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Time-lagged effects of weather on plant demography: drought and *Astragalus scaphoides*

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Abstract. Temperature and precipitation determine the conditions where plant species can occur. Despite their significance, to date, surprisingly few demographic field studies have considered the effects of abiotic drivers. This is problematic because anticipating the effect of global climate change on plant population viability requires understanding how weather variables affect population dynamics. One possible reason for omitting the effect of weather variables in demographic studies is the difficulty in detecting tight associations between vital rates and environmental drivers. In this paper, we applied Functional Linear Models (FLMs) to long-term demographic data of the perennial wildflower, *Astragalus scaphoides*, and explored sensitivity of the results to reduced amounts of data. We compared models of the effect of average temperature, total precipitation, or an integrated measure of drought intensity (standardized precipitation evapotranspiration index, SPEI), on plant vital rates. We found that transitions to flowering and recruitment in year t were highest if winter/spring of year t was wet (positive effect of SPEI). Counterintuitively, if the preceding spring of year $t - 1$ was wet, flowering probabilities were decreased (negative effect of SPEI). Survival of vegetative plants from $t - 1$ to t was also negatively affected by wet weather in the spring of year $t - 1$ and, for large plants, even wet weather in the spring of $t - 2$ had a negative effect. We assessed the integrated effect of all vital rates on life history performance by fitting FLMs to the asymptotic growth rate, $\log(\lambda_t)$. $\text{Log}(\lambda_t)$ was highest if dry conditions in year $t - 1$ were followed by wet conditions in the year t. Overall, the positive effects of wet years exceeded their negative effects, suggesting that increasing frequency of drought conditions would reduce population viability of *A. scaphoides*. The drought signal weakened when reducing the number of monitoring years. Substituting space for time did not recover the weather signal, probably because the weather variables varied little between sites. We detected the SPEI signal when the analysis included data from two sites monitored over 20 yr (2×20 observations), but not when analyzing data from four sites monitored over 10 yr (4×10 observations).

Key words: carryover effects; detecting weather signals; drought; environmental drivers; matrix models; plant demography; space for time substitution.

Introduction

Temperature and precipitation are key drivers of plant population dynamics (e.g., Doak and Morris 2010, Nicole et al. 2011, Salguero-Gómez et al. 2012, Sletvold et al. 2013, Dahlgren et al. 2016) and are essential components for predicting the distribution of species in space and time (Huntley et al. 1995, Carey 1996, Bakkenes et al. 2002, Pearson et al. 2002, Pearson and Dawson 2003, Box 1981). Understanding their combined effects is a prerequisite for predicting immediate effects of climate change (IPCC 2014) on population persistence. Surprisingly, the central importance of precipitation and temperature is not reflected in demographic studies. For example, a review of 396 matrix models in plants (1960 through 2009) found that only 13.1% of the studies linked demographic responses to environmental drivers (Crone et al. 2011, 2013). In recent years, interest in studying the effects of environmental drivers has increased (Ehrlén et al. 2016), perhaps because of growing attention on their importance for predicting species distributions and abundances (Ehrlén and Morris 2015). Although 27.6% of 136 structured population models published between 1995–2015 considered abiotic drivers, only one-half of those were associated with climate (Ehrlén et al. 2016).

Integrating vital rate responses to variation in weather variables and further into demographic models would be valuable for predicting the effect of climate change on population viability. Understanding the environmental drivers of vital rates would also be helpful for projecting population dynamics in any kind of variable environment (Morris and Doak 2002) and for devising appropriate management strategies (e.g., Ehrlén et al. 2005). However, demographic studies are typically conducted over a relatively short time frame (Crone et al. 2011; see Salguero-Gómez et al. [2016] for demographic studies in animals); most studies on plants include less than five transition years (Salguero-Gómez et al. 2015). Short time series may not capture the full range of variation in temperature and precipitation typical for the study area and as a consequence, it may be challenging to detect correlations between environmental drivers and vital rates. The failure to adequately capture environmental variation due to short time series may contribute to the mismatch between predicted and observed population growth rates (Crone et al. 2013).

