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RESEARCH ARTICLE

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Region-specific phenological sensitivities and rates of climate warming generate divergent temporal shifts in flowering date across a species' range

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Abstract

Premise: Forecasting how species will respond phenologically to future changes in climate is a major challenge. Many studies have focused on estimating species- and community-wide phenological sensitivities to climate to make such predictions, but sensitivities may vary within species, which could result in divergent phenological responses to climate change.

Methods: We used 743 herbarium specimens of the mountain jewelflower (*Streptanthus tortuosus*, Brassicaceae) collected over 112 years to investigate whether individuals sampled from relatively warm vs. cool regions differ in their sensitivity to climate and whether this difference has resulted in divergent phenological shifts in response to climate warming.

Results: During the past century, individuals sampled from warm regions exhibited a 20-day advancement in flowering date; individuals in cool regions showed no evidence of a shift. We evaluated two potential drivers of these divergent responses: differences between regions in (1) the degree of phenological sensitivity to climate and (2) the magnitude of climate change experienced by plants, or (3) both. Plants sampled from warm regions were more sensitive to temperature-related variables *and* were subjected to a greater degree of climate warming than those from cool regions; thus our results suggest that the greater temporal shift in flowering date in warm regions is driven by both of these factors.

Conclusions: Our results are among the first to demonstrate that species exhibited intraspecific variation in sensitivity to climate and that this variation can contribute to divergent responses to climate change. Future studies attempting to forecast temporal shifts in phenology should consider intraspecific variation.

KEYWORDS

Brassicaceae, California, climate change, flowering time, herbarium specimens, montane, phenological shifts, *Streptanthus tortuosus*

Evaluating changes in plant phenology is a powerful way to assess the impact of climate change on terrestrial ecosystems because climate and phenology are intimately linked (Menzel et al., 2006, 2020; Cleland et al., 2007). Shifts in flowering and fruiting phenology in response to directional climate change during the past century have been reported in many taxa and ecosystems (Chmielewski and Rötzer, 2001; Fitter and Fitter, 2002; Primack et al., 2004; Forrest et al., 2010; Beaubien and Hamann, 2011; CaraDonna et al., 2014). These shifts can have ecosystem-wide consequences by altering or disrupting plant–pollinator interactions (Miller-Rushing et al., 2010; Huang and Hao, 2018; Kehrberger and Holzschuh, 2019; Kudo and Cooper, 2019) and by influencing competitive interactions among co-flowering plants (such as competition for resources such as pollinators; Forrest et al., 2010; CaraDonna et al., 2014).

Forecasting how species will respond to future changes in climate and predicting the ecosystem-wide consequences of these changes are still major challenges (Ibáñez et al., 2010; Pau et al., 2011; Wolkovich et al., 2014). However, several recent discoveries indicate that such predictions eventually may be within reach. For example, estimates of many species' phenological sensitivity to local climate conditions (i.e., the absolute change in the flowering onset date in response to each 1° increase in temperature) indicate that species differ with respect to how climate influences the timing of their reproduction (Cook et al., 2012; Wolkovich et al., 2012; Park and Mazer, 2018). Generating a sufficient number of regional and site-specific estimates of phenological sensitivity to temperature for a wide range of taxa would improve our ability to predict how the flowering onset dates of entire communities will respond to climate change (Hufft et al., 2018). Similarly, studies of climate-induced phenological mismatches between plants and their pollinators show that mutualistic species interactions can be disrupted by climate change (Kudo and Ida, 2013; Inouye, 2019; Kehrberger and Holzschuh, 2019; but see Iler et al., 2013). Given estimates of the phenological sensitivities of mutualistic (plant–pollinator or plant–disperser) or antagonistic (e.g., plant–herbivore) species pairs or networks, we may be able to forecast the effects of future climatic conditions on these species' associations. Estimating phenological sensitivity within and among taxa is a critical first step toward predicting how future changes in climate will affect the direction and magnitude of phenological shifts and forecasting how these changes may affect ecosystem-wide processes (Menzel et al., 2006; Forrest and Miller-Rushing, 2010; Forrest et al., 2010; Ibáñez et al., 2010; Mazer et al., 2013; Park et al., 2019).

Previous studies investigating phenological sensitivity to climate have largely focused on estimating species-wide sensitivities (Menzel et al., 2006; Cook et al., 2012; Wolkovich et al., 2012; Zhang et al., 2015); however, few studies have been designed to determine whether sensitivities vary within a species (but see Wang et al., 2015; Prevéy et al., 2017; Park et al., 2018; Rafferty et al., 2020; Song et al., 2020), and the consequences of such intraspecific variation in sensitivity to climate are not well understood. Variation in phenological sensitivity within species may be as high as variation in sensitivity among species (as demonstrated by Park et al., 2018), which could result in unequal shifts in the timing of reproduction across a species' range whereby some populations advance or delay their flowering date more quickly than others (Park et al., 2018; Rafferty et al., 2020). Population-specific responses to climate change could reduce phenological synchrony among populations, altering gene flow patterns and disrupting beneficial and antagonistic interspecific relationships (Rafferty et al., 2020). Therefore, determining whether species exhibit intraspecific variability in sensitivity to climate is likely to improve our ability to predict both short- and long-term effects of climate change on the phenology of plant populations and communities. In addition, such studies could help land managers to identify regions within species' ranges that are predicted to experience greater (or lesser) phenological shifts in response to climate change and manage these areas accordingly (Morellato et al., 2016; Olliff-Yang et al., 2020).

Recently, the availability and demonstrated reliability of digitized herbarium records has sparked interest in the use of herbarium-based data to estimate species' phenological sensitivities to a myriad of climate variables including temperature (Robbirt et al., 2011; Davis et al., 2015; Rawal et al., 2015; Park et al., 2018; Daru et al., 2019), the number of frost-free days (Park and Mazer, 2018), precipitation as snow (Park et al., 2018), growing degree days (Mulder et al., 2017; Hufft et al., 2018), and precipitation (Matthews and Mazer, 2016; Love et al., 2019). Given the deep temporal record and broad spatial sampling provided by herbarium records for some of the more well-collected species, these records offer an unprecedented opportunity to explore whether species exhibit intraspecific, regional variation in phenological sensitivity to climate and, if so, whether they exhibit geographic variation in the rate of phenological change over time. In one example, Park et al. (2018) used over 7000 herbarium records representing 30 flowering species distributed across a broad latitudinal range (~30–48°N) in the eastern United States and found that, within species, populations experiencing chronically warmer conditions at lower latitudes are more sensitive to spring temperature than those experiencing chronically cooler conditions at higher latitudes. Due to these regional differences in sensitivity, Park et al. (2018) predicted that populations in chronically warmer regions of a given species' range will advance their phenology more rapidly than populations in chronically cooler regions in response to large-scale warming.

Despite the potential consequences of intraspecific variation in climate sensitivity, few studies have explicitly assessed whether species exhibit differences in sensitivity among populations (Park et al., 2018; Rafferty et al., 2020; Song et al., 2020), and none have used the spatial breadth and temporal depth represented by herbarium specimens to test whether differences in sensitivity may have already resulted in divergent temporal shifts in response to climate change during the past century. In the current study, we aimed to fill this gap and to test the prediction (derived from observations of Park et al.) that individuals sampled from relatively warm regions of a species' range exhibit greater phenological advancement in response to historical temperature increases than those sampled from cooler regions. We used 743 herbarium records representing a 112-year collection period of the mountain jewelflower (*Streptanthus tortuosus* Kellogg; Brassicaceae), a montane wildflower species that spans a wide geographic and climatic range in California. First, we evaluated whether individuals sampled from sites characterized by chronically warm vs. cool conditions differ with respect to their temporal shifts in phenology during the past century. This analysis detected that individuals sampled from warm regions of this species' range exhibited greater phenological advancement than those sampled from cooler regions. Given this observed difference, we then evaluated the relative importance of two, nonmutually exclusive potential drivers of these divergent temporal responses: (1) regional differences in the degree of phenological sensitivity to climate among individuals sampled from warm vs. cool regions, (2) regional differences in the magnitude of climate change experienced by individuals sampled from warm vs. cool regions during the period of collection, or (3) both. To evaluate the potential role of these mechanisms in driving the observed divergent responses, we used these herbarium records to assess whether sensitivity to climate differs between individuals sampled from warm vs. cool regions, and whether climate change occurred uniformly across chronically warm and cool regions of the mountain jewelflower's range.

