PRIMARY RESEARCH ARTICLE

Lagged and dormant season climate better predict plant vital rates than climate during the growing season

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Abstract

Understanding the effects of climate on the vital rates (e.g., survival, development, reproduction) and dynamics of natural populations is a long-standing quest in ecology, with ever-increasing relevance in the face of climate change. However, linking climate drivers to demographic processes requires identifying the appropriate time windows during which climate influences vital rates. Researchers often do not have access to the long-term data required to test a large number of windows, and are thus forced to make *a priori* choices. In this study, we first synthesize the literature to assess current *a priori* choices employed in studies performed on 104 plant species that link climate drivers with demographic responses. Second, we use a sliding-window approach to investigate which combination of climate drivers and temporal window have the best predictive ability for vital rates of four perennial plant species that each have over a decade of demographic data (*Helianthella quinquenervis*, *Frasera speciosa*, *Cylindriopuntia imbricata*, and *Cryptantha flava*). Our literature review shows that most studies consider time windows in only the year preceding the measurement of the vital rate(s) of interest, and focus on annual or growing season temporal scales. In contrast, our sliding-window analysis shows that in only four out of 13 vital rates the selected climate drivers have time windows that align with, or are similar to, the growing season. For many vital rates, the best window lagged more than 1 year and up to 4 years before the measurement of the vital rate. Our results demonstrate that for the vital rates of these four species, climate drivers that are lagged or outside of the growing season are the norm. Our study suggests that considering climatic predictors

1 | INTRODUCTION

Understanding the effects of climate on population dynamics is a central, long-standing quest in ecology (Andrewartha & Birch, 1954; Sutherland et al., 2013). This topic is increasingly salient because climate change is expected to alter dramatically population dynamics of many species, which is key for predicting local extinction risk and species' range shifts (Bellard et al., 2012; Kelly & Goulden, 2008; Urban, 2015). In the last decades, ecologists have been working toward understanding (Harper & White, 1971; Hindle et al., 2019; Sarukhan, 1974) and, more recently, forecasting the effects of climate on population dynamics (Iler et al., 2019; Urban et al., 2016). Models that link climate to biological processes such as population dynamics (Merow et al., 2014; Pagel & Schurr, 2012) have higher predictive ability in novel climates than those based on species occupancy, such as species distribution models (Zurell et al., 2016). However, one challenge in linking climate drivers to demographic processes is to identify the appropriate time window during which climate influences demography, as well as the specific climatic variable that best predicts vital rates (e.g., temperature, precipitation, etc.). This task is challenging because environmental drivers are often correlated, researchers often do not know the most relevant time window nor environmental variable for plant physiological responses to climate, and researchers typically do not have access to long-term data to analyze different temporal windows (Salguero-Gómez et al., 2015).

Investigators often link climate drivers to population dynamics based on pre-existing knowledge of their focal species (van de Pol et al., 2016). The most common approach for plant species is to consider climate within the growing season of the year preceding the vital rate(s) (i.e., survival, development, reproduction; e.g., Chu et al., 2016; Clark et al., 2011). While these choices are supported by strong *a priori* expectations (e.g., Menges & Quintana-Ascencio, 2004), some evidence suggests at least two alternative time windows that might provide better predictive ability. First, several studies show that climate conditions during the dormant season can have a substantial effect on vital rates (Fox et al., 1999; Inouye & McGuire, 1991; Kreyling, 2010). For example, temperature and precipitation during the dormant season influence snowpack, which protects plants from frost damage through insulation (Groffman et al., 2001). A decrease in snowpack has been shown to decrease flower production, most likely through frost damage (Boggs & Inouye, 2012; Inouye & McGuire, 1991). Second, some researchers have found evidence of lagged effects, in which vital rates are affected by climate

more than 1 year prior to the year in which vital rates are measured (Dalgleish et al., 2011; Hacket-Pain et al., 2018; Tenhumberg et al., 2018). For example, decreased snowfall can cause a shortage of soil water later in the season, depleting an individual's stored resources and thus decreasing growth and survival in the following year (Dalgleish et al., 2011). These studies highlight that the most appropriate time window of climate to predict vital rates might not be during the growing season or the current year.

In the literature, authors also tend to select specific climate variables, such as temperature and precipitation, *a priori*, as opposed to using a model selection approach. Authors generally select the climate predictor according to the main limiting factor of the system: for example, precipitation in a warm desert (Huxman et al., 2004; Noy-Meir, 1973). However, testing alternative climate variables is justified when these variables could also affect the limiting resources within a system. For example, in warm deserts, temperature can deplete soil moisture (Sherry et al., 2008), and therefore may be just as likely to predict vital rates as precipitation. Moreover, different climate variables could change idiosyncratically during the upcoming century (IPCC, 2014), disrupting historical correlations between climate variables. The choice of climate variable could thus affect the accuracy of future predictions.

Recently, new statistical techniques have emerged that facilitate selecting a specific climate variable and time window(s) during which this climate variable has a high predictive ability (Ogle et al., 2015; van de Pol & Cockburn, 2011; Teller et al., 2016). Among these, the sliding-window approach (e.g., Brommer et al., 2008; Husby et al., 2010; van de Pol et al., 2016) compares the predictive ability of models whose climate predictor is represented by different time windows (Figure 1). If we subdivide a year into months, then the "time window" is defined as a time period of consecutive month(s). In this scenario, predictive time windows comprise all possible combinations of opening (i.e., beginning) and closing (i.e., end) months during the year. The climatic predictor is then computed by taking an aggregate measure of the monthly climatic values within each window. Although the sliding-window approach holds much promise in increasing predictive ability when linking climatic drivers to demographic processes, it requires large amounts of data. Using simulated datasets, van de Pol et al. (2016) showed that a sample size of 10, referred to either years, sites, or both, was enough to detect strong climate signals reliably (R^2 = 0.4 and 0.8); a sample size of 47 years detected weak climate signals (R^2 = 0.2). These data requirements present a challenge, as the median study duration for plant demography research is 5 years (Salguero-Gómez et al., 2015).
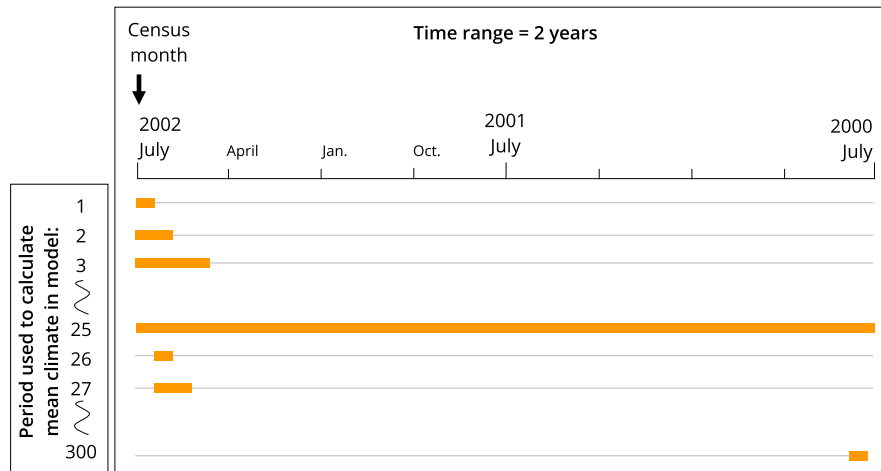
FIGURE 1 Graphical representation of the sliding-window approach, showing time windows in orange. In this article, the sliding-window approach is applied for each of the seven climate variables (three temperature variables, precipitation, snowfall, snow depth, and Standardized Precipitation–Evapotranspiration Index; SPEI). For each climate variable, models are run including the mean climate variable anomaly in all possible time windows within a certain range (in this example, 2 years). Using monthly data, these time windows consist of all possible start and end months. In this example, this means that for model 1 the mean monthly temperature anomaly is calculated in the time window July 2002. The time window for model 2 is July and June 2002, the time window used for model 3 is July, June and May 2002, etc. until model 25 where the time window used are the full 2 years. The time window for model 26 is June 2002, and for model 27 June and May, etc., until 300 different time windows are created for temperature over the 2-year timeframe

