr>
<td>Error</td>
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<td>0.05</td>
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<tr>
<td>Error</td>
<td>0.0001</td>
<td>0.00004</td>
<td>2.16</td>
<td>0.03</td>
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</table>

Table 2 (Continued) Parameter estimates

| Term | Estimate | SE | t ratio | Prob > |t
<table>
<thead>
<tr>
<th></th>
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<td>0.01</td>
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<tr>
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<td>0.04</td>
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<td>&lt; 0.001</td>
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<tr>
<td>Longitude</td>
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<td>2.30</td>
<td>−2.539</td>
<td>0.01</td>
</tr>
<tr>
<td>Year × Longitude</td>
<td>0.003</td>
<td>0.001</td>
<td>2.453</td>
<td>0.01</td>
</tr>
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</table>

Table 2(a) reports the independent effects of each dependent variable and their interactions on $T_{\text{min}}$ from January to March; Table 2(b) reports the effects of these variables on $T_{\text{min}}$ from February–April; Table 2(c) reports the effects of these variables on $T_{\text{min}}$ from March–May. Parameter estimates are the regression intercept and coefficients of each independent variable. $R^2$ values and significant P values (< 0.05) are shown in bold to facilitate comparison across tables.

Panchen et al., 2012). Although phenological responses to precipitation have been less well studied, it appears that the phenological response to precipitation may be less consistent than that with temperature. Some authors have found no effect of precipitation on flowering phenology (Abu-Asab et al., 2001), whereas others have found that increased precipitation results in delayed flowering (Von Holle et al., 2010; Mazet et al., 2013) or earlier phenophase onset dates (Crimmins et al., 2010; Lambert et al., 2010).

In the current study, multiple linear regression models also detected a significant interaction between mean $T_{\text{min}}$ and PPT during late winter and spring (the February–April and March–May windows) affecting flowering DOY. In these windows, the advancing effect of warmer mean $T_{\text{min}}$ was stronger where PPT was higher (Fig. 2a). One proximal explanation for this pattern is that flowering phenology more closely tracks minimum temperatures where precipitation is not limiting. Another interpretation is that, where PPT is relatively high, DOY is delayed (cf. the effects of precipitation as a main effect) and, accordingly, there is greater potential for higher temperatures to advance DOY towards earlier values without risking reproductive failure. Advancing DOY in response to increasing temperature may not be possible where DOY is already relatively early without risking floral failure as a result of late winter or early spring frost events. These interpretations are not mutually exclusive and may both contribute to the interaction. In any case, the ultimate evolutionary or physiological mechanisms underlying these interactions cannot

(a) Response variable: mean $T_{\text{min}}$ (January–March)

(b) Response variable: mean $T_{\text{min}}$ (February–April–May)

(c) Response variable: mean $T_{\text{min}}$ (March–May)
be deduced from these patterns alone; to our knowledge, this is the first report of such a pattern in any wild species.

The temperature × precipitation interaction is also a result of the delaying effect of precipitation being stronger where $T_{\text{min}}$ values are colder, suggesting that future changes in precipitation in the western USA will have greater effects on the flowering time of *T. ovatum* in cooler locations (Fig. 2b, the positive slope of the line representing the minimum value of mean $T_{\text{min}}$ (solid red) is steeper than the slope of the lines representing the mean and maximum values of mean $T_{\text{min}}$ (dashed green and dotted blue)); based on the patterns detected here, any reductions in precipitation will advance flowering, particularly where the climate is relatively cool.

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<th>Table 3 (Continued)</th>
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Table 3 reports the independent effects of year, elevation, latitude and longitude on total precipitation from (a) January–March; (b) February–April; and (c) March–May. Parameter estimates are the regression intercepts and coefficients for each independent variable. $R^2$ values and significant $P$ values (< 0.05) are shown in bold to facilitate comparison across tables.

This result was unexpected; where $T_{\text{min}}$ values are low, flowering is relatively late. Therefore, the delaying effect of high precipitation is strongest where flowering is already delayed. By contrast, we might expect that variation in precipitation would have the strongest effect on the onset of flowering in *T. ovatum* where $T_{\text{min}}$ is highest and flowering is relatively early, that is, precipitation would have a delaying effect where plants are flowering early and there is greater potential for phenology to be delayed. One possible explanation for the observed pattern is that, under warmer climatic conditions, precipitation may freeze and be deposited as snow, requiring additional time for snow to melt and for soils to warm before plants are able to initiate growth and reproduction. Under warmer climatic conditions, by contrast, the effect of precipitation on flowering time is not as strong. Given that very few studies have documented interactions between $T_{\text{min}}$ and precipitation (but see Fu *et al.*, 2014), a better understanding of phenological responses to precipitation is needed if we are to model and forecast phenological changes more effectively, particularly in water-limited ecosystems.

Finally, climatic conditions during the later seasonal windows (FMA and MAM) explained slightly more variation in the flowering phenology of *T. ovatum* than the earlier window. Previous studies have found that the flowering phenology of some taxa is more sensitive to climatic conditions in certain months or seasons than in others (Hart *et al.*, 2014; Mazer *et al.*, 2015), but the mechanism driving this pattern is unclear. In our study, sensitivity to the later seasonal windows
may be caused by the individuals in our study that flowered relatively late (e.g. a flowering DOY > 150, or 30th May; Fig. 2); these plants may be more sensitive than earlier flowering individuals to the more recent climatic conditions (e.g. those observed in FMA and MAM).