METHODS

Study system

Streptanthus tortuosus is a forb that is native to the California Floristic Province. The species flowers between early spring and late summer, depending on its location (e.g., high or low elevation). Vernalization during the winter months is required to induce flowering in *S. tortuosus* (Preston, 1991; Gremer et al., 2019). Plant size, flower size, and flower color (yellow-white, purple, or intermediate) are variable across its range (Preston, 1994; Baldwin et al., 2012; N. L. R. Love, personal observation). The species is pollinated predominantly by bees, but a wide variety of pollinators have been documented visiting flowers, including wasps, flies, butterflies, and beetles. Although *S. tortuosus* is self-compatible, few seeds are set in the absence of effective pollinators (Preston, 1994).

Streptanthus tortuosus has three features that make it a highly suitable species with which to assess intraspecific variation in phenological sensitivity to climate and its potential causes and consequences. First, the species spans a wide variety of climatic conditions in California—from low-elevation, relatively hot and dry foothills to high-elevation, relatively cold, and mesic environments (based on its distribution documented in the California Consortium of Herbaria, www.cch2.org, and in the Global Biodiversity Information Facility, www.gbif.org); consequently, we may expect that different environmental cues may induce the timing of cyclical life events in different habitats, generating intraspecific, regional variation in climate sensitivities. Indeed, it has been demonstrated that, among 21 populations of *S. tortuosus* across an elevation gradient, populations differ with respect to the environmental cues that induce seed germination (Gremer et al., 2019). We may similarly expect flowering phenology to respond to distinct environmental cues across climate gradients. Second, *S. tortuosus* is phenologically sensitive to temperature and precipitation (Love et al., 2019); however, it is unknown whether the degree of sensitivity varies within the species. Third, *S. tortuosus* is well represented by herbarium records that provide a spatially and temporally robust data set with which to detect any regional variation in the magnitude of climate change experienced during the past century and in phenological sensitivity to climate (California Consortium of Herbaria; www.cch2.org).

Phenological scoring

To address our objectives, we assembled 1322 herbarium records from seven herbaria (CAS, CHSC, DAV, OBI, RSA, SFV, and UCJEPS) that represent the spatial range of *Streptanthus tortuosus* (Appendix S1). Herbarium specimens from CAS, CHSC, OBI, and SFV were imaged using an ORTECH Photo e-Box Plus 1419 imaging station (ORTECH Professional Lighting, Chula Vista, CA, USA) at University of California Santa Barbara's Cheadle Center for Biodiversity and Ecological Restoration. Imaged herbarium specimens from DAV, RSA, and UCJEPS were downloaded from the California Consortium of Herbaria 2 portal (CCH2; www.CCH2.org). Before the quantitative phenological scoring of herbarium specimens (described below), we excluded 13 specimens with blurry images, 98 specimens with a recorded collection date that spanned a range greater than three days (e.g., May 1898 or 1–15 May 1898), 20 specimens with no reproductive structures, and 53 specimens with highly overlapping reproductive structures, which preclude obtaining an accurate score. Other criteria for excluding specimens are described below.

To score the phenological status of the remaining 1138 herbarium specimens, we counted the number of buds, flowers, immature, and mature fruits borne by each plant on a given specimen sheet and then used these counts to calculate a quantitative metric of phenological progression—the phenological index (PI)—for each plant according to the phenophase definitions and the ImageJ protocol presented by Love et al. (2019; Eq. 1). The PI represents the degree of phenological advancement of each plant on a given herbarium specimen and recording this value enables the statistical control for variation in phenological stage among specimen sheets when included in phenoclimatic models (Love et al., 2019). To calculate the PI, each class of reproductive unit was assigned a specific value from 1–4 that represents its phenological advancement relative to other classes (buds = 1, flowers = 2, immature fruits = 3, and mature fruits = 4). The proportions of reproductive units in each class were then used to calculate a phenological index (PI) using the following equation:

$$\mathrm{PI} = \sum_{i=1}^{4} P_x i, \tag{1}$$

where P_x represents the proportion of reproductive units in class x and i represents the index value associated with that class (e.g., buds have a value of 1). A given plant with a PI of 1 would represent a plant displaying only buds, while a plant with a PI of 4 would represent a plant bearing only mature fruits. For example, a plant with four buds, nine flowers, 11 immature fruits, and 43 mature fruits would have a PI of 3.38, which would indicate that the plant is relatively late in its phenological advancement. For herbarium specimens with more than one reproductive plant on a single sheet, the phenological indices of all reproductive plants on a given sheet were averaged to produce a mean PI value for the specimen (Appendix S2).

After scoring, each herbarium specimen was georeferenced by either (1) downloading the latitude and longitude from the

California Consortium of Herbaria (www.cch2.org) or (2) by extracting coordinates from the written location description on the specimen label using GeoLocate (www.geo-locate.org). Each set of coordinates was associated with a radius of uncertainty in meters to indicate the precision of the specimen location. We excluded 104 specimens that we were unable to georeference because the location description provided on the label was too general (e.g., Yosemite National Park), 94 specimens with an uncertainty radius greater than 4000 m, and 164 duplicate specimen records. A summary of the exclusion criteria and number of specimens excluded with each criterion can be found in Appendix S3.

The collection date of each remaining specimen was converted into a day of year of collection (DOY) from 1 to 365. The resulting data set included 776 herbarium specimens collected between 4 July 1863 and 9 August 2013 and represented the geographic range of *S. tortuosus* well (Figure 1).

Climate data

We evaluated phenological sensitivity to a set of climate variables that have been found to be important for predicting flowering onset in other taxa (Cleland et al., 2007; Anderson et al., 2012; Park and Mazer, 2018). Climatic conditions (both long-term mean climate and climate during the year of specimen collection) at the collection location of each specimen were characterized by extracting site-specific climate data from Climate NA, a climate data source that downscales gridded PRISM data to scale-free point locations (Wang et al., 2016a). To characterize the temperature during the year in which each specimen was collected (YOC), we extracted the site- and year-specific minimum (Tmin), maximum (Tmax), and mean (Tave) temperatures during winter (average between December and February, when buds are developing) and spring/summer (average between March and August, when flowers are opening and being pollinated). We focused on winter temperatures because *S. tortuosus* requires vernalization to induce flowering (Preston, 1991; Gremer et al., 2019), and thus we might expect it to be sensitive to winter temperatures. We also focused on the spring/summer temperatures because the onset of flowering for this species occurs between March and August, so plants may use temperature as a cue during this period to induce the onset of flowering.

