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Research

Spatial uncertainty in herbarium data: simulated displacement but not error distance alters estimates of phenological sensitivity to climate in a widespread California wildflower

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Herbarium records provide a broad spatial and temporal range with which to investigate plant responses to environmental change. Research on plant phenology and its sensitivity to climate has advanced with the increasing availability of digitized herbarium specimens, but limitations of specimen-derived data can undermine the inferences derived from such research. One issue that has received little attention is collection site uncertainty (i.e. error distance), a measure of confidence in the location from which a specimen was collected. We conducted comparative analyses of phenoclimatic models to determine whether spatial deviations of 2, 5, 15 or 25 km between recorded and simulated collection sites, as well as the error distance reported in digitized records, affect estimates of the phenological sensitivity of flowering time to annual temperature and precipitation in a widespread annual California wildflower. In this approach, we considered both spatial and interannual variation in climatic conditions. Simulated site displacements led to increasingly weak estimates of phenological sensitivity to temperature and precipitation anomalies with increasing distances. However, we found no significant effect of reported error distance magnitude on estimates of phenological sensitivity to climate normals or anomalies. These findings suggest that the spatial uncertainty of collection sites among specimens of widely collected plant species may not adversely affect estimates of phenological sensitivity to climate, even though real discrepancies and georeferencing inaccuracy can negatively impact such estimates. Collection site uncertainty merits further attention as a potential source of noise in herbarium data, especially for research on how plant traits respond to spatial and interannual climatic variation.

Keywords: climate change, error distance, georeferencing, herbarium, phenology, spatial uncertainty

Introduction

Natural history collections are an excellent resource for studying how organisms change over time and space. For plants, wild-collected pressed and dried specimens

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are archived and curated in herbaria. These specimens provide snapshots in time, often over broad geographic gradients and long historical periods, with which researchers can examine spatial and temporal patterns concerning species' phenotypic characteristics, life history and local environmental conditions (Lavoie 2013, Lang et al. 2019). Many herbaria have undertaken digitization efforts to make these records available online, often including high-resolution images of specimens (Soltis 2017, Yost et al. 2020). Herbarium-based research is intensifying thanks in part to this increasing availability of data, revealing species' phenotypic responses, both evolutionary and plastic (adaptive and genetically based versus environmentally induced, respectively), to local and global environmental change (Leger 2013, Heberling et al. 2019, Lang et al. 2019). As this research progresses, so does the need to understand how herbarium records can be used most effectively to answer pressing questions in plant ecology and evolution.

One such area of specimen-based research that relies on herbaria is plant phenology, the study of the timing of seasonal life history stages (Primack et al. 2004, Miller-Rushing et al. 2006, Willis et al. 2017). Changes in the timing of phenological events such as germination and first-flowering date can have serious demographic and evolutionary consequences for plants because these events determine exposure to herbivores, pollinators and favorable (or stressful) environmental conditions (Ehrlén 2015). Links between warming temperatures and the advancing specimen collection dates of angiosperms are often used as evidence of phenological sensitivity to climate – the shift in days of a life history event (e.g. flowering date) per unit change in climate (e.g. degrees Celsius) (Primack et al. 2004, Miller-Rushing et al. 2006, Kopp et al. 2020). Estimates of phenological sensitivity are possible with observational time series data when species are regularly collected in a particular life stage (e.g. flowering or fruiting) and may pertain to many climate or environmental variables (Cook et al. 2012, Mazer et al. 2013). In addition, estimates of phenological change and sensitivity to climate from herbarium specimens tend to be closely aligned with those derived from field observations (Robbirt et al. 2011, Zalamea et al. 2011, Panchen et al. 2012, Davis et al. 2015). The ability to investigate plant responses to environmental variation, including phenological, morphological, genetic and demographic responses, makes the use of herbarium specimens a powerful approach for analyzing how species track changes in climate over broad geographic and taxonomic scales (Cook et al. 2012, Park et al. 2018).

While herbarium specimens can provide a rich historical account of phenotypic change over time and space, several issues should be considered when evaluating the reliability of the data they provide. In addition to potential limitations in sampling breadth and intensity, non-random patterns of collection may bias biological inferences, particularly when investigating the effects of local environmental conditions on plant phenotype (Lang et al. 2019, Panchen et al. 2019). Examples of non-random collection include disproportionately collecting plants from easily accessible locations (e.g.

near roads) or with relatively conspicuous traits (e.g. large plants with many open flowers); preferentially sampling particular taxa (including subspecies) due to their prevalence or attractiveness; unequal sampling among years or seasons; and collector bias, where one or several collectors contribute overwhelmingly to a data set, potentially intensifying any of these biases (Daru et al. 2018, Panchen et al. 2019, Adamo et al. 2021). Consideration of such biases, even when absent or negligible, can inform the criteria used in selecting specimens for analysis and minimize their potential negative effects on any biological inferences drawn. While recent studies have examined the prevalence of collection biases and information uncertainty in herbarium data (Meyer et al. 2016, Daru et al. 2018), as well as accounted or corrected for such biases (Lavoie 2013), there has been no investigation of how the uncertainty in the recorded location of specimens' collection sites (hereafter referred to as collection site uncertainty) might affect interpretations of plant responses to climate, particularly phenological sensitivity.

In digitized herbarium records, collection site uncertainty reflects the confidence in the recorded GPS coordinates from which plants were purportedly collected. When absent from herbarium records, collection site coordinates (latitude and longitude) can be estimated (i.e. georeferenced) with some level of confidence using verbatim locality notes. Records that were georeferenced after specimen collection will usually include a measure of error distance: the linear distance that approximates the radius of a determined area of potential collection locations (Bloom et al. 2018, Yost et al. 2020). Georeferencing can therefore result in specimens with estimated collection sites ranging from high- (small error distance) to low-confidence (large error distance). Information on the proportion of herbarium specimens in North America that have estimates of error distance is not readily available, but a sample of 1 million flowering plant specimens (class: Magnoliopsida) drawn from the Consortium of California Herbaria (accessioned but not necessarily collected within California; downloaded 10 November 2021) included measures of collection site uncertainty for just over half of these records. Values of error distance for these specimens ranged from 0 to 8 851 109 m, although less than 0.1% of these were greater than 50 km. If collection site uncertainty reflects the accuracy of specimen collection locations, then it may consequently affect the accuracy of the local environmental conditions (e.g. temperature and precipitation) associated with a given specimen.