Here we will address two questions. First, we review recent literature that links climate drivers to plant vital rates to evaluate which time windows are used to define climate drivers in plant demographic studies. Second, we apply a sliding-window analysis to long-term datasets of four temperate perennial plant species (*Helianthella quinquenervis*, *Frasera speciosa*, *Cylindriopuntia imbricata*, and *Cryptantha flava*). We focus on several climate variables (temperature, precipitation, snow depth, and a drought index) and ask, for each species: when selecting one climate driver, what is the best time window for predicting plant vital rate responses to climate? We predicted that vital rates will depend mostly on the climate during the respective growing seasons of these plants (Angert et al., 2007; Körner, 2003). However, by explicitly testing for the time window with the best predictive ability, we evaluate how strong the alternative cases are. Our analyses aim to clarify whether, and how often, the dormant season (Hacket-Pain et al., 2018; Kruuk et al., 2015; Sherry et al., 2008; Thompson & Ollason, 2001) and lagged effects (Fox et al., 1999; Harsch et al., 2014; Kreyling, 2010) play a role in the effects of climate on plant demographic processes.

2 | METHODS

2.1 | Literature review

To create a comprehensive overview of what time windows are used to define climate drivers, we conducted a literature review. We investigated two aspects of time windows: (i) the relative time window(s) within the year that are used (annual, growing season,

and/or dormant season) and (ii) how far removed the time windows are from the census date. We used studies published between 1997 and 2017 that contain structured population projection models (either matrix population models [Caswell, 2001] or integral projection models [Easterling et al., 2000]) and that linked macro-climatic drivers to plant vital rates. We identified these studies performing a search on Web of Science using the same Boolean expression employed by Compagnoni et al. (2020; Appendix S1).

For each study (*n* = 76 studies), we identified whether the time window examined for climate driver(s) was within the growing season, dormant season, and/or whether it was an annual driver (i.e., climate aggregated over a 12-month period). If investigators considered multiple drivers across different periods, the study was assigned to all applicable time windows. For example, a study considering the effect of annual and growing season precipitation was assigned to both the annual and growing season time window. As a single study could consider multiple periods, we used Cochran's *Q* tests implemented through the *RVAideMemoire* package (Hervé, 2020) in R (R Core Team, 2018) to test whether certain time windows were considered more often than others (annual, growing season, and dormant season). When Cochran's *Q* test identified significant differences in the selection of periods, McNemar's χ^2 tests (*RVAideMemoire* package; Hervé, 2020) were used for further pairwise comparisons among the three time windows. Second, we identified the length of the timeframe over which climate was considered before each demographic census to quantify how many studies considered lagged time windows (i.e., occurring more than 12 months prior to the census month). For each study, we identified the census date of the vital rates, whether the climate driver(s) were

temperature-related (mean, minimum, etc.) or precipitation-related (including precipitation, snowfall, soil moisture, etc.), and the date of the time window(s) considered for the climate driver relative to the census date. We chose temperature and precipitation because most studies investigated at least one climate driver that could be classified as one of these two categories. When a study tested both temperature and precipitation, we scored both of these as present for the study. We included the presence of a climate driver if it was considered by the author, and regardless of significance of the results, the model types used, and whether it was analyzed for its effect on population growth rate or only one vital rate. We tested whether temperature and precipitation were considered equally often as possible climate drivers across biomes. As temperature and precipitation could both be considered in the same study, we again used McNemar's χ^2 tests.

2.2 | Demographic modeling

2.2.1 | Study species and study sites

To identify which climate variables and time windows best predict plant vital rates, we applied the sliding-window analysis to long-term datasets. We identified four perennial plant species datasets for our demographic modeling that had over a decade of demographic data. Our selected species come from biomes whose growing season is clearly defined by an abiotic limitation: temperature for montane habitats (Bryson, 1974) and precipitation for arid habitats (Huxman et al., 2004; Noy-Meir, 1973).

Montane species

We used data collected in the West Elk Range of the Colorado Rocky Mountains, USA, on two herbaceous montane plant species, *Helianthella quinquenervis* (Hook.) A. Gray and *Frasera speciosa* Douglas ex Griseb. *Helianthella quinquenervis* (Asteraceae), the aspen sunflower, is a long-lived iteroparous perennial (Inouye & Taylor, 1979) for which three populations were censused across its elevation range for up to 15 years (Iler et al., 2019). In this study, we used data from 1998 to 2012 for the "mid" population (38°57.5′N, 106°59.3′W, 2886 m a.s.l.), 2005 to 2012 for the "high" population (38°58.612′N, 106°58.690′W, 3407 m a.s.l.), and 1999 to 2012 for the "low" population (38°51.774′N; 107°09.556′W, 2703 m a.s.l.). *Frasera speciosa* (Gentianaceae), the monument plant or green gentian, is a long-lived semelparous perennial (Inouye, 1986) whose population was censused in an alpine meadow at 3750 m, near Cumberland Pass (Che-Castaldo & Inouye, 2011). This population was censused for 47 years (1973–2019).

Populations of both *H. quinquenervis* and *F. speciosa* were censused annually in July, which is in the middle of the growing season (roughly June–August, Iler et al., 2019). Each census measured survival, size, reproduction, and the number of reproductive structures of each plant. Size was measured as the number of rosettes for *H. quinquenervis* and as the number of leaves in the basal rosette for *F.*

speciosa. The reproductive measurements of *H. quinquenervis* and *F. speciosa* are the number of flowering stalks and the number of flowers, respectively. Climate data for the three *H. quinquenervis* populations were estimated using PRISM (PRISM Climate Group, Oregon State University, n.d.) because separate weather stations were not available for each population (Figure S1.1). Climate data for the single population of *F. speciosa* come from the closest NOAA (National Oceanic and Atmospheric Administration, USA) weather station that has data going back to the 1970s (18 km away from the population, Figure S1.2), retrieved using the R package rnoaa (Chamberlain, 2019).

Arid species

We used data from a cactus, *Cylindriopuntia imbricata* (Haw.) DC., and an herbaceous perennial, *Cryptantha flava* L. (A. Nelson) Payson. For *C. imbricata* (Cactaceae), the tree cholla cactus, we used 15 years of data (2004–2018) from a population located at the Sevilleta National Wildlife Refuge, a Long-Term Ecological Research site (SEV-LTER) in central New Mexico, USA (34°20′5.3″N, 106°37′53.2″W, 1660 m a.s.l.; see [Miller et al., 2009] and [Ohm & Miller, 2014] for more details). *Cryptantha flava* (Boraginaceae), Brenda's yellow cryptantha, is a short-lived iteroparous perennial. The data used in this study come from a population near Redfleet State Park, Utah, USA (40°35′42.63″N, 109°25′55.92″W, 1790 m a.s.l.). Demographic monitoring was set up in several plots, distributed among six blocks (see Lucas et al., 2008 for details). The dataset contains 16 years of demographic information (1997–2012; Salguero-Gómez et al., 2012).