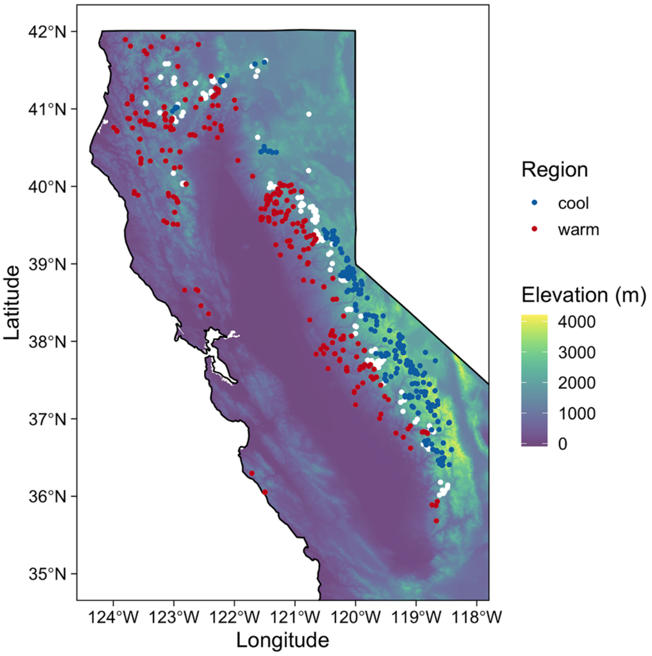

FIGURE 1 Locations of *Streptanthus tortuosus* specimens collected in cool regions (blue circles; $n = 299$) and warm regions (red circles; $n = 294$) of the species' range. The white circles are those records for which the collection site represents the middle 20% of the temperature range of *S. tortuosus* ($n = 150$). These records were removed prior to the warm vs. cool region comparisons

To characterize the onset and length of the growing season during the YOC, we downloaded the day of year of onset of the frost-free period (bFFP) and the number of frost-free days (NFFD) at each specimen collection location (Table 1). To characterize precipitation during the YOC, we downloaded the cumulative annual precipitation as snow (PAS) and the cumulative annual precipitation (MAP, which includes PAS; Table 1). The earliest historical climate data available through ClimateNA is 1901; thus, specimens collected before 1901 (33 specimens) were excluded from the final data set (Appendix S3). The site-specific YOC data were extracted for 743 specimens with collection dates ranging from 17 May 1902 to 9 August 2013. To characterize the long-term mean or chronic temperature conditions at each collection site, we extracted the long-term mean (90-year; 1901–1990) of the mean annual temperatures (MATs).

Delimiting cool vs. warm regions

To delimit which specimens were collected in chronically cool vs. chronically warm regions of the mountain jewelflower's range, we first used the distribution of long-term mean MAT among all collection sites to calculate 10 quantiles (i.e., deciles). Then, to create a more explicit comparison between cool vs. warm regions, we removed the central two deciles (deciles 5 and 6) from the data set ($n = 150$, Appendix S4). Below, we refer to the data set from which these two deciles were removed as the "reduced data set" ($n = 593$). Specimens representing the lower four deciles (1–4) were considered to be collected from chronically cool regions ($n = 299$), while the upper four deciles (7–10) were considered to be collected from chronically warm regions ($n = 294$; Appendix S4). The cool vs. warm regions were defined by the chronic conditions at each given specimen collection site (Figure 1); however, these regions align well with geographic subregions within the borders of California (Jepson Flora Project, 2021). In this study, warm regions correspond geographically to the Klamath and North Coast Ranges, and the Sierra Nevada Foothills. Cool regions correspond to the High Sierra Nevada. The mean DOY between regions was compared using a Welch two-sample *t*-test in R version 3.6.1 (R Core Team, 2019).

TABLE 1 Summary of the linear regression conducted to detect the effect of collection year on the day of year of collection (DOY) while controlling for geographic variables (latitude, longitude, and elevation) among (a) all specimens ($n = 743$) and (b) among specimens in the reduced dataset ($n = 593$) to compare shifts in cool ($n = 299$) vs. warm ($n = 294$) regions

(a) Independent variable	**Estimate**	**SE**	***t* ratio**	**$P > \|t\|$**
Intercept	216.89	127.57	1.70	0.09
Phenological index	16.88	1.02	16.57	**<0.001**
Year	−0.10	0.027	−3.75	**<0.001**
Elevation	0.029	0.0010	27.94	**<0.001**
Latitude	5.02	1.07	4.68	**<0.001**
Longitude	1.02	1.22	0.84	0.40

Source of variation	**df**	**SS**	***F* ratio**	***P***
Intercept	1	1073	2.89	0.09
Phenological index	1	101899	274.45	**<0.001**
Year	1	5219	14.06	**<0.001**
Elevation	1	289774	780.45	**<0.001**
Latitude	1	8121	21.87	**<0.001**
Longitude	1	259	0.70	0.40
Error	737	273642		
R^2				0.70

(b) Term	**Estimate**	**SE**	***t* ratio**	**$P > \|t\|$**
Intercept	−116.07	133.99	−0.87	0.39
Phenological index	17.33	1.13	15.35	**<0.001**
Year	−0.090	0.030	−2.99	**0.0029**
Temperature region [C]	1.06	1.78	0.59	0.55
Elevation	0.029	0.0017	17.17	**<0.001**
Latitude	4.31	1.28	3.37	**<0.001**
Longitude	−0.33	1.46	−0.23	0.82
Year × temperature region [C]	0.10	0.030	3.43	**<0.001**

Analysis of variance source	**df**	**SS**	***F* ratio**	***P***
Intercept	1	270	0.75	0.39
Phenological index	1	84698	235.56	**<0.001**
Year	1	3224	8.97	**0.0029**
Temperature region	1	127	0.35	0.55
Elevation	1	105952	294.68	**<0.001**
Latitude	1	4087	11.37	**<0.001**
Longitude	1	19	0.05	0.82
Year × temperature region	1	4226	11.75	**<0.001**
Error	585	210340		
R^2				0.74

Detecting temporal shifts in phenology

To assess phenological shifts during the 112-year collection period (1902–2013), we constructed two multiple linear regressions designed to detect the effect of collection year on DOY. The first model was designed to detect a shift among all specimens pooled ($n = 743$) and included the phenological index (PI), year of collection (YOC), and geographic variables (elevation, latitude, and longitude) as predictor variables (Eq. 2).

$$\begin{aligned} \mathrm{DOY} = {} & b_0 + b_1(\mathrm{PI}) + b_2(\mathrm{YOC}) + b_3(\mathrm{Latitude}) \\ & + b_4(\mathrm{Longitude}) + b_5(\mathrm{Elevation}) + \varepsilon \end{aligned} \tag{2}$$

The second model was designed to determine whether the magnitude and/or direction of phenological shifts depends on the long-term mean climatic conditions to which collection sites were exposed (i.e., cool vs. warm regions). This model was constructed using the reduced data set and included DOY as the response variable and the PI, year of collection, geographic variables, temperature region (cool or warm), and the year × temperature region interaction as predictors. The geographic variables were included to control for the possibility that non-random sampling across the collection period could confound the detection of the temporal shifts in phenology (Eq. 3).

$$\begin{aligned} \mathrm{DOY} = {} & b_0 + b_1(\mathrm{Phenological\ Index}) \\ & + b_2(\mathrm{Year\ of\ Collection}) + b_3(\mathrm{Latitude}) \\ & + b_4(\mathrm{Longitude}) + b_5(\mathrm{Elevation}) \\ & + b_6(\mathrm{Temperature\ Region}) \\ & + b_7(\mathrm{Year\ of\ Collection})(\mathrm{Temperature\ Region}) \\ & + \varepsilon \end{aligned} \tag{3}$$

Estimating region-specific sensitivities to climate

To determine whether individuals sampled from cool vs. warm regions collectively differ in their estimated sensitivities to climate (i.e., the absolute change in the DOY in response to each one-unit increase in the climate variable), we constructed 11 multiple linear regressions (one for each climate variable listed in Table 2) designed to detect the effect of climate during the YOC on DOY (Eq. 4). Each model included DOY as the response variable, while the temperature region (cool vs. warm), the PI (to control for variation in phenological stage among specimens), and one of the 11 climate variables of interest were included as the predictors. In addition, the models designed to estimate sensitivity to temperature, bFFP, or NFFD included the YOC MAP as an independent variable; these models therefore controlled for variation in MAP when detecting the sensitivity of DOY to temperature-based variables. Similarly, the models designed to estimate the sensitivity to MAP or PAS included YOC