In theory, large error distances could indicate relatively large discrepancies between the recorded and the actual sites of specimen collection, although error distance itself indicates only the potential for collection site coordinates to be incorrect when uncertainty is substantial. Such uncertainty may be of little consequence in herbarium research that uses coarse (i.e. low spatial resolution) measures of climate. For example, estimates of phenological sensitivity in studies using climate data obtained from meteorological stations located several kilometers away from collection sites (e.g. ≥ 25 km; Hart et al. 2014, Davis et al. 2015, Ellwood et al.

2019, Banaszak et al. 2020) may be only modestly influenced by collection site uncertainty. Recently, however, herbarium-based phenological research has investigated responses to climate across large geographic areas using finer-grained (i.e. high spatial resolution) climate data estimated at specimens' listed coordinates (Munson and Long 2017, Berg et al. 2019, Kopp et al. 2020). The increasing availability of high-resolution climate data can improve our understanding of plant sensitivity to climate, but any effects of collection site uncertainty are likely to be more pronounced if or when such uncertainty reflects spatial accuracy and therefore the accuracy of local climate data.

The potential effects of large error distances on estimated phenology–climate relationships may also depend on the form of climatic variation being analyzed. Research on phenological responses to climate has typically used one of three different forms of climate variables, the most common being the climatic conditions recorded during the year of specimen collection. The other two are 1) the average conditions at a given site over long historical periods (normals) and 2) the year- and site-specific deviations in climate from these long-term averages (anomalies). Differences among sites in long-term normals describe how conditions vary geographically across space while year-to-year variation in anomalies describes how sites' conditions vary through time (Hodgson et al. 2011, Munson and Long 2017). Consequently, phenological variation explained by climate normals may reflect adaptation to local climates among populations as well as phenotypic plasticity across a species range. On the other hand, phenological variation explained by climate anomalies may only reflect phenotypic plasticity in response to interannual variation in climate, barring instances of rapid short-term evolution. Only a handful of studies have estimated biological responses to multiple forms of climatic variation (Bontrager and Angert 2016, Waterton et al. 2020, Mazer et al. 2021, Love and Mazer 2022), and recent evidence shows that species' phenological sensitivity to climate may depend on the dimension of climatic variation being analyzed (geographic versus interannual) (Munson and Long 2017, Delgado et al. 2020, Pearson et al. 2021). For traits such as flowering time that may respond to climate change via both adaptive evolution and plasticity (Anderson et al. 2012), studying the effects of both normals and anomalies on the estimation of phenological sensitivity can improve our understanding of the causes of phenological shifts in response to ongoing global change.

Here, we investigate the effects of spatial deviation and collection site uncertainty in herbarium specimens on the relationship between flowering phenology and local temperature and precipitation in an annual California wildflower, *Nemophila menziesii* (Boraginaceae). The potential for error distance to reflect the accuracy of georeferenced coordinates led us to hypothesize that greater collection site uncertainty weakens the statistical relationship between phenology and climatic predictor variables. To test this hypothesis, we used a series of comparative models with *N. menziesii* herbarium records to address the following questions: 1) how does the simulated displacement of specimen coordinates affect the

parameter estimation and performance of phenoclimatic models? 2) Does the magnitude of error distance reported in digitized specimens affect estimates of phenological sensitivity to annual temperature and precipitation? And 3) does error distance or simulated displacement differentially affect estimates of sensitivity to geographic versus interannual variation in temperature and precipitation (normals versus anomalies, respectively)? Whether or not collection site uncertainty affects the results of phenoclimatic (and other trait-climate) models has implications for how herbarium specimens are selected for analysis and can reveal the value of accurate georeferencing in specimen-based research.

Methods

Study species

Nemophila menziesii (Boraginaceae), commonly known as baby blue eyes, is an herbaceous winter annual widely distributed from Oregon to Baja California with its center of diversity in California. Populations are distributed across broad temperature and aridity gradients (Supporting information) and exhibit geographic variation in morphology, physiology and phenology (Cruden 1972); *N. menziesii* tends to flower earlier in the spring at lower elevations. Plants often grow on partially shaded slopes in oak woodlands, coastal sage scrub and grasslands, and typically germinate after autumn or winter rains and flower in early spring (Platenkamp and Shaw 1993). The large number of herbarium specimens available for this species, its broad geographic distribution, and the high phenological variation observed across California make *N. menziesii* a promising model with which to investigate phenological sensitivity to climate and the effects of error distance on estimates of sensitivity.

Herbarium specimens

Digitized herbarium records of *N. menziesii* were obtained from the Consortium of California Herbaria (CCH): 1676 records were downloaded from the original CCH1 portal in September 2019, and 1535 additional records were downloaded from the newer CCH2 portal in December 2019 (data from CCH1 and CCH2 may be accessed from: <https://ucjeps.berkeley.edu/consortium/>). All specimens used were collected within California. Within and between these two sets of data, duplicate records (those that had matching catalog numbers or were collected within ~1 km of one another on the same date) were removed. Records missing latitude and longitude values were manually georeferenced using the online utility software GEOLocate (<www.geo-locate.org/>), which uses the point-radius method (Wieczorek et al. 2004) with user-entered specimen locality notes (e.g. text descriptions of collection sites, distances from landmarks and other location descriptors) to estimate collection coordinates and an uncertainty radius (error distance) in meters (Rios and Bart 2010). After cleaning, the dataset contained 1677

unique *N. menziesii* records representing specimens collected from 1901 to 2019. Each record includes: a unique specimen identifier, date of collection, day of year of collection (DOY; 1–365), decimal latitude and longitude (converted from degrees, minutes and seconds when necessary), elevation above sea level (m) (obtained from USGS elevation data with the elevatr package in R when absent; Hollister et al. 2021) and collection notes (e.g. locality, habitat, co-occurring taxa). DOY in this data set ranged from 20 to 242. For the analyses below, we assumed that specimen DOY approximates peak/mean flowering date (cf. Robbirt et al. 2011, Jones and Daehler 2018), since collections of showy annual species such as *N. menziesii* are typically made when plants are in flower. Upon visual inspection, all 1136 specimens with digitized images had at least one open flower present. While some of the 541 specimens for which images were unavailable may lack open flowers, we assume that any influence this might have had on our models was negligible. Approximately 70% of our specimens, including those that we georeferenced ourselves as well as many of those downloaded from CCH2 with previously recorded GPS coordinates, had a measure of error distance (m), which indicates the uncertainty associated with the estimation of collection site coordinates. When georeferencing specimens without coordinates, we excluded records for which there was exceptionally low confidence in collection sites (estimated error distance > 15 km), although a handful of previously georeferenced specimens had error distances > 15 km (Supporting information).