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One possible reason for omitting the effects of temperature and precipitation in demographic studies is the difficulty in detecting tight associations between vital rates and environmental drivers because the information from time series data is typically insufficient for unravelling the complex mechanisms leading from variation in weather variables to population fluctuations (Knape and de Valpine 2011). Our ability to detect the signal of weather variables on population dynamics is influenced by the way we choose to aggregate temperature and precipitation data. For example, precipitation can be summed up by day, month, season, or year. If we aggregate by season, we need to choose the months to be included in that season. The best choice of weather variables to include depends on the bias-variance trade-off between the risk of over-fitting against the risk that an important variable would be missed (e.g., Hastie et al. 2009:220). Moreover, any type of aggregation bears the risk of losing information about the actual sequence of environmental events that led to observed vital rates. This is particularly problematic if the effects of weather variables are context dependent. For instance, the detrimental effects of frost in spring depends on whether the chilling and heating requirements were sufficient to break winter dormancy (Campoy et al. 2011).

An additional challenge for detecting the effect of weather variables on plant vital rates are situations where the effects are delayed. For instance, water availability during the growing season controls the amount of resources plants can use for growth and reproduction. Perennial plants may allocate some of the available resources to storage thereby influencing plant vital rates in future growing seasons. In low productivity environments a single growing season may not be sufficient to exceed the resource threshold required for reproduction, and plants rely on accumulating resources in storage pools (e.g., roots or rhizomes; Ehrlén and Van Groenendael 2001) over more than a single growing season. Storing resources also increases survival in the presence of environmental stress. This is particularly relevant in seasonal habitats where the amount of stored resources has a direct effect on next year's regrowth and plant size is positively correlated with survival, flowering and seed production (e.g., Ellner and Rees 2006, Tenhumberg et al. 2008, 2015). Even in seasonal habitats, the investment into growth can extend beyond the current growing season as indicated by size of individuals being positively correlated among years (Ehrlén and Van Groenendael 2001). Detecting delayed effects of weather variables on the demography of perennial plants may require statistical models that explicitly include time lags.

Teller et al. (2016) demonstrated an elegant statistical method that uses functional linear models (FLMs) of lagged weather data. A functional linear model is a smooth spline $f(x)$ whose values are multiplied by a vector of observed data z_x and then summed. If the vector of observed data is a time series of environmental values such as monthly precipitation, the resulting estimated spline function clearly identifies how much each month contributes to the observed response. The model is

$$\eta(y_{i,t}) = \sum_{j=0}^{k} \beta_j x_{i,t,j} + \sum_{m=0}^{n} f(m) z_{i,t,m} \qquad (1)$$

where $y_{i,t}$ is the response at site i in year t. The first term is a vector of k linear predictors as in a usual linear or generalized linear model. The second term is the functional linear term of the environmental driver variable $z_{i,t,m}$ for each site i, time t, and m months before July of year t; n is the maximum number of lags considered. In principle, additional functional linear terms could be included in the same model, but increasing complexity will naturally lead to an increase in the amount of data required to successfully fit the model. This approach solves the bias–variance trade-off by searching the space of possible weighted sums to minimize prediction error using cross-validation (Wood 2017). Minimizing prediction error identifies an optimal level of complexity (Hastie et al. 2009:220).

A prerequisite for successfully fitting FLMs is the availability of a sufficient number of independent observations of vital rates under different environmental conditions. Simulation results from Teller et al. (2016) indicate that at least 20–25 observations of the response y are required to detect climate signals. This requirement is a severe limitation for analyzing demographic data with functional linear smooth splines because most demographic studies are much shorter than 20 yr (Crone et al. 2011, Salguero-Gómez et al. 2015). A possible alternative to using long time series at single sites is to use shorter time series from several sites. In this case, it is essential for the locations to be far enough apart to experience different weather at least to some extent. How well this space for time substitution works is an open question. Teller et al. (2016) did explore the effect of correlations within a time series and found the method robust to correlations. They also found the method robust to cross-correlations between different weather drivers, but this is not the same situation as spatial correlations within a single weather driver.