Annual demographic censuses were conducted in May for both species, coinciding with the beginning of the growing season for *C. imbricata* (May–September; Miller et al., 2009) and *C. flava* (April–July; Salguero-Gómez et al., 2012). Each census measured survival, size changes (growth/shrinkage), probability of reproduction, and number of reproductive structures of each individual. For *C. imbricata*, size measures consisted of plant height, maximum width, and the width perpendicular to the maximum width. *Cryptantha flava*'s size was measured as the number of rosettes. Reproductive structures quantified during the annual censuses were flower buds and flowering rosettes for *C. imbricata* and *C. flava*, respectively. Climate data for *C. imbricata* were obtained from the nearest climate station of the SEV-LTER (<0.1 km, Figure S1.3, Moore, 2016). Data for *C. flava* came from the nearest NOAA station (16.6 km, Figure S1.4).

2.2.2 | Analyses

2.2.1 | Baseline models

We modeled vital rates based on generalized linear mixed models that followed previous studies published by the data originators. Because of data limitations, and for consistency with previous literature, all vital rate models are density-independent. Testing for density dependence would require data on the location of each individual and possibly the location of other species, which are not available for our species. Baseline models did not include climate drivers,

were size-dependent, and included year as a random intercept. We used a log-transformed size predictor in all models to improve model fit. For *C. imbricata*, size was calculated as the log-transformed volume (cm^3) of an individual, calculated as a cone using plant height and average width. For *H. quinquenervis* in every baseline model, population was added as a fixed effect (Iler et al., 2019) and block was used as a fixed effect for *C. flava* (Salguero-Gómez et al., 2012). Plot identity was added to every baseline model for *C. imbricata* as a random effect (Elderd & Miller, 2016).

Survival and changes in size were modeled as dependent on the size in the previous year (Table S3.1). Because *F. speciosa* is semelparous, survival for this species was modeled conditional on not flowering. Data for *C. flava* suggested senescence, with decreased survival at larger sizes; therefore, the survival baseline for this vital rate also included a quadratic response to size (Table S3.1) as we assume size correlates with age. For *H. quinquenervis*, *C. imbricata*, and *C. flava*, flowering probability and number of reproductive structures were modeled as a function of size during the same census (Table S3.1). For *F. speciosa*, the flowering probability and flower numbers (in year *t* + 1) were modeled as dependent on size of the previous census (year *t*). In this species, size was not measured at the time of flowering (except for flowering stalk height and number of flowers).

Survival and flowering probability were modeled as Bernoulli regressions. Because the size measure of *C. imbricata* is continuous, the size change model for this species was modeled as a Gaussian regression. The size change model of the other species, which have count data as size variables, was modeled as Poisson regressions. Flower numbers also consisted of count data and thus were also modeled as Poisson regressions. See Table S3.1 for an overview of the full set of baseline models.

2.2.2 | Climate variables

We tested a total of seven climate variables for *F. speciosa* and five climate variables for the other species, based on monthly temperature or monthly precipitation anomalies. Previous studies have shown that temperature, precipitation, snow cover, and drought indices (which integrate temperature and precipitation) can be key drivers of population dynamics (e.g., Dalgleish et al., 2011; Doak & Morris, 2010; Salguero-Gómez et al., 2012; Siepielski et al., 2017; Tenhumberg et al., 2018). We used climate anomalies rather than absolute values because plants are expected to be adapted to their mean climate (Peterson et al., 2018), and should therefore respond to climatic anomalies. We considered both average and extreme temperature anomalies because climate extremes have also been shown to influence vital rates (Easterling, Meehl, et al., 2000). Specifically, mean minimum and mean maximum temperature should correlate with limitations to vegetation processes. For example, the mean minimum temperature should influence nighttime respiration costs (Criddle et al., 1997; Maier et al., 1998; Wright et al., 2006) while the mean maximum temperature should influence photorespiration costs (Hagemann & Bauwe, 2016). The monthly climate variables included total precipitation (*P*), mean average daily temperature (T_{avg}),

mean maximum daily temperature (T_{mean_max}), and mean minimum daily temperature (T_{mean_min}). We used precipitation data, and the latitude of our study populations, to calculate a drought index, the Standardized Precipitation–Evapotranspiration Index (SPEI), on a scale of 12 months, using the *SPEI* R package (Beguería & Vicente-Serrano, 2017). Finally, for *F. speciosa*, we also included monthly snowfall (S_{fall}) and mean snow depth (S_{depth}). S_{fall} and S_{depth} were not available for the separate populations of the other montane species, *H. quinquenervis*. We used *P*, SPEI, S_{fall}, S_{depth}, and T_{avg} to quantify the cumulative effect of water availability and temperature on vegetation processes. We used S_{fall}, and S_{depth} to account for the physical effects of snow. Finally, we used T_{min_mean} and T_{max_mean} to quantify the effect of climatic extremes in driving demographic rates.

We calculated climate anomalies as a z-score, by subtracting the monthly climate mean from each annual monthly value, and dividing by the standard deviation of the monthly climate. We calculated the means and standard deviations of monthly climate across a minimum period of 30 years (World Meteorological Organization, 2017). However, for *C. imbricata*, we could only calculate climate anomalies for the 20-year period (1998–2018) during which climate data were available.

We computed the climatic predictors of our generalized linear models using the climate observed from the start of the annual census backwards (e.g., if survival was measured in mid-July 2018, we considered the monthly climate anomalies starting in July 2018; see Figure 1). Our demographic datasets consist of censuses made on the same month each year. As a result, the start and end months of the range tested for climate signals were the same across years for each species.

Our time range started from the census where the response variable was measured (e.g., survival or flower probability). Thus, for all vital rates and species except for *F. speciosa*, our range includes the month during which the response variable was measured in year *t* + 1, and the preceding 36 months. For *F. speciosa*, we considered a more extended range; 6 years for survival and size changes, and 4 years for fertility. While this increased range increased the possibility of spurious correlations, previous research indicates that this species commits to flowering 4 years before flowering (Inouye, unpublished), and increases the number of leaves in the rosette every 4 years on average (Inouye, 1986), suggesting it may be particularly slow growing and prone to lagged climate effects.

2.2.3 | Sliding-window analysis

We identified the climate driver with the best ability to predict demographic rates using the sliding-window approach (van de Pol et al., 2016, Figure 1), implemented with the *climwin* package (Bailey & van de Pol, 2016) in R (R Core Team, 2018). This package compares the predictive ability of models that include climate from all possible time windows within a specified time frame (range). Because our data are monthly, possible time windows include windows of 1-month duration, 2-month duration, and all the way up to the full extent of the range tested. Moreover, all possible starting months

were considered for each window duration. In other words, a time window of 2 months could start 2 months before and end at the census date, or it could start 7 months before and end 5 months before the census month. Subdividing a range of 3 years into the constituting 36 months implies testing the predictive ability of 703 time windows of each climate driver for each response variable. The monthly climate variables were aggregated within each window by taking the mean.