Climate data

To investigate effects of simulated spatial deviation and reported error distance on estimates of phenological sensitivity to climate in *N. menziesii* herbarium specimens, we used two forms of climate variables: 100-year climate normals (long-term averages) and anomalies (year-of-collection deviations from normals). Climate data were obtained from ClimateNA ver. 6.40, an application that provides downscaled and interpolated point-location monthly, seasonal and annual climate data (Wang et al. 2016). We extracted year-of-collection mean annual temperature (MAT) and cumulative annual precipitation (CAP) (identical to mean annual precipitation, MAP, reported in other papers) data for every year from 1901 to 2019 for each of 1677 *N. menziesii* specimen collection sites. Year-of-collection conditions at a given site reflect both long-term and interannual sources of climatic variation but tend to be strongly correlated with climate normals (Mazer et al. 2020) (Supporting information). Annual temperature was averaged across the 12 months in a year while annual precipitation was summed across months. We calculated 100-year MAT and CAP normals as the average conditions at a specimen's site of collection from 1901 to 2000 and MAT and CAP anomalies as the conditions in the year of specimen collection minus the long-term normals at that location. We used a 100-year normal period instead of the more commonly used 30-year period in order to capture more historical variation from across the species' range since

many of our specimens were collected before 1990. The inclusion of both normals and anomalies in our analyses allowed us to investigate phenological sensitivity to climate across two scales of variation: sensitivity to geographic climatic variation and sensitivity to interannual climatic variation. This approach has been used recently by others investigating phenological sensitivity to climate (Munson and Long 2017, Mazer et al. 2021, Pearson et al. 2021).

Statistical analyses

Phenoclimatic models

Using all 1677 *N. menziesii* herbarium records, we constructed simple linear models (referred to below as phenoclimatic models) to investigate the relationship between DOY, our response variable, and four climatic predictor variables: MAT normals, CAP normals, MAT anomalies and CAP anomalies. The slope of these relationships (the partial regression coefficient of each predictor) describes the phenological sensitivity – the change in mean flowering date per unit change in climate – to geographic or interannual variation in MAT/CAP. Although we use DOY as a proxy for flowering date in *N. menziesii*, we use the term 'phenological sensitivity' for these coefficients to reflect the fact that other phenophases of interest can be analyzed and interpreted in the same way. Elevation, latitude and longitude were included as predictors to control for variation in DOY not explained by MAT or CAP and to improve model fit. All predictors were tested as fixed effects and no interactions were included. All partial regression coefficients were standardized (predictors were mean-centered and scaled by one standard deviation) to facilitate comparisons of their effects on DOY. Climate normals and anomalies were generally uncorrelated ($|r| <$ 0.15, Supporting information). Model residuals and variance inflation factors (VIF; a metric designed to detect correlations among predictor variables in regression analyses) were examined to ensure that there was no strong multicollinearity among climatic predictors of interest and that our models met the assumptions of ordinary least squares (OLS) regression (also known as linear regression). VIF values for all climatic predictors were below 4. Below, we describe how these models were used to examine the effects of simulated displacements and collection site uncertainty on estimates of phenological sensitivity to MAT and CAP. All analyses were conducted in R (<www.r-project.org>) and all scripts and data used in these analyses are available in a Dryad digital repository (<https://doi.org/10.25349/D9X893>).

Collection site simulations

To investigate how discrepancies between the actual and recorded collection locations of our specimens might affect the performance of phenoclimatic models, we simulated new coordinates (latitude and longitude) for all specimens for which the recorded error distance was ≤ 2 km (n = 743) ('high-confidence' collections). For each of these records, we used the geosphere package in R (Hijmans 2021) to select new coordinates located 2, 5, 15 and 25 km away from the

recorded collection site in a random direction. This provided four simulated collection sites per record, each located 2–25 km away from the listed site. We refer to the distance between these new sites and the originally reported collection sites as 'simulated displacements' to distinguish them from the error distance reported for records during georeferencing. New elevation data for these locations were obtained using the elevatr package in R (Hollister et al. 2021). MAT and CAP normals and anomalies for all simulated sites were calculated using data extracted from ClimateNA based on sites' latitude and longitude. DOY values for each record were not altered. We replicated these simulations 200 times for each displacement distance, resulting in a total of 800 simulated locations per original high-confidence specimen collection. Due to the proximity of some recorded collection sites to bodies of water, the number of usable simulated sites per displacement distance iteration varied from 709 to 743 (new sites located in water were excluded). Phenoclimatic models identical to those above were fit using these data, with the same model tested for each of the four displacement distances and each of the 200 iterations. We compared model results representing the four sets of simulated displacements, examining model parameters (e.g. partial regression coefficients of climatic predictors, the standard error around these coefficients and model adjusted R^2 values) for each predictor and displacement distance as estimates averaged across all 200 test iterations.

Effects of reported error distance

To determine whether collection site uncertainty estimated during the georeferencing of herbarium specimens affects the performance of phenoclimatic models, we investigated the effects of error distance using two modeling approaches. First, herbarium records were divided into four categories of uncertainty to determine whether model outputs differed among data sets comprised of specimens representing different levels of collection site uncertainty. We constructed four data sets that included 1) all records (including those for which no error distance was reported) (n = 1677), 2) records that reported any measure of error distance (n = 1166), 3) records reporting an error distance ≤ 5 km (n = 1033) and 4) high-confidence records reporting an error distance ≤ 2 km (n = 743). In this sequence, these data sets reflect an increasing confidence in collection location as error distances decrease. These categories are not mutually exclusive: the larger data sets (e.g. all records, any records with error distance) include records also present in the smaller data sets (e.g. error distance ≤ 2 km). As in the analyses of the simulated displacements described above, we focused on how the estimated regression coefficients and adjusted R^2 values (a goodness-of-fit measure) differed among the phenoclimatic models applied to each data set. Second, we analyzed phenoclimatic models in which error distance was included as a covariate, using the data set of all records (including those with no measure of error distance) to determine whether collection site uncertainty had any direct effects on DOY and whether estimates of sensitivity to MAT and CAP normals

and anomalies differed significantly from our original model. We ran two separate models with our full data set, one with error distance as a continuous quantitative predictor and one with error distance as a categorical variable (mutually exclusive bins = 0–2, 2–5, 5–10, 10–15, > 15 km and error = NA) (see the Supporting information for category sizes).