In this paper, we use FLMs to unravel the effects of weather variables on the demography of the perennial wildflower, *Astragalus scaphoides*, using a long-term data set collected at four different sites with the longest time series being 26 continuous years of demographic monitoring. Water availability is probably the most limiting factor for accumulating resources in the environment of *A. scaphoides* but the evidence for this is mixed. Observational analyses (Crone and Lesica 2004) and water addition experiments (Crone and Lesica 2006) did not detect a significant effect of water on flowering patterns, but flowering was significantly reduced in an extreme drought year (Gremer and Sala 2013). We expect that the effect of weather variables on vital rates are delayed in this species because *A. scaphides* can store and reallocate resources over time (Crone et al. 2009, Gremer et al. 2010) and it exhibits biannual flowering peaks (Crone and Lesica 2004, Crone et al. 2005), probably because plants require more than one flowering season to accumulate sufficient nutrients for reproduction (Isagi et al. 1997, Satake and Iwasa 2000). We hypothesized that water availability has immediate and delayed effects: High water availability during the growing season will have immediate positive effects on survival, flowering, and growth. If a large proportion of the plants flower pollen is unlikely to be limited and seed production will be high (Crone et al. 2009). The high seed production depletes the pool of non-structural carbohydrates (NSC; Crone et al. 2009), which reduces NSC availability in the following season with likely negative consequences for growth, survival, and reproduction. Hence, we hypothesized that high water availability in the previous

year reduces survival, growth, and flowering in the following year. *A. scaphoides* also exhibits whole-plant dormancy (staying underground for one or more growing seasons). Gremer et al. (2010) found that dormant plants have lower NSC at the beginning of the growing season compared to emergent plants, and accumulate nonstructural carbohydrates via remobilization of structural carbon into available forms. Hence we hypothesized that high water availability in the previous year also increases the probability of plants entering dormancy.

We fitted FLMs of temperature, precipitation, and drought intensity to explore weather effects on vital rates, an integrated measure of life history performance $log(\lambda_t)$, and the observed change in population size $\log(N_{t+1}/N_t)$. Finally, we examine the utility of swapping spatial replication for duration of a time series using subsets of the real data, and a semiparametric power analysis using bootstrapped weather data.

Methods

Study system

A. scaphoides is a long-lived pea plant (Fabacae) with an average life expectancy of approximately 21 yr (Ehrlèn and Lehtilä 2002). This species is endemic to high-elevation sagebrush steppes in southwestern Montana and east-central Idaho. Our study sites were located near Lemhi Pass on the Montana–Idaho border, where summers are typically dry with a mean annual precipitation of approximately 250–300 mm. The dry conditions suggest that resource accumulation by plants is likely water limited and individuals may need more than one growing season to accumulate sufficient resources for exceeding the threshold required for flowering (Isagi et al. 1997, Satake and Iwasa 2000). Resource limitation likely contributes to the observed biannual flowering peaks of *A. scaphoides* populations (Crone and Lesica 2004, 2006, Crone et al. 2005, 2009). Here, we present annual vital rates estimated from a long-term monitoring data set collected by Lesica and Crone (E.g., Lesica 1995, Crone and Lesica 2004, 2006); we use these to quantify the effect of weather variables on vital rates and population growth rates using FLMs.

Monitoring data

A. scaphoides was monitored at four different sites near Lemhi Pass on the Montana–Idaho border. Sheep Corral Gulch (Montana), and Haynes Creek (Idaho) were established in 1986, McDevitt Creek (Idaho) in 1988, and Reservoir Creek (Montana) in 2003. Haynes Creek was not monitored from 2000 to 2002. The distances between the study populations ranged between 9.3 km and 52.9 km. At each site, plants were mapped annually to the nearest 10 cm along two 50 × 1 m transects, and plant ID, number of inflorescences, fate, size class, and number of seed pods were recorded. The population was divided into four different stages: small vegetative plants (one to five leaves), large vegetative plants (six or more leaves), flowering plants, and dormant plants. A plant was considered dormant if it stayed underground for at least one growing season, but reappeared in a later year.