TABLE 2 Regression coefficients (a) representing the estimated change in the climate variables during the 112-year collection period in cool vs. warm regions independent of model covariates (latitude, longitude, elevation, and cumulative mean annual precipitation (MAP) or mean annual temperature (MAT)), and (b) the estimated sensitivity of *Streptanthus tortuosus* to each climate variable in cool versus warm regions independent of model covariates (cumulative mean annual precipitation and the phenological index). When the two-way interaction between the climate variable and temperature region (cool vs. warm) is significant at $\alpha = 0.95$ (indicating that the estimates differ between cool vs. warm regions), an estimate for each region is reported. When the interaction is not significant, a single estimate for both regions is reported. The ratio of the warm to cool region coefficient estimate is listed when the coefficient differs significantly between regions. Full model summaries for estimating the magnitude of climate change during the past century and the estimated sensitivities to climate are presented in Appendix S7 and S8, respectively

	(a) Estimated change during the past century			(b) Sensitivity to climate		
Climate variable	Cool	Warm	Warm:cool ratio	Cool	Warm	Warm:cool ratio
MAT (°C)	1.34 ± 0.20***			−4.46 ± 0.58***	−8.31 ± 0.51***	1.86
Winter Tmin (°C)	0.93 ± 0.42*	2.3 ± 0.41***	2.47	−2.91 ± 0.49***	−5.84 ± 0.47***	2.01
Winter Tmax (°C)	1.15 ± 0.27***			−2.91 ± 0.53***	−5.97 ± 0.44***	2.05
Winter Tave (°C)	1.38 ± 0.26***			−3.55 ± 0.56***	−6.56 ± 0.47***	1.84
Spring/summer Tmin (°C)	1.89 ± 0.36***	3.19 ± 0.35***	1.68	−3.64 ± 0.57***	−7.08 ± 0.50***	1.94
Spring/summer Tmax (°C)	NS			−4.02 ± 0.44***	−6.22 ± 0.40***	1.55
Spring/summer Tave (°C)	1.47 ± 0.22***			−4.42 ± 0.51***	−7.85 ± 0.46***	1.78
bFFP (days)	−12.78 ± 4.55***	−32.98 ± 4.48***	2.58	0.27 ± 0.07***	0.52 ± 0.04***	1.93
NFFD (days)	31.47 ± 6.96***	54.52 ± 6.86***	1.73	−0.16 ± 0.04***	−0.32 ± 0.02***	2.00
MAP (mm)	NS	428 ± 118***		0.0092 ± 0.0013***		
PAS (mm)	−145.87**	NS		0.016 ± 0.0036***	0.142 ± 0.022***	8.88

*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

MAT as an independent variable. The two-way interaction between temperature region (cool vs. warm) and the YOC climate variable of interest was also included to determine whether sensitivity of DOY to the climate variable differed between regions (Eq. 4).

$$\begin{aligned}\mathrm{DOY} = {} & b_0 + b_1(\text{Temperature Region}) \\ & + b_2(\text{Phenological Index}) \\ & + b_3(\text{Climate Variable}_{\mathrm{YOC}}) \\ & + b_4(\mathrm{MAP}_{\mathrm{YOC}} \text{ or } \mathrm{MAT}_{\mathrm{YOC}}) \\ & + b_5(\text{Temperature Region}) \\ & \times (\text{Climate Variable}_{\mathrm{YOC}}) + \varepsilon\end{aligned} \tag{4}$$

Estimating region-specific changes in climate through time

To determine whether the magnitude of climate change experienced by individuals sampled from cool vs. warm regions differed during the 112-year collection period, we constructed 11 multiple linear regressions (one for each climate variable listed in Table 2) designed to detect the effect of specimen collection year on the YOC climate at a given specimen's collection location (Eq. 5). Each model included the climate variable of interest as the response variable, the temperature region (cool vs. warm), the YOC, the geographic variables (latitude, longitude, and elevation), and the YOC MAP (for models estimating changes in temperature, bFFP, or NFFD) or YOC MAT (for models estimating changes in MAP or PAS) as main effects. The geographic variables were included to control for the possibility that spatially nonrandom sampling across the collection period could confound the detection of the direct relationship between climate and year. The YOC × temperature region (cool vs. warm) interaction was also included in the model to determine whether the estimated magnitude of climate change over the 112-year collection period differed between regions (Eq. 5).

$$\begin{aligned}\text{Climate Variable}_{\mathrm{YOC}} = {} & b_0 + b_1(\text{Temperature Region}) \\ & + b_2(\text{Year of Collection}) \\ & + b_3(\text{Latitude}) + b_4(\text{Longitude}) \\ & + b_5(\text{Elevation}) \\ & + b_6(\mathrm{MAP}_{\mathrm{YOC}} \text{ or } \mathrm{MAT}_{\mathrm{YOC}}) \\ & + b_7(\text{Temperature Region}) \\ & \times (\text{Year of Collection}) + \varepsilon\end{aligned} \tag{5}$$

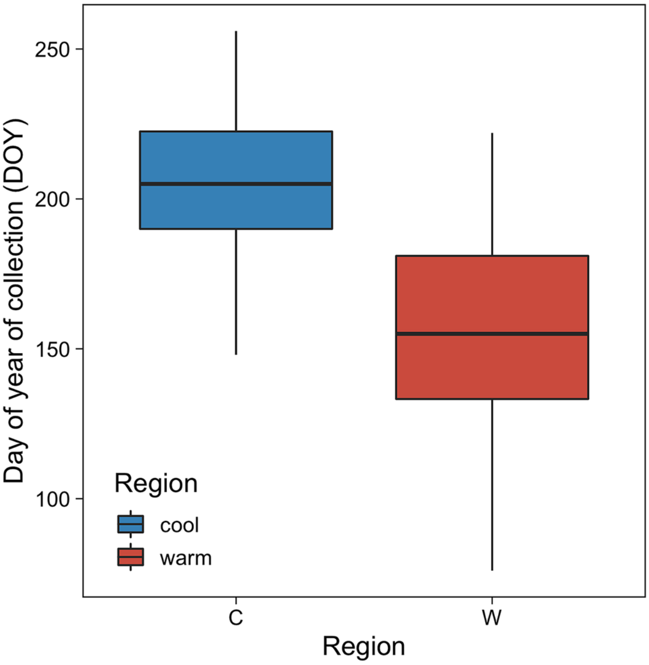

FIGURE 2 Box and whisker plots representing the distribution of the day of year (DOY) of specimens collected in cool (blue) and warm (red) regions. The horizontal line within each box represents the median, and the lower and upper hinges correspond to the first and third quartiles, respectively. The lower and upper whiskers extend to the smallest and largest values of DOY

We chose to seek evidence of region-specific temporal phenological shifts, sensitivity to climate, and climate change by assessing these effects in discrete warm vs. cool regions rather than by assessing the interaction between long-term mean MAT (as a continuous variable) and year or seasonal temperature because long-term mean MAT is highly correlated with some of the 11 climatic variables of interest (e.g., correlation with winter Tmin: $r = 0.95$; with spring/summer Tmin: $r = 0.97$) and with some of the geographic variables (e.g., correlation with elevation: $r = -0.95$). To avoid difficulties in interpreting the output of multiple regressions when there is multicollinearity among predictor variables and to maintain consistency and comparability among all models, we chose to assess region-specific phenological responses in warm vs. cool regions.

All multiple linear regressions conducted for this study were constructed using OLS regression and type III sum of squares with the lm() function and car package in R (Fox and Weisberg, 2019). All analyses were performed in R version 3.6.1 (R Core Team, 2019).

Relative importance of regional differences in sensitivity vs. differences in the magnitude of climate change

To evaluate the relative importance of regional differences in sensitivity vs. regional differences in the magnitude of climate change in driving the observed differences in the phenological advancement through time between regions, we calculated the ratio between estimates of both climate change and sensitivity to climate in cool vs. warm regions. If, for example, the ratio between the magnitudes of climate change in warm vs. cool regions (e.g., Δ winter Tmin in warm regions/Δ winter Tmin in cool region) was consistently higher than the ratio between the sensitivity to climate variables in warm vs. cool regions (e.g., warm region sensitivity to winter Tmin/cool region sensitivity to winter Tmin), then we may infer that regional differences in the magnitude of climate change are more important than regional differences in sensitivity in explaining the observed difference between regions in temporal phenological shifts. Conversely, if the ratio between sensitivities in warm vs. cool regions was higher than that between the magnitudes of climate change in cool vs. warm regions, then differences in the degree of sensitivity may be more important in driving observed differences in temporal phenological shifts.