Results

Below, we present the results of the phenoclimatic models applied to all herbarium records pooled, followed by the results of models applied to simulated site displacements, and finally the results of analyses on the effects of reported specimen error distance on phenoclimatic models.

Phenological sensitivity in *N. menziesii*

All four climate variables, MAT and CAP normals and anomalies, explained a significant proportion of variation in DOY in our full data set (n = 1677 records). Controlling for latitude, longitude and elevation, higher long-term and anomalous MAT had an advancing effect on DOY while higher long-term and anomalous CAP had a delaying effect on DOY (Fig. 1) (Table 1, all records included). Phenological sensitivity to annual temperature was comparable for long-term normals and anomalies (Fig. 1a and c, respectively). Sensitivity to annual precipitation, however, was higher in response to variation across space than in response to interannual variation (Fig. 1b and d). In addition to climate, geographic location also explained variation in DOY. Controlling for MAT and CAP, specimens collected from higher elevations had earlier DOYs, on average, than those from lower elevations. Since latitude and longitude are highly collinear in this dataset, we focus below only on the effects of MAT and CAP normals and anomalies on DOY, for which all parameter VIF values were less than 4.

Effects of simulated displacement on phenological sensitivity to climate

In the analyses of simulated sets of coordinates for herbarium records, the effect of collection site displacement on estimates of phenological sensitivity to MAT and CAP depended on the type of climatic predictor. While all of the models analyzing simulated data sets explained a statistically significant proportion of the variance in specimen DOY (p < 0.0001), the significance of individual climatic predictors differed among them. As the simulated distance from recorded sites increased, average estimates of absolute sensitivity to climate anomalies declined (Fig. 2). The effect on DOY of interannual variation in MAT and CAP became statistically non-significant when the locations used to assign climatic conditions were displaced, on average, 5 km (2 km for CAP anomalies) or more from recorded collection sites. On the other hand, the regression coefficients of MAT and CAP normals remained statistically significant with increasing location mismatch,
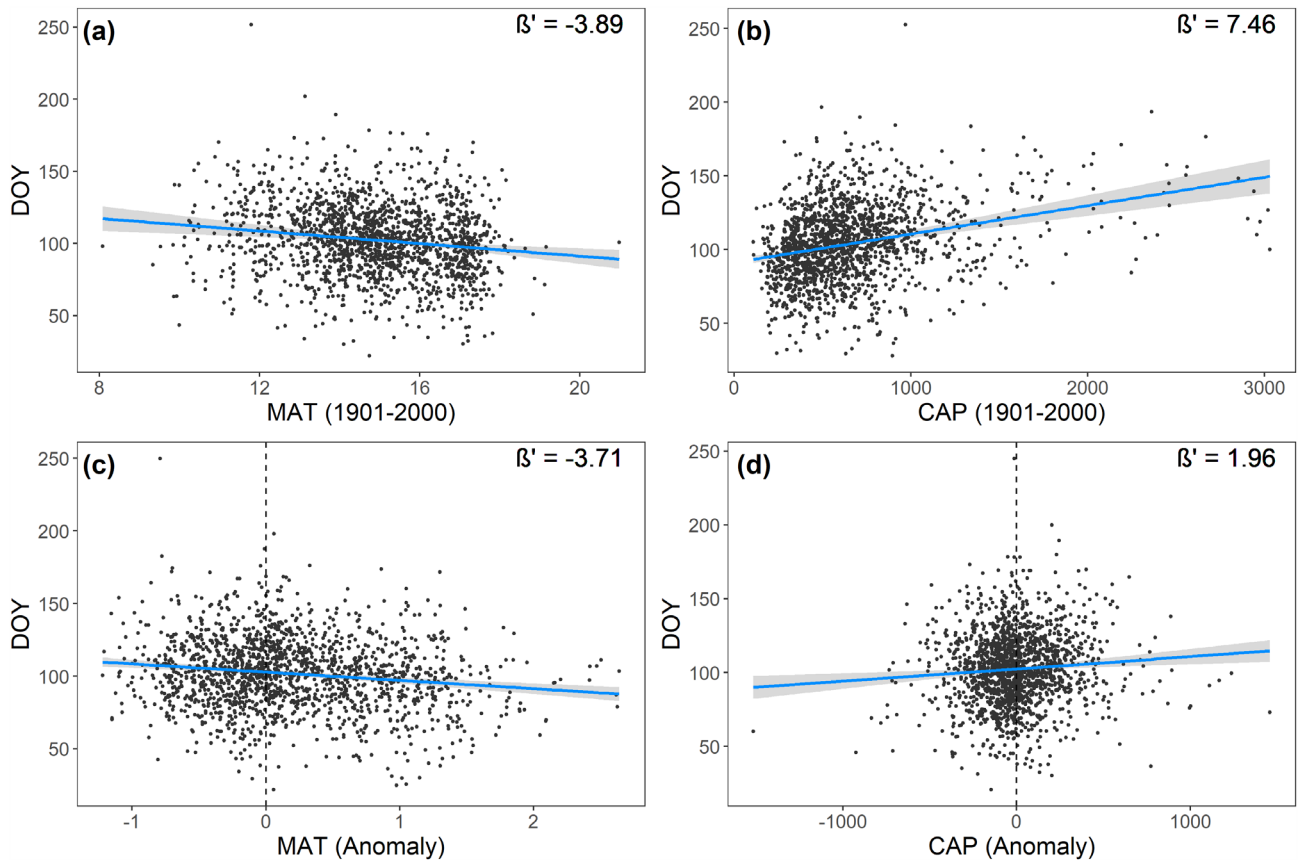
Figure 1. Leverage plots displaying the independent effects of climatic predictors on specimen DOY, controlling for elevation, latitude and longitude for all records (n = 1677). Plots show the effect on DOY of long-term (a) MAT (mean annual temperature, °C) and (b) CAP (cumulative annual precipitation, mm), as well as anomalous (c) MAT and (d) CAP. Partial regression coefficient estimates β′ were estimated using mean-centered and scaled (SD = 1) predictors. Shaded bands represent 95% confidence intervals (CIs). Vertical dashed-lines in (c) and (d) indicate 0-value anomalies (no difference between collection year and historical average climate). Each point represents one herbarium specimen.

although the average absolute sensitivity of DOY to these predictors increased slightly. The 95% confidence intervals for these estimates were also larger than those calculated for MAT and CAP anomalies. Further examination revealed that simulated displacements led to higher mean standard deviations of predictor variables for climate anomalies (but not for

normals) as displacement distance increased (averaged across all iterations) (Supporting information).