The sliding-window analysis included a single linear effect of climate for each vital rate and species. This resulted in a total of seven models for each vital rate for the montane species, and five models for each vital rate of the arid species, for which the predictive ability of all time windows was tested. We selected the best model (and thus best climate driver) using AIC_c. We subtracted the AIC_c of the baseline models (i.e., models not considering climate) from the AIC_c of the climate models. The climate driver with the lowest AIC_c was selected for further analysis. We focus on identifying a single, best climate variable for each vital rate. Additional climate variables may also predict vital rates, and over different timeframes, but our goal was to assess whether the best climatic predictor occurred within a timeframe that is typically considered (e.g., the growing season). Additionally, adding multiple climatic predictors would amplify the number of climate windows, increasing the chance of spurious correlations (see section below). Finally, we evaluated the predictive ability of our selected climate driver models. This was done by comparing the AIC_c scores of the selected climate driver models with the models using the same climate variable observed during the most recent growing season.

2.2.4 | Potential for spurious correlations

Due to the high number of windows tested in our analysis, we examined potential spurious correlations between the climate drivers and vital rates. There are two ways in which selected models might reflect a spurious relationship. First, due to the high number of models tested, significant climate signals could arise by chance. Second, there may be a correlation between the selected climate driver and other time windows and/or climate variables. To address the first possibility, we used a randomization procedure that randomizes the date of the demographic data (van de Pol et al., 2016). This randomization removed the observed correlation between response variable and climatic drivers. However, this randomization maintained the original data structure, as well as the structure of the climate variables. Then, we re-ran the sliding-window analysis described above, saving the AIC_c of the best model. This model selection was done 2000 times, creating a distribution of the best AIC_c values obtained on each randomized dataset. This distribution was then used to test whether the AIC_c of the best model found in the sliding-window analysis is due to chance, indicating a spurious correlation.

To address the second possibility that there is a correlation between the selected climate driver and other climate drivers, we investigated the influence of correlation between competing climatic windows. While high correlations would not decrease the predictive

abilities of the selected climate drivers, they could indicate that the causal relationship could be found in other time windows and/or climate variables. We first quantified the autocorrelation between the selected climate window, and all other competing windows. We then also tested the correlation between the selected climate window and the climate windows of all the climate variables that were not selected.

3 | RESULTS

3.1 | Literature review

Out of 76 studies (Table S1.1) with 246 different populations of 103 plant species, few considered the possibility of climate effects in the dormant season, or the possibility of lagged effects. The studies had a mean duration of 8.04 years (with a range of 1–40 years). A total of 11 studies had a duration greater than 15 years, and all studies selected climate drivers a priori, rather than using a model selection approach such as the sliding window. We found that researchers do not consider different periods (annual, growing, and dormant season) equally when examining the effects of temperature (χ^2 = 7.294, df = 2, p = 0.026) and precipitation (χ^2 = 19.471, df = 2, p < 0.001) on vital rates (Figure 2). When authors considered temperature as a possible climate variable, the growing season was considered significantly more often than the dormant season (χ^2 = 8.642, df = 1, p = 0.003). Moreover, a tendency emerged for climate effects in an annual period to be investigated more often
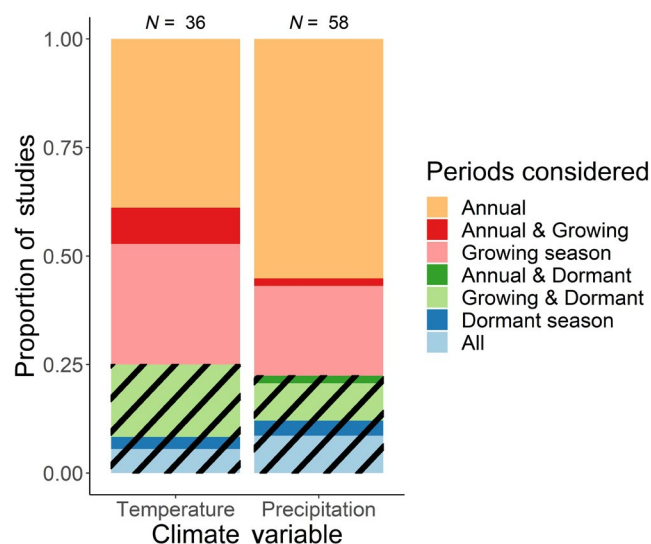
FIGURE 2 The literature review reveals that 25% or fewer studies examining temperature and precipitation as climate drivers explicitly consider climate during the dormant season. Studies that include temperature and/or precipitation drivers are categorized by the periods within the year over which climate is considered as a potential driver (annual, dormant season, and growing season). The black lines indicate studies that explicitly include dormant season as a possible climate driver

than in the dormant season (χ^2 = 3.375, df = 1, p = 0.066). When authors investigated precipitation, the annual timeframe was most commonly considered (Figure 2). Authors considered the annual period (χ^2 = 15.625, df = 1, p < 0.001) and the growing season (χ^2 = 5.063, df = 1, p = 0.024) significantly more often than the dormant season. Additionally, authors also investigated precipitation during an annual period more often than during the growing season (χ^2 = 4.5, df = 1, p = 0.034).

A total of 85% of the examined studies (n = 65 out of 76 studies) considered windows inside the transition year only (Figure 3b shows Arid studies; all studies can be found in Figures S1.1 and S1.2). Of the 11 studies including lagged windows, only six considered two full years prior to the census. Finally, only the publications from arid biomes had a strong preference of one type of climate driver over the other. Studies in arid regions investigated precipitation climate drivers significantly more often (χ^2 = 9.091, n = 17, df = 1, p = 0.003) than temperature.

3.2 | Demographic modeling

3.2.1 | Potential for spurious correlations

Randomizations showed that of the 16 climate signals detected, 13 had a significantly low chance of being spurious results (p < 0.05;

Appendix S6). On the other hand, the climate drivers selected for the survival of *F. speciosa* (p = 0.369; Figure S6.5) and for the size changes and flower numbers in *C. imbricata* (p = 0.217; Figure S6.10 and p = 0.520; Figure S6.12, respectively) did have a chance of being spurious. We therefore did not present the results for these three climate drivers.

Correlation results showed that shorter windows have fewer auto-correlations or correlations with other climate variables (e.g., Figure S9.4), whereas longer windows have many other neighboring windows that are highly correlated, both within the same climate variable and in others (e.g., Figure S9.14). Correlation was more common between the temperature climate variables (e.g., Figure S9.1), between P and SPEI (e.g., Figure S9.6), and between snowfall and depth (e.g., Figure S9.5). Correlation was less common between P and SPEI, and between the temperature and snow variables (but see Figures S9.9 and S9.12).