RESULTS

Our data set spanned a 112-year collection period from 1902–2013 (Appendix S5). The mean DOY among all specimens ($n = 743$) was 182 (1 July; SD = 35.04, range: 76–256; Appendix S6). Specimens sampled from cool regions were, on average, collected 50 days later than those sampled from warm regions (95% CI: 45.04–54.96 days, $t = 22.23$, $P < 0.001$; Figure 2). The mean DOY among specimens sampled from cool regions ($n = 299$; 90-year MAT range: −0.5–6.46°C) was 205 (24 July; SD = 23.59, range: 148–256) and from warm regions ($n = 294$; 90-year MAT range: 9.46–16.9°C) was 155 (4 June; SD = 31.12, range: 76–222; Figure 2).

Temporal shifts in flowering date

Among all specimens ($n = 743$), we detected a 10-day advancement in flowering DOY over the past 100 years (estimate = −0.10 ± 0.03 days/year, $t = -3.75$, df = 1, $P < 0.001$) independent of phenological status and geographic location (Table 1b; Figure 3A). This temporal shift, however, differed significantly between warm and cool regions. We detected a 19-day advancement in flowering date among specimens sampled from warm regions (estimate = −0.19 ± 0.04 days/year, $t = -4.61$, df = 1, $P < 0.001$), but we found no evidence of a temporal shift among specimens sampled from cool regions ($t = 0.29$, df = 1, $P = 0.77$; Table 1b; Figure 3B). The model designed to detect a temporal shift in flowering DOY among all specimens explained 70% of the variance in DOY, while the model designed to detect temporal shifts in warm vs. cool regions using the reduced data set accounted for 74% of the variance in DOY (Table 1).

Region-specific sensitivity to climate

Increased annual and seasonal temperatures advanced flowering DOY among all specimens in the reduced data set,

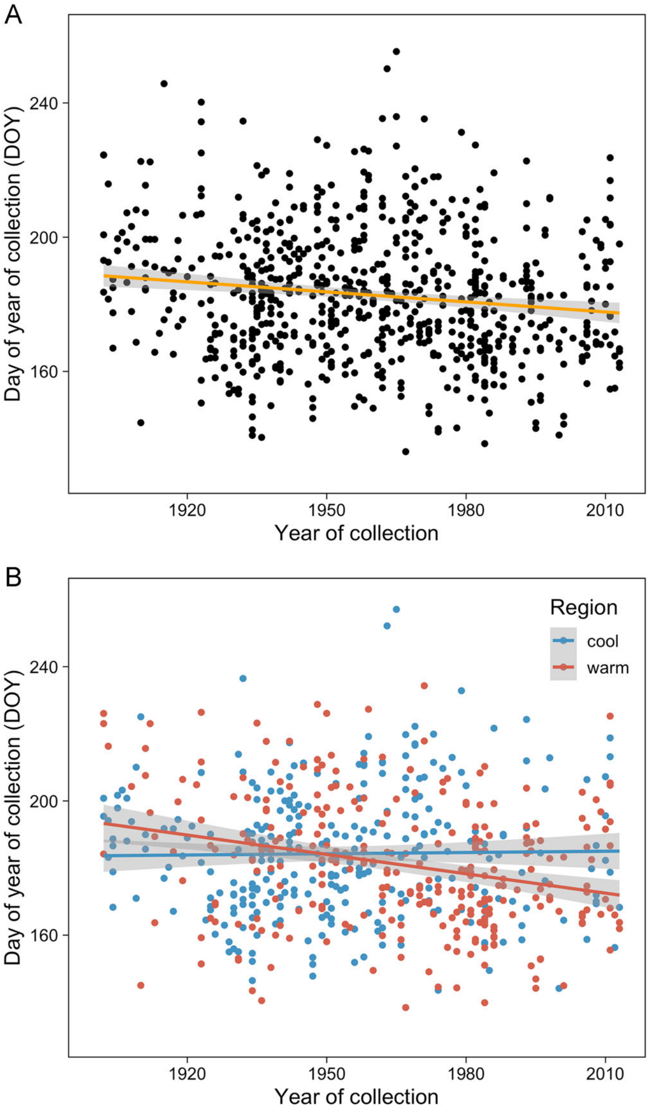

FIGURE 3 The relationship between the day of year of collection (DOY) and year for (A) all specimens in the final data set ($n = 743$) and (B) those specimens collected in cool (blue points; n = 299) and warm (red points; $n = 294$) regions

but those sampled from warm regions were more sensitive than those from cold regions to all of the temperature-related climate variables (MAT; winter Tmin, Tave, Tmax; and spring/summer Tmin, Tave, Tmax) tested in this study independent of geographic location and phenological status (Table 2). For example, among specimens sampled from warm regions, flowering DOY advanced 5.84 ± 0.47 days per 1°C increase in winter Tmin, while among specimens sampled from cool regions, flowering DOY advanced only 2.91 ± 0.49 days per 1°C increase in winter Tmin (temperature region × winter Tmin: $t = 4.33$, df = 1, $P < 0.001$; Figure 4A, Table 2b; Appendix S7). Similarly, among specimens sampled from warm regions, flowering DOY advanced 7.08 ± 0.50 days per 1°C increase in the mean minimum temperature during spring and summer, while among specimens sampled from cool regions, flowering DOY advanced only 3.64 ± 0.57 days per 1°C increase in spring/summer Tmin (temperature region × spring/summer Tmin: $t = 4.46$, df = 1, $P < 0.001$; Figure 4B, Table 2b; Appendix S7). The seven models designed to estimate the sensitivity of *S. tortuosus* to temperature-related variables in cool vs. warm regions explained 72–77% of the variance in DOY (Appendix S7).

Similarly, specimens sampled from warm regions were more sensitive to the onset of the growing season (as estimated by the bFFP) and the length of the growing season (as estimated by the NFFD). Earlier onset and longer growing seasons advanced flowering DOY among all specimens in the reduced data set, but these effects were strongest among specimens sampled from warm regions (Table 2). Among specimens sampled from warm regions, a 1-day advance in the onset of the growing season advanced flowering DOY by 0.52 ± 0.04 days, while in cool regions a 1-day advance in the onset of the growing season advanced flowering DOY by only 0.27 ± 0.07 days (temperature region × bFFP: $t = -3.27$, df = 1, $P = 0.001$; Figure 3C, Table 2b; Appendix S7). The models designed to estimate the sensitivity of flowering DOY to the bFFP and NFFD explained 73% and 72% of the variance in DOY, respectively (Appendix S7).

Among all specimens in the reduced data set, increased precipitation (as measured by MAP and PAS) delayed flowering DOY. The two-way interaction between MAP and temperature region was not significant, indicating that the effect of MAP on flowering DOY did not significantly differ between cool and warm regions (temperature region × MAP: $t = 1.81$, df = 1, $P = 0.07$; Table 2b; Appendix S7). In both cool and warm regions, flowering DOY was delayed 0.92 days per 100-mm increase in MAP (MAP: estimate = 0.0092 days/mm; $t = 7.21$, df = 1, $P < 0.001$; Table 2b; Appendix S7). Specimens sampled from warm regions were more sensitive to PAS than those from cool regions (warm: estimate = 0.14 ± 0.02 days/mm; cool: estimate = 0.016 ± 0.003 days/mm; temperature region × PAS: $t = -5.82$, df = 1, $P < 0.001$; Table 2b; Appendix S7). Both models designed to estimate the sensitivity of flowering DOY to MAP and PAS explained 75% of the variance in DOY (Appendix S7).