As displacement from specimens' original coordinates increased, the average standard error of the estimated regression coefficients increased while model adjusted R^2 values decreased (Fig. 3). Changes in these parameters

Table 1. Partial regression coefficients from models examining the effects of long-term and anomalous MAT and CAP on specimen DOY. Each column contains standardized regression coefficient estimates (β′) and standard errors (SE) for a subset of *N. menziesii* specimens. Each subset represents a different range of specimen error distance described by the column headings, with sample sizes in parentheses. Partial regression coefficients (β′) are mean-centered and scaled by 1 standard deviation. *p < 0.05, **p < 0.01. All predictors were included as fixed effects. VIF values for latitude and longitude were abnormally high (> 4).

|	All records (n = 1677)		Records with any error distance (n = 1166)		Records with error ≤ 5 km (n = 1033)		Records with error ≤ 2 km (n = 743)	
	Adj. R^2 = 0.3075		Adj. R^2 = 0.2981		Adj. R^2 = 0.3060		Adj. R^2 = 0.2923	
Predictor	β′	SE	β′	SE	β′	SE	β′	SE
MAT (100Y)	**−3.89****	1.04	**−4.25****	1.18	**−5.32****	1.26	**−5.66****	1.51
CAP (100Y)	**7.46****	0.91	**7.32****	1.12	**6.82****	1.19	**7.33****	1.48
MAT (Anom.)	**−3.71****	0.61	**−2.78****	0.72	**−3.06****	0.76	**−3.06***	0.94
CAP (Anom.)	**1.96****	0.60	**2.32****	0.72	**2.34****	0.76	**2.01***	0.94
Elevation	**9.42****	1.14	**8.75****	1.30	**8.18****	1.40	**7.97****	1.65
Latitude	1.24	1.78	0.19	2.03	1.29	2.17	0.46	2.65
Longitude	**6.79****	2.07	**5.78***	2.35	**7.40****	2.56	**7.68***	3.07
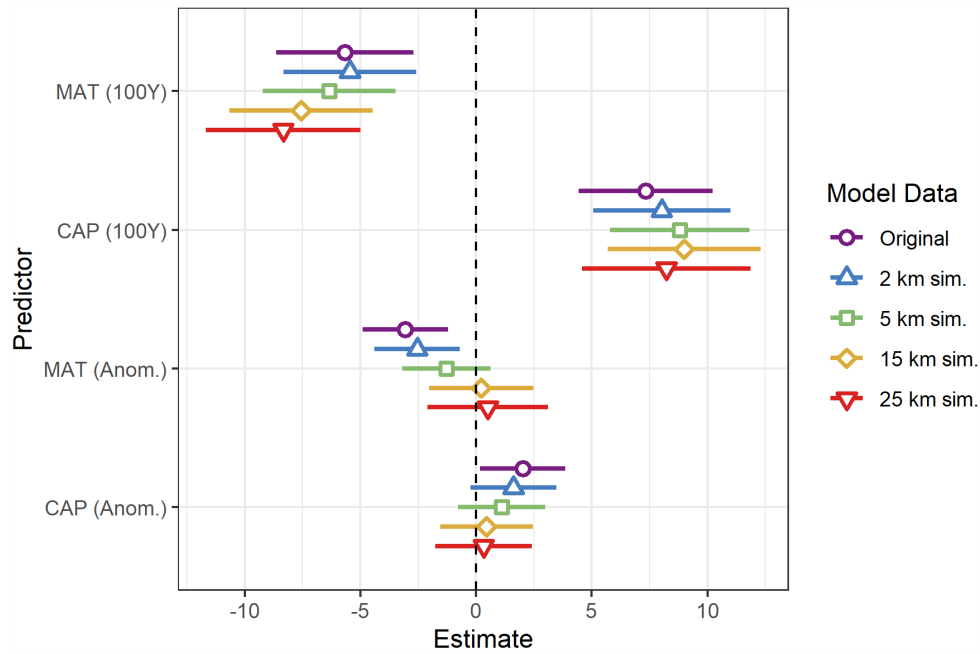
Figure 2. Standardized estimates of phenological sensitivity to MAT (mean annual temperature, °C) and CAP (cumulative annual precipitation, mm) 100-year normals and year-of-collection anomalies, partitioned by data set and controlling for latitude, longitude and elevation. Coefficient estimates and 95% confidence intervals (horizontal bars) of the sensitivities based on simulated data are averages from the model outputs of 200 replicates for each displacement distance. 'Model Data' specifies the data sets in which records were displaced either 2, 5, 15 or 25 km from their recorded locations and for which new climate and elevation data were assigned. 'Original' data refer to the herbarium records for which error distances were ≤ 2 km (n = 743). All five models explained a statistically significant proportion of the variance in DOY (p < 0.0001), but the mean effect of climate anomalies on DOY did not differ from 0 in the models for which simulated displacements were ≥ 5 km for MAT anomalies or ≥ 2 km for CAP anomalies. Coefficient estimates are mean-centered and scaled by 1 standard deviation.

were lower for models applied to sets of records for which sites were displaced 2 or 5 km than for those applied to records for which sites were displaced 15 and 25 km. Simulated displacements of 15 and 25 km resulted in a ~6.8 and ~9.8% average reduction, respectively, in model fit (Fig. 3), although these reductions were much higher in some iterations.