3.2.2 | Sliding-window analysis

We found that in many cases the climate variable most predictive of demographic rates fell outside of the growing season, and many climatic predictors were lagged (i.e., their effect occurred farther back than one transition year; Figure 4). One climate driver had a time window that resembled the growing season: average temperature
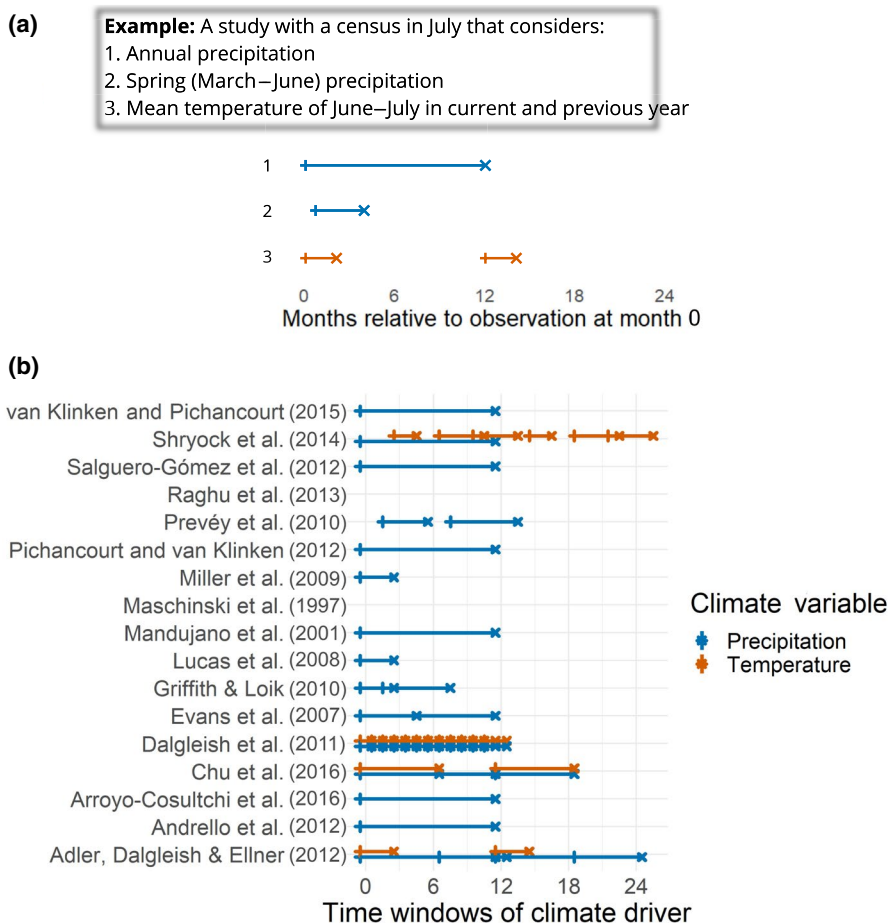
FIGURE 3 Few studies consider climate drivers more than 12 months prior to the census month. (a) shows the hypothetical example with written climate driver descriptions and the appropriate time windows in graphical form. (b) shows the subset of studies conducted in arid regions. The time windows that are considered in studies conducted in two biomes; arid and temperate coniferous forest relative to the census of the response variable. Few studies consider the potential for lagged effects (climate drivers more than 12 months prior to the census). Both precipitation and temperature drivers are included
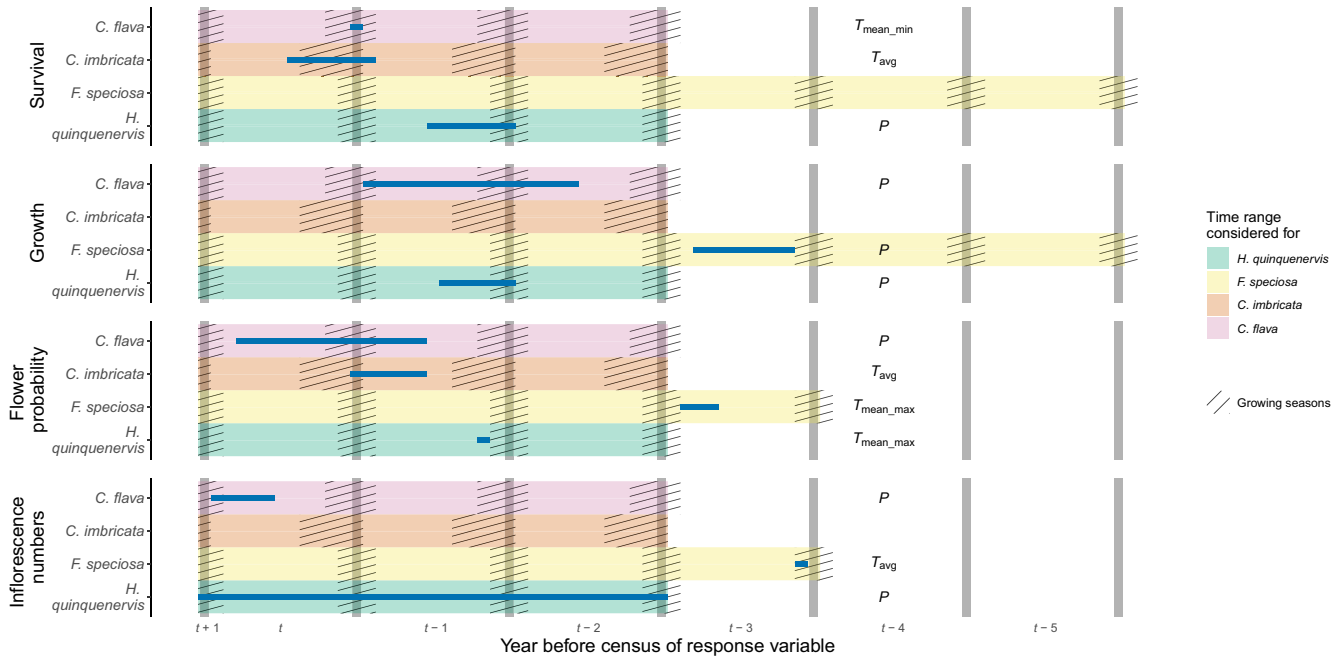
FIGURE 4 The climate drivers that best predict vital rates in *Helianthella quinquenervis*, *Frasera speciosa*, *Cylindriopuntia imbricata*, and *Cryptantha flava* mostly fall outside the growing season and before the first year prior to the population census. For each vital rate and each species, the time window with the best predictive ability is shown with blue horizontal lines. The best driver is listed on the right side of the graph. The grid lines indicate census months and the shaded areas show the time range considered in the sliding-window analysis. The dashed areas indicate the growing seasons for each population

for *C. imbricata* survival extends 1 month before and after the growing season (Figure 4). Other windows included only 1 month during the growing season or fell fully outside the growing season (e.g., *C. flava* survival and *F. speciosa* changes in size, respectively, Figure 4). Moreover, lagged windows were common: out of the 13 non-spurious time windows, six open and close before the transition year (i.e., >1 year before the census in time t), and one window closes in the transition year, but opens in year $t-1$ (*C. flava* flower probability, Figure 4). We also found windows spanning more than 12 months. We found that eight of the 13 best climate predictors were related to temperature. Finally, all but one of the selected models with a time window different from the growing season had AIC_c scores that were at least 2 units lower than models with time windows in the recent growing season (Appendix S5).