Region-specific changes in climate through time

Among temperature-related variables, we detected long-term temporal increases in MAT, winter Tmin, winter Tave, winter Tmax, spring/summer Tmin, and spring/summer Tave independent of geographic location and MAP during the YOC (Table 2a; Appendix S8). Warm regions experienced a greater degree of temporal change in winter and spring/summer minimum temperatures than cool regions. During the past century, winter minimum temperatures increased an estimated 2.3 ± 0.41°C in warm regions vs. 0.93 ± 0.42°C in cool regions (temperature region × year:

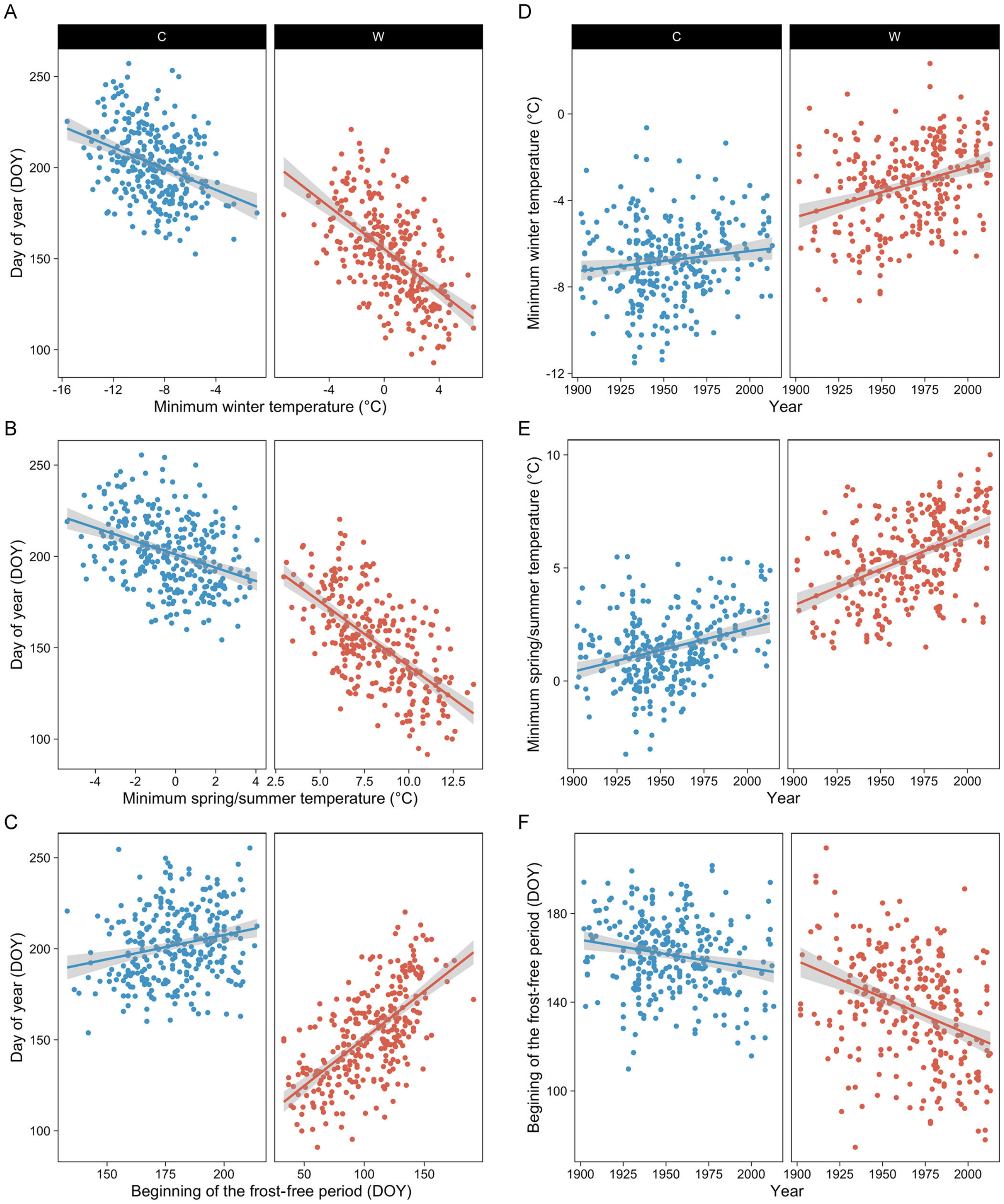

FIGURE 4 Partial regression plots representing the sensitivity of *Streptanthus tortuosus* to (A) minimum winter temperature, (B) minimum temperature during spring and summer, and (C) the day of year of the beginning of the frost-free period independent of model covariates (cumulative mean annual precipitation and the phenological index) in cool versus warm regions. The remaining plots (D–F) show how these same variables have shifted during the 112-year collection period independent of model covariates (latitude, longitude, elevation, and cumulative mean annual precipitation). Individual slopes for each of these relationships are listed in Table 2

$t = -2.35$, df = 1, $P = 0.019$; Figure 4D, Table 2a; Appendix S8). Similarly, spring/summer minimum temperatures increased an estimated 3.19 ± 0.35°C in warm regions vs. 1.89 ± 0.36°C in cool regions during the past century (temperature region × year: $t = -2.57$, df = 1, $P = 0.01$; Figure 4E, Table 2a; Appendix S8). The degree of temporal change in MAT, winter Tmax, winter Tave, and spring/summer Tave was similar between cool and warm regions (i.e., the year × temperature region interaction was not significant; Table 2a). We detected no evidence that the maximum temperature during the spring/summer growing season had changed in either temperature region ($t = 1.52$, df = 1, $P = 0.13$; Table 2a; Appendix S8). The seven models designed to detect changes in annual and seasonal temperature among sampled locations during the past century explained 84–93% of the variance in temperature (Appendix S8).

Similarly, we detected long-term temporal changes in the day of year of onset of the growing season (as estimated by bFFP) and the length of the growing season (as estimated by NFFD) independent of geography and MAP in the YOC. In the case of both variables, the degree of change experienced by specimens sampled from warm regions was greater than that experienced by specimens sampled from cool regions. The beginning of the frost-free period has advanced an estimated 32.98 ± 4.48 days in warm regions vs. 12.78 ± 4.55 days in cool regions during the past century (temperature region × year: $t = 3.16$, df = 1, $P = 0.0017$; Figure 4F, Table 2a; Appendix S8). The growing season has lengthened by an estimated 54.42 ± 6.86 days in warm regions vs. 31.47 ± 6.96 days in cool regions during the past century (temperature region × year: $t = -2.35$, df = 1, $P = 0.019$; Table 2a; Appendix S8).

We detected a long-term mean increase in MAP in warm regions but no evidence of a change in MAP in cool regions during the past century (Table 2). Specimens sampled from warm regions experienced an increase of 428 ± 118 mm of cumulative MAP during the past 100 years, while those sampled from cool regions experienced no significant change in MAP (temperature region × year: $t = -3.87$, df = 1, $P < 0.001$; Table 2a; Appendix S8). We detected a decrease of 146 ± 47 mm in PAS in cool regions (temperature region × year: $t = -2.92$, df = 1, $P = 0.004$; Table 2a; Appendix S8), but no significant change in warm regions during the past century. The models designed to detect temporal changes in precipitation independent of geography and MAT in the YOC explained 30% of the variance in MAP and 90% of the variance in PAS among all sampled locations during the 112-year collection period (Appendix S8).

Relative importance of regional differences in sensitivity vs. regional differences in the magnitude of climate change

Cool and warm regions differ with respect to both the magnitude of climate change experienced by individuals and the estimated phenological sensitivity to climate among individuals (Figure 4, Table 2). With respect to minimum temperatures, the bFFP, the NFFD, and MAP, individuals sampled from warm regions have experienced a greater degree of change and also exhibit a higher degree of phenological sensitivity to these variables (Table 2). For example, relative to cool regions, warm regions have experienced a 2.47× and 1.68× greater increase in winter Tmin and spring/summer Tmin, respectively, and individuals sampled from warm regions are 2.01× and 1.94× more sensitive to winter Tmin and spring/summer Tmin, respectively, than those sampled from cool regions (Figure 4A, B, D, E). Similarly, warm regions have experienced a 2.58× greater advancement in the bFFP and individuals sampled from warm regions are 1.93× more sensitive to the bFFP than those sampled from cool regions (Figure 4C, F).