Effects of error distance on phenological sensitivity to climate

We found negligible effects of reported specimen error distance on estimates of phenological sensitivity to MAT and CAP normals and anomalies. Of the four error distance subsets, results of models analyzing records with 0–2 km error
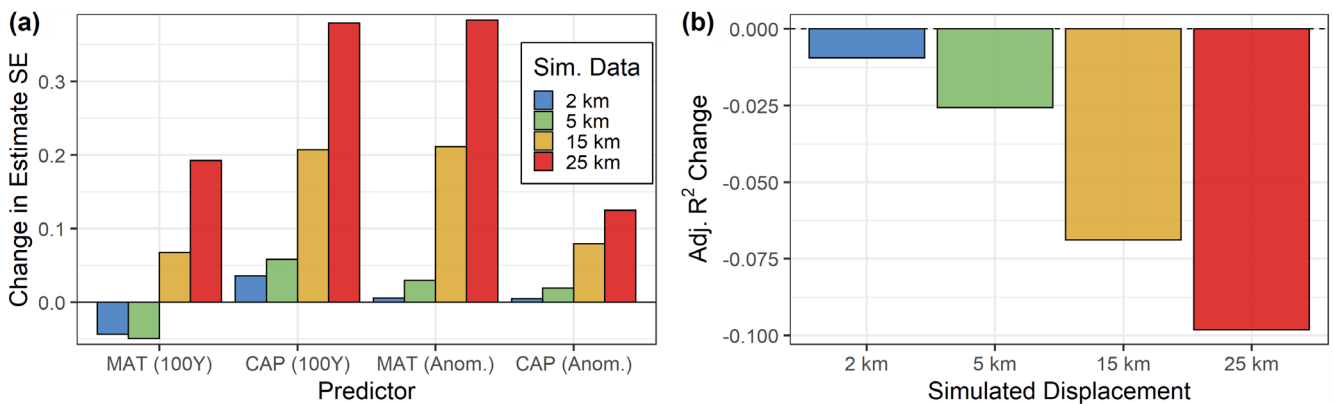

Figure 3. Average changes in phenoclimatic models' (a) regression coefficient standard errors (SE) and (b) adjusted R² values among sets of simulated data relative to models based on high-confidence records' (error distance ≤ 2 km) unaltered collection locations. Simulated data refers to data sets where records were displaced either 2, 5, 15 or 25 km from their original high-confidence collection sites and for which new climate and elevation data were obtained. In (a), climatic predictors include MAT (mean annual temperature, °C) and CAP (cumulative annual precipitation, mm) 100-year normals and year-of-collection anomalies.

distance were similar to those analyzing records of lower confidence error distance categories (Table 1). Highly overlapping 95% CIs of regression coefficients indicated that there were no statistically significant differences in estimates of phenological sensitivity among the different error distance categories (Fig. 4), although the effect of long-term MAT on DOY became stronger with increasing confidence in site locations. The standard error and 95% CIs of the coefficient estimates increased with more restrictive error bins, for which samples sizes were smaller, and were generally larger for MAT and CAP normals than anomalies. Adjusted R^2 values for models applied to error distance subsets were lower than that of the complete data set, although by no more than 0.02. Compared to the analyses of simulated collection locations described above, changes in model adjusted R^2 values among error distance categories were much lower. When included as a covariate in our model analyzing all records, error distance had no significant effect on DOY, neither as a continuous nor as a categorical predictor variable ($p > 0.05$) (Supporting information). In addition, there were no qualitative differences in the effects of the four climatic predictors on DOY when comparing the models with and without error distance as a covariate.

Discussion

Our analyses generated two major findings. Using digitized herbarium records of *Nemophila menziesii*, among which ~70% of specimens had a reported measure of uncertainty (error distance) associated with their collection location, we found that the inclusion of records with relatively large or missing error distances does not significantly alter the statistical relationship between local temperature and

precipitation and flowering time relative to analyses of data sets excluding such records. Second, using simulated collection site coordinates, we found that discrepancies of ≥ 5 km in geographic collection location reduced the magnitude and statistical significance of estimates of phenological sensitivity to interannual variation in climate. In spite of the weak effects of reported error distance on estimates of phenological sensitivity in our analyses, simulated geographic deviations in collection site and, consequently, local climatic conditions resulted in altered estimates of phenological sensitivity to climate. Although we cannot evaluate with precision the accuracy of the georeferenced collection locations in our herbarium-derived data, as discussed below, it seems likely that these georeferenced collection locations are sufficiently accurate to provide robust estimates of phenological sensitivity to climate regardless of the value of error distance reported in *N. menziesii* specimens. Whether this applies to other widespread species is a question requiring further investigation.

Collection site displacement affects estimates of phenological sensitivity

While variation in error distance among *N. menziesii* herbarium records did not greatly affect estimates of phenological sensitivity, our simulations of intentionally displaced coordinates did. Compared to high-confidence herbarium records (error distance ≤ 2 km), average estimates of phenological sensitivity to MAT and CAP anomalies became increasingly weak as the magnitude of coordinate displacement exceeded 2 km (Fig. 2). In contrast, sensitivity to 100-year normals changed little and even increased with greater displacement distances, particularly for MAT. In
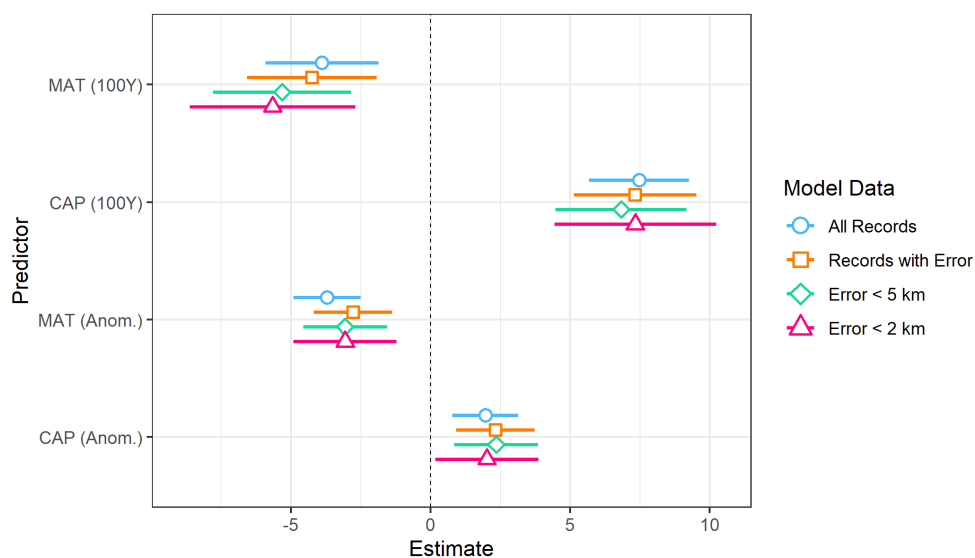