For *H. quinquenervis*, we found that precipitation (*P*) from July in year $t-1$ (July$_{t-1}$) to January in year $t-1$ (January$_{t-1}$) has the best predictive ability for survival from year *t* to year $t+1$ (with 59.32 AIC units lower than the baseline; from now on presented as $\Delta AIC_c = -59.32$; Figure 4; Table S5.1). *P* in this time period has a positive effect on survival of *H. quinquenervis* (Figure 5). An increase of two standard deviations (from mean −SD to mean +SD) changed survival probability of an average-sized individual from 79.5% to 96.0% (Figure S8.1). Size changes were best predicted by *P* from July$_{t-1}$ to December$_{t-1}$ ($\Delta AIC_c = -51.33$; Figure 4; Table S5.2). *P* during this time window had a positive effect on *H. quinquenervis* (Figure 5). An increase of 2-SD in *P* increased the size in year $t+1$ by 43.8% (for an average-sized individual; Figure S8.1). Flower probability was best predicted by mean maximum temperature (T_{mean_max}) in September$_{t-1}$ ($\Delta AIC_c = -67.2$;

Figure 4; Table S5.3). A 2-SD increase in T_{mean_max} decreased flower probability from 85.0% to 1.5% (Figure 6; Figure S8.2). Finally, the number of flowering stalks was best predicted by *P* from July$_{t-2}$ to July$_{t+1}$ ($\Delta AIC_c = -31.66$; Figure 4; Table S5.4), which is the full time range in our analysis. An increase of 2-SD increased the number of flowering stalks by 70.2% (Figure 6; Figure S8.2).

Frasera speciosa changes in size were best predicted by *P* in September$_{t-3}$ to April$_{t-3}$ ($\Delta AIC_c = -9.52$; Figure 4; Table S5.6), where an increase of 2-SD decreased size in $t+1$ by 4.1% (Figure 5; Figure S8.1). Flower probability was best predicted by T_{mean_max} from March$_{t-3}$ to May$_{t-3}$ ($\Delta AIC_c = -11.69$; Figure 4; Table S5.7), when a 2-SD increase increases flower probability from 0.02% to 0.16% (Figure 6; Figure S8.2). Finally, average temperature (T_{avg}) in August$_{t-3}$ best predicted the number of flowers ($\Delta AIC_c = -12.99$; Figure 4; Table S5.8). A 2-SD increase in temperature increased the number of flowers by 38.0% (Figure 6; Figure S8.2). All vital rates of *F. speciosa* had at least one secondary climate variable whose predictive ability was close to the best models (i.e., within 2 AIC_c units; T_{mean_max}, *P*, and T_{mean_max} for size changes, flower probability and flower numbers, respectively; Table S5.6–5.8).

Our results show that for *C. imbricata*, survival was best predicted by T_{avg} from April$_{t-1}$ to October$_t$ ($\Delta AIC_c = -8.43$; Figure 4; Table S5.9). An increase in temperature of 2-SD during this period decreased survival probability (Figure 5) from 98.7% to 95.9% for an average-sized individual (Figure S8.1). There was also a second climate variable with a ΔAIC_c score that was within 2 units of the selected survival model (T_{mean_max}; Table S5.9). The best predictor for flower probability was T_{avg} from December$_{t-1}$ to May$_t$ ($\Delta AIC_c = -9.88$;

FIGURE 5 The model prediction for survival and changes in size with the best climate driver plotted against the datapoints for *Helianthella quinquenervis* ("mid" population), *Frasera speciosa*, *Cylindriopuntia imbricata*, and *Cryptantha flava* (Block I). Climate effect was calculated on three levels; mean climate anomaly during this time window as well as + and – one standard deviation climate anomaly. The vertical blue lines are the mean size of the individuals used to parameterize the models. Data used for the model parameterization are also plotted. In the survival column, the points are the binned proportions of survival, with the size of the points proportional to the number of observations in each bin. The points in the changes of size column are individual observations
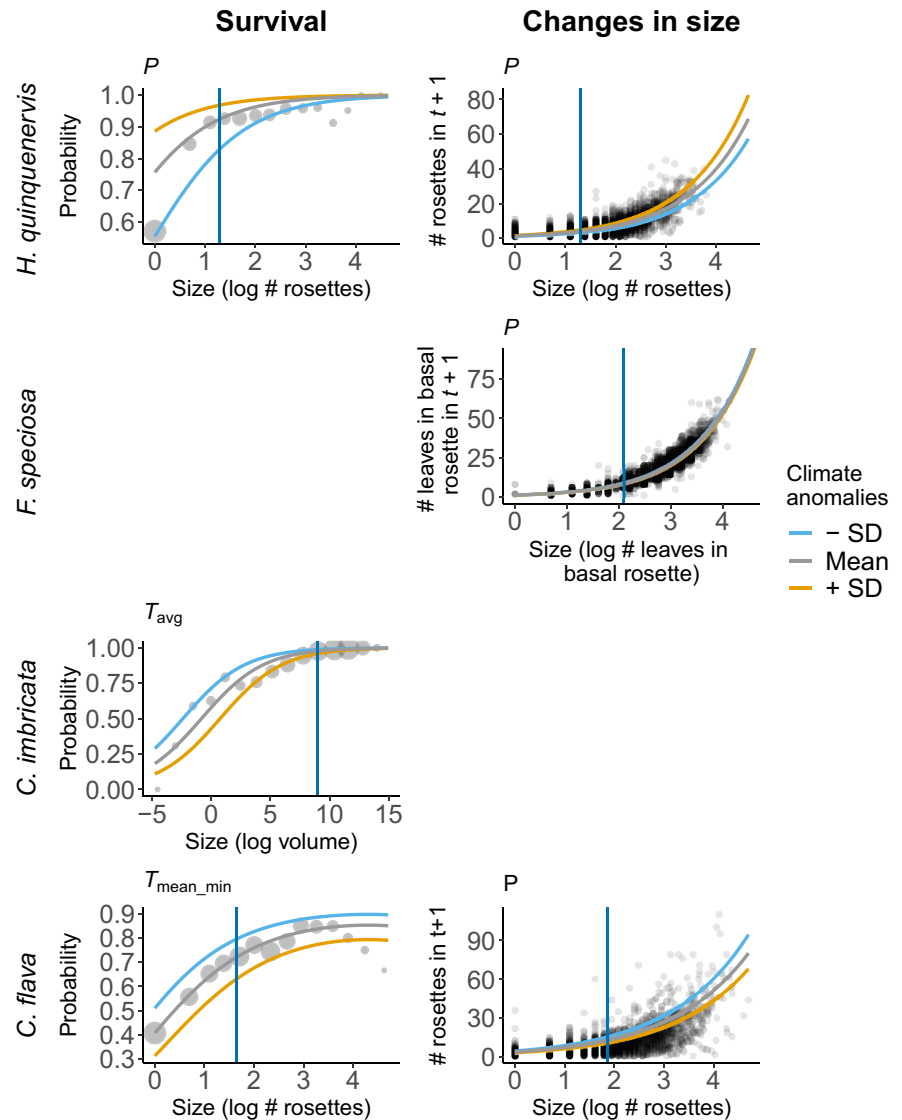

Figure 4; Table S5.11), where flower probability increased from 0.9% to 5.9% with a 2-SD increase in T_{avg} (Figure 6; Figure S8.2).