DISCUSSION

This study demonstrates that, based on data derived from herbarium specimens collected across a species' range, the degree of phenological sensitivity to climate and the magnitude of phenological shifts through time in response to climate change can vary within species. During the 112-year collection period examined here, flowering date advanced significantly among individuals of *Streptanthus tortuosus* collected in relatively warm regions but exhibited no evidence of advancement among those collected in cool regions. The evidence presented here suggests that the difference in temporal shifts in flowering date between cool and warm regions is likely driven by both (1) intraspecific variation in phenological sensitivity to climate variables and (2) differences in the magnitude of climate change experienced by individuals and populations in cool vs. warm regions. These results and their implications are discussed in detail below.

Regional differences in phenological advancement

The results presented here add to the mounting evidence that plants have responded to climate change (specifically, increases in temperature) by advancing their flowering date (Parmesan and Yohe, 2003; Cleland et al., 2007; but see Banaszak et al., 2020); however, our study is one of the few to detect intraspecific variation in the magnitude of temporal shifts within a wide-ranging species (Prevéy et al., 2017; Rafferty et al., 2020). Among all individuals of *S. tortuosus* sampled in this study, flowering date advanced 10 days during the past century, but this pattern was driven by the advancement of individuals collected in warm regions, which exhibited a 20-day advancement in flowering date (Figure 3, Table 1). Individuals collected in relatively cool regions exhibited no evidence of advancement in flowering date (Figure 3B, Table 1b).

Biases inherent in herbarium-based phenological data may influence estimates of phenological shifts through time (Lavoie, 2013; Daru et al., 2018). For example, specimens are collected nonrandomly through space and time; therefore, it is possible that temporal shifts in phenology detected in herbarium-based studies reflect changes in sampling locations through time rather than true responses to climate change. For example, if more recent collections represent specimens in warmer locations where flowering occurs earlier, then an advancement in collection date through time would result that may be wrongfully interpreted as an advancement in phenology. In addition, reproductive specimens may be collected at any phenological stage between budding and fruiting, limiting our ability to reliably use the DOY as an estimate of flowering date (Love et al., 2019). Moreover, this variation could potentially introduce noise or bias into models estimating phenological shifts. In this study, we addressed these potential biases by controlling for both collection location and phenological stage (as estimated by the phenological index) in models designed to estimate phenological shifts, providing us with greater confidence in our estimates of phenological shifts through time.

By seeking evidence for intraspecific, regional variation in phenological advancement, studies may detect nonuniform shifts in phenology across species' ranges; and such divergent phenologies may have several ecological consequences that merit investigation. First, intraspecific differences in phenological advancement among populations may reduce flowering synchrony and pollen-mediated gene flow, thereby affecting processes such as local adaptation or population divergence (Ison et al., 2014; Wang et al., 2016b; Rafferty et al., 2020). Second, non-uniform shifts in phenology may alter population- or region-specific interactions with other organisms (e.g., pollinators, herbivores, competitors; Elzinga et al., 2007; Kudo and Ida, 2013). Third, divergent shifts in phenology may expose some populations to novel conditions (e.g., increased exposure to frost or drought; Franks et al., 2007; Inouye, 2008) or to novel interactions (e.g., plant–plant, plant–herbivore, plant–pollinator interactions; Fabina et al., 2010; Forrest et al., 2010; Theobald et al., 2017). Given these consequences and their potential impact on plant survival, fitness, and population persistence (Fabina et al., 2010; Forrest and Miller-Rushing, 2010; Anderson et al., 2012; Springate and Kover, 2014), assessing the spatial complexity of temporal phenological shifts will help us to forecast the ecological consequences of climate change.

Regional differences in phenological sensitivity to climate

Higher temperature during the year of specimen collection advances flowering date (DOY) in both cool and warm regions; however, relative to individuals sampled from cool regions, individuals in warm regions were about twice as phenologically sensitive to all of the temperature and growing season length variables (i.e., bFFP and NFFD) examined in this study (Figure 4, Table 2). In addition, individuals in warm regions flower earlier than those in cool regions (Figure 2). This intraspecific pattern—where individuals in relatively warm regions both flower earlier and are more phenologically sensitive to temperature—is consistent with the few other studies that have investigated regional variation in temperature sensitivity within species (Menzel et al., 2006; Wang et al., 2015; Park et al., 2018; Song et al., 2020). Moreover, the intraspecific pattern detected here is consistent with the interspecific patterns of temperature sensitivity estimated from many other herbarium-based and field-based studies (i.e., species or communities that flower earlier and/or occur in warm climates are more sensitive to temperature than those that flower later and/or occur in cooler climates; Menzel et al., 2006; Rutishauser et al., 2009; Cook et al., 2012; Wolkovich et al., 2012; Park et al., 2018). The consistent patterns at various taxonomic and ecological scales suggest that the underlying drivers may be similar and could reflect variation in phenological sensitivity due to differences in life-history strategies (Kudoh et al., 1995; Caffarra and Donnelly, 2011; Li et al., 2014), differences in the reliability of temperature cues (Lapenis et al., 2014; Park et al., 2018), or differences in the abiotic drivers of selection on plant phenology (Theobald et al., 2017).

Contrary to the intraspecific pattern detected in this study, where individuals in warm regions are more sensitive to temperature than those in cool regions, Prevéy et al. (2017) found that, among 47 plant species occurring in the Arctic tundra, conspecific populations occupying relatively cool regions at higher latitudes were more sensitive to temperature than those occupying warm regions at lower latitudes. These contrasting patterns suggest that spatial variation in temperature sensitivity may differ among biomes (Ernakovich et al., 2014; Carbognani et al., 2018). However, despite detecting a pattern that contrasts with the findings presented here, Prevéy et al. (2017) also found that interspecific and intraspecific patterns in temperature sensitivity matched—species, as well as conspecific populations, in warmer regions were less sensitive to temperature than those in cooler regions, again suggesting that drivers underlying inter- vs. intraspecific variation in phenological sensitivity may be similar.

Our study highlights the importance of considering intraspecific variation when estimating temperature sensitivity, especially when using these estimates to predict a species' phenological responses to future climate change (Forrest and Miller-Rushing, 2010; Pau et al., 2011; Wolkovich et al., 2014). For example, if a species' sensitivity is estimated by assessing its response to interannual variation in climate at a single (or even a few, spatially close) study site(s), it may not accurately capture the spatial complexity of temperature sensitivity across that species' range. Predictions derived from these estimates could potentially over- or underestimate temporal phenological shifts and consequently inaccurately assess the impact of climate change on species and their interactions with other organisms.

Temporal shifts in phenology are explained by sensitivity to climate and the magnitude of climate change in warm regions

Because of their spatial and temporal sampling breadth, herbarium-based data are uniquely suited to test how well estimated phenological sensitivities explain temporal shifts in phenology that have already occurred in response to climate change during the past century. For example, in the present study, minimum temperature during the flowering period (spring/summer) of *S. tortuosus* in warm regions has increased an estimated 3.2 ± 0.3°C during the past century and, based on the sensitivity of flowering time to spring/summer Tmin exhibited by individuals in warm regions, we would predict the increase in spring/summer Tmin to result in a 18.60–26.83 day advancement of DOY among individuals in warm regions over the past century (Figure 4B, E; Table 2). This predicted phenological shift is similar to the observed 19.0 ± 3.0 day advancement among individuals in warm regions during the past century that was detected in this study. In addition to spring/summer Tmin, the predicted temporal advancement of DOY in warm regions in response to increases in winter Tmin (10.15–17.1 days) and advances in the onset of the bFFP (13.68–20.98 days) are also similar to the observed advancement (Table 2). The 428 ± 118 mm increase in MAP in warm regions during the past century is predicted to delay flowering date by 2.85–5.02 days and may have slightly counteracted the advance caused by increasing temperatures and advancing bFFP.