Figure 4. Standardized estimates of phenological sensitivity to MAT (mean annual temperature, °C) and CAP (cumulative annual precipitation, mm) 100-year normals and year-of-collection anomalies derived from the analysis of four data sets, each characterized by a different range of error distances, controlling for latitude, longitude and elevation. 'Model Data' specifies the different error distance groupings: all records (n = 1677); records with any error distance (n = 1166); records with 0–5 km error distance (n = 1033); and records with 0–2 km error distance (n = 743). Horizontal bars represent 95% confidence intervals. Coefficient estimates are mean-centered and scaled by 1 standard deviation.

N. menziesii, inaccurate georeferencing should therefore have a greater impact on estimates of phenological sensitivity to interannual variation in climate, which explains less variation in DOY than geographic variation in climate, although inferences concerning sensitivity to both forms of climatic variation may be susceptible to the effects of collection site inaccuracy. Whether herbarium-based estimates of phenotypic responses to climate are more susceptible to the effects of inaccurate georeferencing for climate anomalies versus normals will likely depend on the relative influence of interannual versus geographic variation in climate on a given trait for a given species.

In addition to changes in the estimates of phenological sensitivity to climate when collection locations were displaced, the standard error around these estimates increased and the goodness-of-fit of phenoclimatic models decreased with increasing displacement (Fig. 3). The relatively large changes in these measures when displacements exceeded 5 km suggest that, for *N. menziesii*, such deviations have the potential to substantially undermine inferences based on the parameter estimates from phenoclimatic models. While spatial uncertainty deserves further attention in specimen-based research, the results presented in Fig. 3 demonstrate that spatial accuracy has clear consequences for modeling the relationships between species' traits and the local environment. Our findings on the effects of collection site displacement could be used to help establish a reasonable threshold for acceptable error distances when defining specimen inclusion criteria, although spatial inaccuracy is not the same as collection site uncertainty and such decisions should depend on species-specific factors as well (e.g. distribution, climate sensitivity, collection biases). Given that the error distance associated with a particular specimen's GPS coordinates indicates only the potential for these coordinates to be inaccurate, the effect of collection site uncertainty on trait-climate models should depend on 1) the extent to which spatial uncertainty reflects spatial inaccuracy and 2) the spatial heterogeneity of environmental predictor variables. For example, large values of error distance might influence the outputs of phenoclimatic models only when the accuracy of corresponding georeferenced coordinates is low, and this effect would be magnified with occurrence data that spans steep climatic gradients (i.e. climate is highly variable across short distances).

Effects of error distance on phenological sensitivity

In the large sample of herbarium specimens analyzed here (n = 1677), error distance – the uncertainty radius attributed to the georeferenced location of collected specimens – had little impact on measures of flowering time sensitivity to MAT and CAP normals and anomalies estimated from phenoclimatic models (Table 1, Fig. 4). The absence of significant differences in climatic predictor partial regression coefficients among different error distance categories illustrates a negligible effect of collection site uncertainty on estimates of phenological sensitivity in *N. menziesii*. Contrasted with our

results on the effect of simulated displacements on estimates of sensitivity, the results of this analysis suggest that collection site uncertainty is generally not indicative of collection site accuracy: the inclusion of records with relatively large error distances did not significantly affect the strength of the estimated climatic effects on flowering time, as might be expected if larger levels of uncertainty correspond to greater deviations from true collection locations. Estimates of error distance in *N. menziesii* specimens, even when large or not reported, should therefore have little effect on the quantitative inferences derived from phenoclimatic models.

To our knowledge, the analyses presented here on the effects of spatial uncertainty on estimates of phenological sensitivity to climate are the first of their kind, although others have drawn attention to the importance of examining geographic uncertainty when making ecological inferences (Feeley and Silman 2010, Naimi et al. 2014, Meyer et al. 2016). For example, in species distribution models using vertebrate occurrence records, Naimi et al. (2014) found a greater negative effect of positional uncertainty on model accuracy when the spatial association among environmental predictor variables was low compared to when spatial association among variables was high. In our analyses, moderate spatial autocorrelation was present among long-term climate normals and geographic predictors (but not model residuals; data not shown). However, we have no reason to believe that this obscured any meaningful effect of error distance in the analytical approaches we used. More research using other ecological models and with other well-collected plant species, particularly those with different life histories and occupying regions with high levels of climatic heterogeneity, will help to elucidate the consequences of spatial uncertainty on the inferences derived from herbarium-based research.

Sensitivity to geographic versus interannual variation in climate

The estimates of phenological sensitivity in *N. menziesii* presented here are similar to those reported in other herbarium-based studies (Primack et al. 2004, Matthews and Mazer 2015, Davis et al. 2015, Park et al. 2018), but few investigators to date have estimated the independent effects of both geographic and interannual variation in climate on phenological sensitivity (but see Hodgson et al. 2011, Munson and Long 2017, Delgado et al. 2020). The influence on phenology of geographic variation (indicated by variation among collection sites in climate normals) versus interannual variation in climate (estimated as site-specific climate anomalies measured in the year of collection) may differ because different mechanisms of phenotypic change are associated with each. Phenological variation across space likely results from both phenotypic plasticity and local adaptation to long-term chronic conditions whereas phenological change among years at a given site should result primarily from phenotypic plasticity, particularly for perennial species (Hodgson et al. 2011). Munson and Long (2017) analyzed phenological sensitivity to climate in C3 and C4 grasses across a large region of

the western US and found that, although sensitivity differed among species and functional groups, geographic climate variation (normals) typically explained as much or more variation in DOY than interannual climate variation (anomalies) across species, results that are consistent with those presented here. More recently, however, estimates of phenological sensitivity to climate normals versus anomalies were found to be similar in two *Clarkia* congeners (Mazer et al. 2021). Further research and statistical approaches, such as year-detrending estimates of phenological sensitivity (Iler et al. 2017), are needed to more clearly decipher the independent roles of evolutionary adaptation and plasticity in determining phenological responses estimated using herbarium data.