Finally, for *C. flava*, the best predictor for survival probability was T_{mean_min} in May$_t$ (ΔAIC_c = −12.71; Figure 4; Table S5.13). Survival decreased from 79.5% to 63.0% with a 2-SD increase of T_{mean_min} in this period (Figure 5; Figure S8.1). The second best climate variable for predicting survival (T_{mean_max} from September$_t$ to January$_t$) also had a low ΔAIC_c score (ΔAIC_c = −12.35). Changes in size were best predicted by P from Dec$_{t-2}$ to April$_{t-1}$ (ΔAIC_c = −14.03; Figure 4; Table S5.14). Average-sized individuals in year t were 27.9% smaller in $t + 1$ when P increased with 2-SD in this period (Figure 5; Figure S8.1). Flower probability was best predicted by P from December$_{t-1}$ to February$_t$ (ΔAIC_c = −13.07; Figure 4; Table S5.15). A 2-SD increase in P increased flower probability of an average-sized individual from 10.5% to 31.3% (Figure 6; Figure S8.2). The number of flowering rosettes was also best predicted by P, but from December$_t$ to April$_t$ (ΔAIC_c = −12.14; Figure 4; Table S5.16). Number of flowering rosettes increased by 54.3% with a 2-SD increase in precipitation over this timeframe (Figure 6; Figure S8.2).

4 | DISCUSSION

Changes in climate are projected to be heterogeneous across space and time (IPCC, 2014). Thus, it is important for ecologists to select the right climate variables and time windows to understand and forecast responses of their specific study systems/locations to current and future climate (van de Pol et al., 2016). We found that plant population ecologists typically only consider in their demographic models the climate during the transition year, over either annual or growing season time frames. This choice makes the implicit assumption that climatic effects on vital rates—and thus emergent population dynamics—are short term. However, our sliding-window analyses reveal that in the four species for which we have long-term (>10 years) demographic data, lagged windows are the rule rather than the exception. Moreover, our analyses demonstrated that the influence of climate drivers on demography often occurred outside of the most-recent growing season. Thus, these results indicate that lagged climate variables and dormant season climate might be important drivers of plant population dynamics. Consequently,
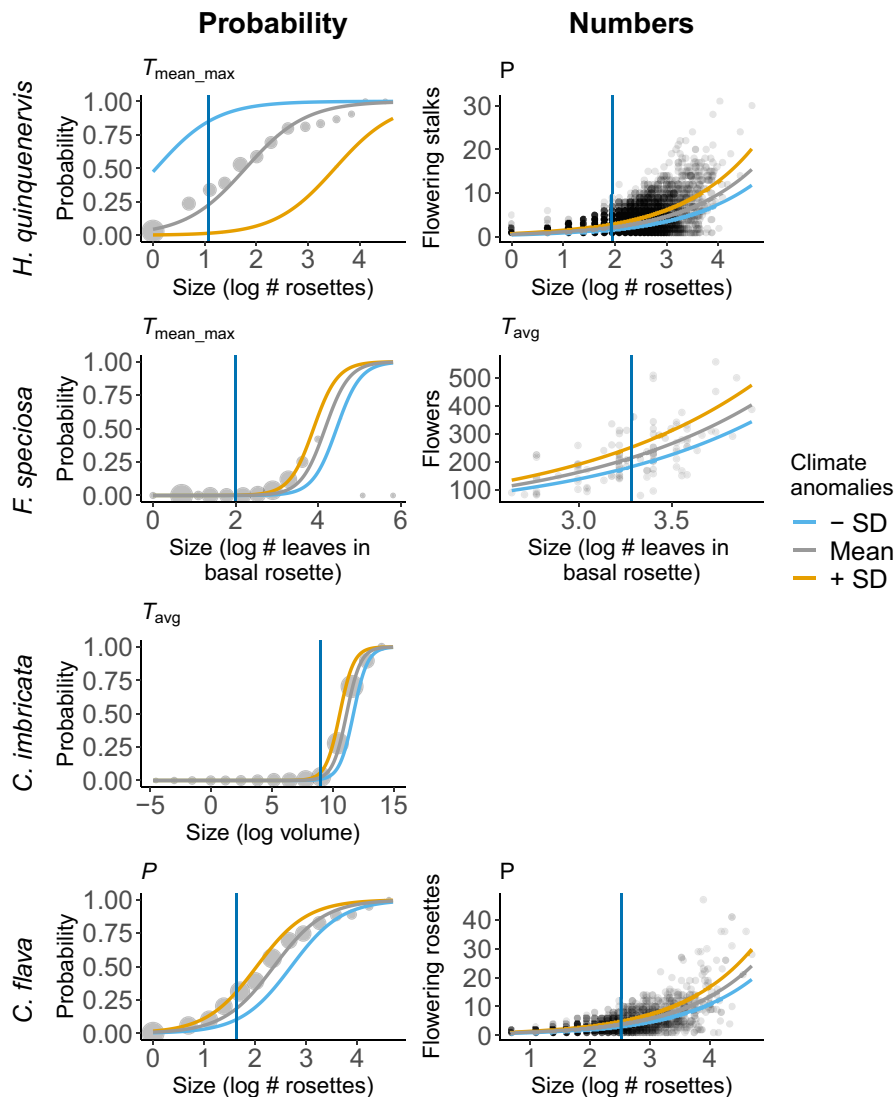
FIGURE 6 The model prediction for flower probability and numbers with the best climate driver plotted against the datapoints for *Helianthella quinquenervis* ("mid" population), *Frasera speciosa*, *Cylindriopuntia imbricata*, and *Cryptantha flava* (Block I). Climate effect was calculated on three levels; mean climate anomaly during this time window as well as + and − one standard deviation climate anomaly. The vertical blue lines are the mean size of the individuals used to parameterize the models. In the probability column, the points are the binned proportions of flower probability with the size of the points proportional to the number of observations in each bin. The points in the number column are the individual observations

investigators are justified in considering dormant season and lagged climate as (*a priori*) climate predictors.

Our results suggest that lagged climate might commonly mediate the effect of climate on vital rates. The literature provides some key examples of how a lagged effect of climate could result from physiological mechanisms. For instance, in *Astragalus scaphoides*, Tenhumberg et al. (2018) found a lagged negative effect of spring precipitation on survival. This lagged effect was linked to the biannual flowering peaks of this species (Crone & Lesica, 2004) where a large proportion of individuals flower after a wet spring. This flowering peak led to depleted non-structural carbohydrate stores in the following year (Crone et al., 2009), which negatively influenced survival (Tenhumberg et al., 2018). The prevalence of lagged effects we report here across our species could result from similar physiological mechanisms. Correlating residuals from the changes in size models from 1 year to the next revealed significant negative relationships for *H. quinquenervis* and *F. speciosa* (data not shown), but not *C. flava*. This finding suggests that the former two species

could be similarly limited by resources after a year of better than average growth.

Another way in which plant physiology might result in lagged climate effects is the preformation of leaves and inflorescences. Belowground bud banks are common among herbaceous plants (Ott et al., 2019). For instance, in alpine environments, up to 4 years can be required for each leaf and inflorescence to progress from initiation to functional and structural maturity (e.g., Diggle, 1997; Garcia et al., 2011). This preformation happens in *F. speciosa* as well 4 years before emergence (Inouye, 1986). Accordingly, the climate most influential to the changes in number of leaves and flowering probability in *F. speciosa* occurs 4 years before the census (Figure 4). Our second result on flowering probability agrees with another analysis carried out on this same *F. speciosa* dataset. Flowering by *F. speciosa* is correlated with summer precipitation 4 years prior to inflorescence emergence (Inouye, in prep). Our analysis selected mean maximum temperature, rather than precipitation occurring 4 years prior to flowering as the best predictor

of flowering probability; however, precipitation was a close second best model (Table S5.7). Temperature was also a significant predictor of flowering, with a 2-year lag, of *Veratrum tenuipetalum* (Melanthiaceae) in the same habitats as lower-altitude *Frasera* populations (Iler & Inouye, 2013).