Given that (1) individuals in cool regions are sensitive to temperature and other temperature-related variables (e.g., bFFP and NFFD), and that (2) the temperature has changed during the 112-year observation period—why are we unable to detect any temporal shift in phenology among individuals sampled from cool regions? One possibility is that individuals in cool vs. warm parts of species ranges may rely on different cues to induce flowering. For example, many alpine wildflowers are phenologically sensitive to the date of snowmelt (Totland and Alatalo, 2002; Kudo and Hirao, 2006; Inouye, 2008; Carbognani et al., 2018). Because individuals of *S. tortuosus* in cool regions primarily occur in high elevation, alpine environments, the date of snowmelt may be an important cue to induce flowering (Figure 1). While we did not test for the direct effects of snowmelt date on DOY in this study, it is likely strongly correlated with the bFFP (the date on which temperatures are consistently above 0°C). In cool regions, the predicted temporal advancement of flowering date based on the sensitivity of individuals to the bFFP in response to the 12.8 ± 4.3 day advancement in the bFFP during the past century is 1.7–5.8 days (Table 2). Given that the standard error of the estimated temporal shift in flowering date is ±3 days, the slight advancement of flowering date predicted by the advance in the bFFP may be too small to detect due to background variation in flowering date in response to interannual variation in climate (Figure 3B, Table 1b). Moreover, compared to specimens collected in warm regions, those collected in cool regions are underrepresented in more recent years, when the effects of warming may have been expressed more strongly (due to accelerating climate change), potentially hindering our ability to detect a significant phenological shift (Appendix S5).

We found that the greater temporal advancement of flowering date among specimens in warm regions vs. those collected in cool regions is explained by both (1) a higher sensitivity to phenologically important climate variables and (2) a greater increase in temperature (especially minimum temperatures), and consequently, a greater advance in the onset of spring (as measured by the bFFP) experienced by individuals collected in warm regions (Figures 3B, 4; Table 2). This study is one of the first to demonstrate that differences in both sensitivity and the degree of climate change experienced among populations contribute to regional differences in the magnitude of temporal shifts in phenology (Prevéy et al., 2017). Given these results, future studies using models to predict changes in phenology and species interactions should consider both differences in the degree of sensitivity to climate and the expected magnitude of climate change when forecasting impacts (Cleland et al., 2007; Forrest and Miller-Rushing, 2010; Pau et al., 2011). Additionally, by hindcasting temporal shifts in phenology using estimated sensitivities to various climate variables, we can assess the predictive capacity of these sensitivities and thus may be able to improve the accuracy of predictions regarding future shifts in phenology in response to continuing climate change.

Relative importance of regional differences in sensitivity vs. the magnitude of climate change

One of the goals of this study was to evaluate which of the potential drivers—regional differences in the magnitude of climate change vs. regional differences in the degree of sensitivity to climate—may be more important in explaining differences in the observed phenological advancement through time between the regions. We found that, among the five climate variables (winter Tmin, spring/summer Tmin, bFFP, and NFFD) that differed between regions with respect to both the magnitude of change in that variable during the past century and the degree of phenological sensitivity to that variable, warmer regions exhibited about twice the magnitude of climate change as cool regions, and the plants sampled from warm regions were approximately twice as sensitive as those sampled from cool regions (Table 2). For example, spring/summer Tmin increased 1.68 times as fast in warm regions than cool regions, and individuals in warm regions are about 1.94 times as sensitive to spring/summer Tmin (Table 2) as individuals in cool regions. Moreover, neither the ratio between the regional magnitudes of climate change nor between regional degrees of sensitivity was consistently higher than the other (Table 2). Based on the evidence presented here, the two factors may be similarly important in driving divergent phenological shifts during the past century. To our knowledge, our study is the first to assess the relative importance of the magnitude of climate change vs. the degree of phenological sensitivity in driving temporal shifts in phenology and this comparative framework may be useful to assess the relative importance of these two factors for the many species that are well represented by herbarium specimens.

CONCLUSIONS

This study is one of the few to demonstrate that herbarium-based data can be used to detect regionally distinct phenological patterns when incorporating fine-scale phenological scoring (Park et al., 2018; Song et al., 2020). The results presented here directly support the prediction, first introduced by Park et al. (2018), that, collectively, plants sampled from regions where those plants exhibit higher sensitivity to temperature will advance their phenology more rapidly in response to warming than those sampled from regions which collectively exhibit lower sensitivity to temperature. Furthermore, we found that this divergent response was also driven by regional differences in the magnitude of climate change. Our findings highlight the need to measure both phenological sensitivity to climate and the magnitude of climate change experienced over a given time period when trying to explain intra- or interspecific variation in the magnitude of phenological change in response to directional changes in climate. Our study also adds to the mounting evidence that herbarium records are useful sources of phenological data (Davis et al., 2015; Willis et al., 2017; Jones and Daehler, 2018), and reinforces the need to preserve these valuable natural history collections while also expanding our capacity to extract high-quality and meaningful phenological data from imaged specimens (e.g., through using machine learning methods; Blagoderov et al., 2012; Lorieul et al., 2019; Goëau et al., 2020; Pearson et al., 2020).

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AUTHOR CONTRIBUTIONS

N.L.L.R. and S.J.M. both conceived of this project. N.L.L.R. led the effort to collect and analyze the data. Both N.L.L.R. and S.J.M. contributed to writing the paper.

OPEN RESEARCH BADGES

This article has been awarded Open Materials and Open Data badges. All materials and data are publicly accessible via the Open Science Framework at https://github.com/natalielrlove/region-specific-pheno-responses.git and https://doi.org/10.5281/zenodo.4299389. Learn more about the Open Practices badges from the Center for Open Science: https://osf.io/tvyxz/wiki.

DATA AVAILABILITY STATEMENT

The full ($n = 743$) and reduced ($n = 593$) data sets are available at Zenodo (https://doi.org/10.5281/zenodo.4299389), and the R scripts used to construct all models conducted here can be found at GitHub (https://github.com/natalielrlove/region-specific-pheno-responses.git).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Numbers of specimens from each herbarium included in the final dataset and in the reduced data set with the middle 20% of the temperature range of *S. tortuosus* removed ($n = 150$ specimens) that was used for cool vs. warm region comparisons.

Appendix S2. The distribution of phenological indices (PIs) among (A) sites of collection of all specimens ($n = 743$) and (B) sites where specimens were collected in cool (shown in blue; $n = 299$) and warm (shown in red; $n = 294$) regions.

Appendix S3. Criteria for excluding herbarium specimens from the final data set and the number of specimens removed based on each criterion.

Appendix S4. The distribution of mean long-term (90-year) mean annual temperatures (MAT) among (A) sites of collection of all specimens ($n = 743$) and (B) sites where specimens were collected in cool (shown in blue; $n = 299$) and warm (shown in red; $n = 294$) regions.

Appendix S5. The distribution of specimen collection years among (A) sites of collection of all specimens ($n = 743$) and

(B) sites where specimens were collected in cool (shown in blue; $n = 299$) and warm (shown in red; $n = 294$) regions.

Appendix S6. The distribution of the day of year of specimen collection (DOY) among (A) sites of collection of all specimens ($n = 743$) and (B) sites where specimens were collected in cool (shown in blue; $n = 299$) and warm (shown in red; $n = 294$) regions.

Appendix S7. Parameter estimates and summary statistics for the multiple linear regressions conducted to detect the effect of each climate variable of interest on the specimen day of year of collection (DOY) in cool vs. warm regions while controlling for the phenological index and the mean annual precipitation (MAP) or mean annual temperature (MAT) among specimens in the reduced data set ($n = 593$).

Appendix S8. Parameter estimates and summary statistics for the multiple linear regressions conducted to detect the effect of the year on the each climate variables of interest in cool vs. warm regions (year × temperature region) while controlling for geographic variables and the mean annual precipitation (MAP) or mean annual temperature (MAT) among specimens in the reduced data set ($n = 593$).

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