Our objective in the current study was to use simple regression models to explore the influence of spatial uncertainty and inaccuracy on estimates of phenological sensitivity to climate, not to construct the most predictive or comprehensive model of phenological variation in *N. menziesii*. For annual plant species such as *N. menziesii* whose phenophases exhibit strong seasonality, monthly and seasonal climatic conditions (e.g. winter, spring) may be as or more predictive of phenology than annual conditions (Hereford et al. 2017). Here, we chose to use MAT and CAP as climatic predictors because they explain significant variation in DOY, are strongly correlated with seasonal climate parameters (e.g. $r = 0.76$ for minimum spring temperature ~ MAT 100-year normals and $r = 0.77$ for minimum spring temperature ~ MAT anomalies; Supporting information), are available from most climate databases, and have been used to predict phenological responses to climate in other plant species (Wolkovich et al. 2013, Munson and Long 2017, König et al. 2018). While using standardized partial regression coefficients in our models prevented us from forecasting future consequences of phenological sensitivity (e.g. days advancement per degree Celsius warming), it allowed us to compare the relative influence of predictors with different units of measurement on DOY, as well as how error distance might affect this influence. We hope that these modeling and statistical approaches may serve as templates with which to initiate other investigations of the effects of collection site uncertainty on phenological (and other trait) sensitivity to climate. More complex approaches and finer-tuned climate data can also provide greater insight into the biological underpinnings of species' phenological patterns than we have demonstrated here. How and why phenological sensitivity to climate varies within *N. menziesii* is a focus of ongoing investigation.

Specimen georeferencing and further considerations

The estimation of collection site uncertainty relies primarily on the methods by which specimens are georeferenced. Advancing technology has likely improved the efficiency of georeferencing, but it is not known whether the accuracy of coordinate estimation has improved through time. In addition, previously georeferenced herbarium records may have used protocols or resources (e.g. GEOLocate) different from those used in the current study to estimate collection sites and error distances (Murphey et al. 2004, Guo et al. 2008), emphasizing the need

for standardized georeferencing guidelines in herbarium-based research. Relatively few of the *N. menziesii* records analyzed here reported an error distance ≥ 10 km, and a large number of records had no measure of error distance (Supporting information). The confidence and accuracy of collection locations in these specimens lacking error distance cannot be quantified. Further investigation of the effects of error distance (or lack thereof) and georeferencing protocol on phenoclimatic models would complement the results presented here.

Phenological research is not the only context in which collection site uncertainty may affect ecological inferences. The examination of location uncertainty in natural history records has been of much interest in species distribution modeling (SDM), for which different investigators have used different protocols and levels of uncertainty as criteria for data inclusion. Bloom et al. (2018) reviewed previous georeferencing efforts in SDM to develop a new georeferencing protocol and found that a higher resolution of spatial occurrence data resulted in more accurate climate envelopes and model predictions of habitat suitability in *Saxifraga austromontana*. Similarly, Feeley and Silman (2010) found positive effects of rigorous georeferencing on the precision of species habitat ranges estimated from SDMs, especially in mountainous regions with greater environmental heterogeneity. Considerations of other issues in specimen-based research are also warranted. Uncertainty in estimates of climatic predictors, for example, may affect model predictions and reduce statistical power, as demonstrated with spatial climate variables in SDMs (Stoklosa et al. 2015).

The potential for error distance and other artifacts of natural history collections (e.g. sampling bias) to affect ecological and evolutionary inferences should be addressed in more contexts to better understand their influence. A larger, multi-species approach to exploring the questions examined here can help to address the generality of these findings by considering whether factors such as geographic distribution, life history and sensitivity to climate might influence the effects of error distance on model performance. Populations and species that are extremely sensitive to climate or that are found in highly heterogeneous environments (e.g. distributed across steep elevation or aridity gradients), for example, may be more susceptible to negative effects of coordinate uncertainty in trait-climate modeling. Similarly, species with contrasting sensitivities to climate may differ in their susceptibility to statistical noise or bias generated by error distance. In considering what artifacts may introduce bias or noise to analyses of natural history collections, it may be useful to treat spatial uncertainty as a potential bias itself: an artifact of occurrence data that could affect later inferences. Finally, factors other than error distance or sampling bias may also influence spatial accuracy and uncertainty in herbarium research. For example, collectors may sometimes provide the coordinates of a nearby landmark or field station instead of a specimen's actual point of collection. These and other possibilities underscore the importance of rigorous and repeatable collection practices, detailed field notes and a standardized georeferencing protocol.

Conclusion

While other herbarium-based studies on phenology have detailed their own georeferencing protocols and drawn attention to the importance of addressing spatial uncertainty, none have investigated the effects of collection site uncertainty on phenoclimatic models. Our findings suggest that estimates of phenological sensitivity may be insensitive to collection site uncertainty when statistical models are applied to well-sampled and widely collected taxa such as *N. menziesii*. If so, researchers examining such taxa may not need to restrict their analyses to specimens for which collection site uncertainty is relatively low. Our findings represent an important first step toward determining the robustness of trait–climate modeling when analyzing natural history observations for which observation locations are subject to spatial uncertainty. Both a greater consideration for the potential effects of error distance as well as a standardized protocol for georeferencing and estimating error distance can lead to improvements in model accuracy in studies of trait–climate relationships using natural history observations. The increasing use of herbarium collections in ecological and evolutionary research necessitates a careful consideration of the factors that influence the biological conclusions we draw from our analyses. Improving phenoclimatic models, as well as other trait-climate modeling approaches, is of particular importance for researchers studying the effects of climate change on the phenotypes of organisms using natural history observations.

Author contributions

Devin E. Gamble: Conceptualization (lead); Investigation (lead); Methodology (lead); Supervision (lead); Writing – original draft (lead); Writing – review and editing (supporting). **Susan J. Mazer**: Conceptualization (supporting); Investigation (supporting); Supervision (supporting); Writing – review and editing (lead).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.25349/D9X893> (Gamble and Mazer 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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