An alternative hypothesis to explain lagged climate drivers during the dormant season is their indirect effects. Indirect effects of climate drivers occur when these influence certain biotic drivers, such as soil microbiomes or pollinators, rather than plant physiology. Examples include the reported long, lagged window in which precipitation has a negative effect on the growth of *C. flava*. Yu et al. (2019) showed that under wetter conditions, *B. eriopoda*, a C_4 grass, had a competitive advantage over *C. imbricata*. Indirect effects can also include interspecific (Aschehoug et al., 2016) or intraspecific density dependence (Dahlgren et al., 2016). Specifically, lagged climate drivers for survival could point to intraspecific density dependence, but we do not find such lagged climate drivers for our species. Previous authors who emphasized the importance of dormant season climate also pointed to indirect biotic effects (Kreyling, 2010; Stahl et al., 2006). Accordingly, biotic drivers are known to have large effects on population growth rates (Morris et al., 2020). Identifying possible indirect effects of climate on vital rates would require additional data on, for example, insect populations (Stahl et al., 2006) or the soil community (Bever et al., 1997; Maherali, 2020), and is an exciting area for future research.

The mechanisms by which dormant season climate influences vital rates likely depend on the habitat. For example, snow cover duration during the dormant season might be important for vital rates of montane and cold desert species such as *C. flava* (which requires vernalization to flower), whereas physiological activity outside of the growing season might be important for arid species. In the montane species *F. speciosa*, the dormant season was important for size changes and flower probability. Less precipitation during the winter might be linked to earlier snow melt, a longer growing season, and more growth. An earlier snow melt might also correlate with a warmer T_{mean_max}, which led to a higher probability of flowering. Snow melt timing generally has a substantial effect on the dynamics or physiology of alpine plant populations (Campbell, 2019; Iler et al., 2019; Wipf et al., 2009). However, it is possible that dormant season snowfall and snow depth anomalies do not correlate well with snow melt timing, or that the ecological effects of snow cover on vital rates might be nonlinear (e.g., because snow cover insulates the ground only above the 40 cm threshold; Cline, 1997).

The climate driver that best predicted the flowering of our arid species, *C. imbricata*, is most likely linked to the importance of physiological processes during the dormant season. Both our results and Czachura and Miller (2020) found that flowering probability was positively affected by temperature anomalies observed during the dormant season. Wetter and cooler seasons might allow dormant season photosynthetic activity, as has been documented in other species, such as winter annuals (Regehr & Bazzaz, 1976) and conifers in oceanic climates (Waring & Franklin, 1979).

We hypothesize that the diversity of selected climate variables and time windows could explain an earlier finding showing

mostly uncorrelated vital rates in *C. imbricata* and *H. quinquenervis* (Compagnoni et al., 2016). Specifically, our results suggest that vital rates might fluctuate independently because they respond to a diversity of climatic windows, climate drivers, and effect sizes. Testing this hypothesis would also require ruling out the effect of other factors producing positive or negative correlations among vital rates, such as density dependence and individual-level trade-offs between vital rates.

Despite the computational burden of our sliding-window analyses, we still make assumptions that could be relaxed by more complex models. First, we assumed that each month within the time window is equally important. However, generalized additive models (Teller et al., 2016) and regularization (Tredennick et al., 2017) can estimate the effect sizes, and therefore the relative importance, of single monthly or seasonal climate anomalies. This could be especially important in the long windows such as the flower numbers of *H. quinquenervis*, which includes several growing and dormant seasons. Second, we focused on selecting only one climate driver per vital rate, which allowed us to address the main question of this article: what are the best climate variables and time windows for our species, and how do these relate to what is common in the literature? However, other research questions could benefit from selecting multiple drivers (van de Pol et al., 2016), for example, when maximizing predictive ability of predicting population trends under climate change. Finally, we did not consider more complex relationships between climate and vital rates, such as nonlinear effects (Ehrlén et al., 2016), density dependence (Gornish, 2013), climate and size interactions (Iler et al., 2019), and interactions between vital rate parameters. Including these factors could increase the predictive ability of vital rate models or even change the climate driver selected. Our approach is an important first step in assessing the relative importance of climate conditions that fall outside of typically considered time windows in studies of plant demography.

When selecting the best climate driver, closely related time windows, or different climate variables can have similar model support. Selecting among climate variables, nine of our vital rates had a climate variable with a much lower ΔAIC_c (at least 2 units) than all other variables (e.g., Table S5.2), but other vital rates had at least one other climate variable with ΔAIC_c scores close to the best climate driver (e.g., Table S5.6). This lack of a clear winner could indicate highly correlated climate drivers, complex relations between vital rates and climate mentioned previously or a strong influence of more than one climate driver (van de Pol et al., 2016). When multiple models have similar support, investigators can opt to perform model averaging. However, the ability of these models to predict future responses to climate might still be low. For example, when correlations between separate climate drivers are high, it may be impossible to establish causality. This is especially relevant when predicted climatic changes include novel correlations between climatic drivers (IPCC, 2014).

In this analysis, we have used large-scale, macro-climatic predictors which, however, can differ from the micro-climate experienced by plants (Scherrer & Körner, 2010). This can be especially important when investigating plant populations in spatially variable habitats,

such as montane grasslands (Körner, 2003; Oldfather & Ackerly, 2019). Because it is currently unclear how climatic anomalies correlate at the macro- and micro-scale, employing micro-climatic conditions in a sliding-window analysis could improve our understanding of timeframes over which climate affects vital rates.

Our results motivate several recommendations for researchers with shorter-term datasets for which the sliding-window method may not—yet—be feasible, and for those with longer-term datasets. In short-term datasets, a sliding-window method has a high chance of not detecting the climate signal, or identifying true signals as spurious through the randomization tests (van de Pol et al., 2016). We therefore suggest to first compare the predictive ability of climatic predictor types over larger and fewer timeframes (e.g., "dormant season temperature"), rather than continuously sliding climatic windows. According to our findings, these climate predictors should include both precipitation and temperature during the growing season, the dormant season, and in previous years. Second, considering natural history information (e.g., presence of belowground bud banks, or of dormant season physiological activity) when selecting climate drivers can improve the chance of selecting relevant time periods (including lagged time windows). Third, with shorter datasets, researchers should account for potential overfitting, for example by performing cross-validation (Wenger & Olden, 2012) or by fitting regularized regression models (Dahlgren, 2010). Finally, for the researchers with longer-term datasets, we encourage the use of model selection methods to select climate drivers. In these cases, it is vital to consider the life-history information of their specie(s) to select a time range that allows for appropriate lagged effects. This time range should include climate drivers during the growing and dormant season.

DATA AVAILABILITY STATEMENT

The demographic datasets of all four species used for the demographic modeling are available online (*H. quinquenervis*; https://doi.org/10.5061/dryad.863c8sk, *Frasera speciosa*; https://osf.io/ qubhx/, *Cylindriopuntia imbricata*; https://doi.org/10.6073/pasta/dd06df3f950afe4a4642306182237d13, *Cryptantha flava*; https://doi.org/10.6084/m9.figshare.c.3306537.v1. The R code used in all the analyses is available on GitHub at github.com/SanneE1/Climate-windows.

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SUPPORTING INFORMATION

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