One limitation of the current study is that the models included only contemporaneous temperature and rainfall (i.e. climatic parameters experienced in the same set of months). Mazer et al. (2015) found that, for some Californian native woody species, the effects on a phenophase’s DOY of $T_{\text{min}}$ during 1 month were dependent on the level of rainfall in another month. For example, precipitation in one winter month influenced an individual plant’s sensitivity to $T_{\text{min}}$ experienced in a subsequent month. The examination of the effects of nonsynchronous combinations of temperature and rainfall was beyond the scope of the current study, but the variance in DOY explained by multivariate models might be increased by including such interactions.

### Temporal changes in temperature and rainfall

Seasonal $T_{\text{min}}$ values varied across the > 100 yr of observation (1895–2009) in our climatic dataset, but the direction of change was dependent on the location of observation. Observations from the western coastal portion of $T. \text{ovatum}$’s range revealed that minimum temperatures have decreased across the observation period, whereas, in the eastern inland portion of the range, minimum temperatures have increased. Lebassi et al. (2009) reported similar patterns for summer temperature over a 50-yr observation period (from 1948 to 2004) in California: summer temperatures have become cooler at low-elevation coastal sites, which are open to marine air penetration, whereas summer temperatures at inland sites have increased in recent years. Likewise, the temporal changes in precipitation are complex, with the direction of change depending on location. In the January–March window, long-term temporal changes in PPT were dependent on latitude, whereas, in March–May, the temporal change in precipitation was dependent on longitude. To our knowledge, the fact that temporal trends in temperature and/or precipitation vary regionally has not previously been accounted for in studies of the responses of species to climate change, and is an important consideration for any widespread species, in which long-term pheno- logical patterns in one part of its range may differ from those in another part of its range as a result of regional variation in the direction or magnitude of climate change.

Climate models for the Pacific Northwest generally predict warmer and similar to slightly wetter conditions in the future; the climate models available in The Nature Conservancy’s online climate wizard tool (http://www.climatewizard.org/; accessed 9 November 2014), for example, predict warmer springs (March–May) and relatively little change in precipitation in the Pacific Northwest by the 2080s (Girvetz et al., 2009). We found that warmer spring $T_{\text{min}}$ values were associated with advanced flowering and the delaying effect of precipitation was more pronounced where $T_{\text{min}}$ values were lower. If the climate predictions hold true for this region, we expect the inter-annual trend in the flowering phenology of $T. \text{ovatum}$ to shift towards earlier flowering in the upcoming decades.

### Long-term temporal changes in flowering date

Given the complexity of long-term temporal changes in climatic variables that affect flowering phenology, it is not surprising that the long-term temporal trend in flowering date was similarly complex and location dependent. Surprisingly, few studies have emphasized the importance of considering location- or region-specific trends in phenology (but see Cocu et al., 2005, who found location-specific trends in aphid phenology across Europe), perhaps because most studies have been limited to local or regional scales.

Interestingly, the model including geographic variables and collection year explained a larger proportion of the variation in flowering date than any of the models with seasonal climatic variables (48% (Table 4) vs 34–36% (Table 1)). Although geographic parameters are a good proxy for (and probably capture most)
variation in climate, other abiotic factors that affect phenology are also likely to vary geographically and may account for the additional explained variance (e.g. day length, duration of the warmest part of the day, soil nutrients or temperatures, and the intensity of herbivory). Moreover, each season may explain some portion of the variance in flowering DOY, independent of other seasons, a possibility not explored here (as each three-month window was modeled independently). Finally, biotic factors, such as the timing of pollinator availability and abundance, could determine the optimum flowering time in different regions. If so, natural selection could result in local adaptation and differentiation among populations in flowering time that is somewhat independent of local climatic conditions.

Using natural history collections as a data source

The geographic distribution of *Trillium ovatum* is well represented by the specimens included in our dataset (Fig. 1). Although herbarium specimens have been used to extend the temporal coverage of phenological datasets (Primack et al., 2004; Robbirt et al., 2011; Panchen et al., 2012), here we show that they can also expand geographic coverage, which allowed us to describe relationships with geographic variables and to capture a wider range of climatic conditions. Many natural history collections are now being digitized, making information contained within them more accessible, and allowing researchers to document phenological information without physically visiting herbaria or requesting loan specimens (Park, 2012, 2014).

As shown here, data derived from natural history collections can be used to detect phenological relationships with climate and provide a reference point for comparison with future phenological research. *Trillium ovatum* is a focal species for two national-scale phenological monitoring programs in the USA, the USA National Phenology Network (www.usanpn.org) and Project Budburst (http://budburst.org/), and we expect that contemporary phenological data across its native range will be increasingly accessible via these online platforms. These herbarium-derived data and results represent a 122-yr time series that will provide a baseline on which to interpret phenological data that are reported to these programs in the future.

Acknowledgements

The authors gratefully acknowledge University of California, Santa Barbara (UCSB) student interns, who invested considerable time and effort in the examination of hundreds of herbarium specimens; Danica Taber for her assistance in data management and organizing undergraduate schedules; and Kimberly Crispin for retrieving PRISM data. The authors also thank the herbaria that loaned specimens, particularly Dr Jennifer Thorsch, and UCSB Cheadle Center For Biodiversity and Ecological Restoration for hosting the borrowed specimens and for providing space to work with them. The authors acknowledge funding from the National Park Service Climate Change Response Program (Cooperative Agreement H8C07080001).

Author contributions

E.R.M. and S.J.M. planned and designed the research. E.R.M. acquired the herbarium loans, supervised student interns and managed the data. E.R.M. led the data analysis, and E.R.M. and S.J.M. discussed all analyses, results and interpretations. E.R.M. led the writing and preparation of the manuscript. E.R.M. and S.J.M. contributed to the editing of the manuscript.

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