We estimated vital rates from a subset of the data: two populations that were monitored continuously from 1988 to 2014 (Sheep Corral Gulch and McDevitt Creek) and two populations that were monitored continuously during 2003–2014 (Haynes Creek and Reservoir Creek). We used generalized mixed effects models with year as a random effect to calculate annual estimates of the following stage specific vital rates: survival, flowering probability conditioned on survival, dormancy conditioned on survival and not flowering, growth/shrinkage conditioned on survival and not flowering or not being dormant, and number of small, large, and flowering recruits (i.e., small, large, and flowering plants, respectively) produced by flowering plants. The number of recruits was estimated using a Poisson distribution with log-link and other vital rates were estimated using a binomial distribution with logit-link (function glmer in the lme4 package in R). We combined those vital rate estimates into annual matrix models and calculated asymptotic growth rates, $\log(\lambda_t)$, for each matrix. The corresponding life cycle graph of *A. scaphoides* is displayed in Fig. 1, and vital rates and population projection matrices are listed in Appendix S1.

Data sets used for FLM analyses

We included five different subsets of monitoring data in the FLM analyses:

(1) All estimates from the short and long time series for a total of 70 observations (2 sites × 25 yr + 2 sites × 10 yr); (2) all estimates for McDevitt Creek and Sheep Corral Gulch for a total of 50 observations (2 sites × 25 yr); (3) the last 20 yr (1994–2014) for McDevitt Creek and Sheep Corral Gulch for a total of 40 observations (2 sites × 20 yr); (4) the first 20 yr (1989–2009) for McDevitt Creek and Sheep Corral Gulch for a total of 40 observations (2 sites × 20 yr); (5) the last 10 yr (2004–2014) for all four sites for a total of 40 observations (4 sites × 10 yr). Subsets 3, 4, and 5 are chosen to have the same sample size regardless of the number of sites involved. We used subset 1 for our main analyses to understand the effect of weather on *A. scaphoides* demography. Next, we used the subsets 2–5 to explore if the availability of less data (shorter time series, fewer sites, and space for time swap) would have eliminated detection of the weather signal.

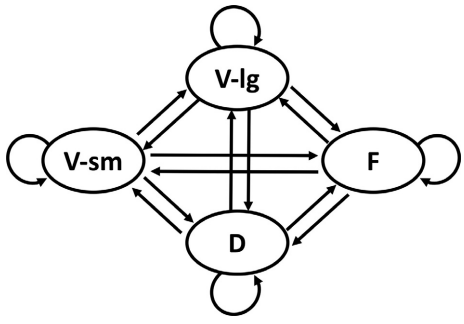

Fig. 1. Life cycle graph of *Astragalus scaphoides*, modeled after Lesica (1995). The arrows indicate transitions between four different plant stages: V-sm (small vegetative plants with one to five leaves), V-lg (large vegetative plants with six or more leaves), F (flowering plants), and D (dormant plants).

Weather data

We downloaded daily rainfall and temperature data for each study site from the PRISM Climate Group (data *available online*).[6] For the smooth spline analysis (Teller et al. 2016), we used the temperature averaged for each month and the rainfall summed up over each month. Then we calculated the one-month standardized precipitation evapotranspiration index (SPEI; Vicente-Serrano et al. 2010), which quantifies the beginning, duration, and magnitude of drought conditions compared to normal conditions. This index takes into account both precipitation and scaled potential evapotranspiration (PET) using the Thornthwaite method (Thornthwaite 1948) and thus captures the main impact of increased temperature on water demand. This index has been used to analyze effects of drought on agricultural (Potop et al. 2012) and a variety of ecological systems (e.g., Vicente-Serrano et al. 2012, 2013, Cavin et al. 2013, Drew et al. 2013, Lévesque et al. 2013). Studying the effect of drought on population demography is especially important for nutrient limited systems such as in our study system because drought affects nutrient availability, which determines plant population growth rates (e.g., Gotelli and Ellison 2002, Brys et al. 2005, Colling and Matthies 2006). To visualize the general trend of changing drought conditions over the monitoring periods at the four study sites we calculated 12-month SPEIs (package SPEI version 1.7; Beguería and Vicente-Serrano 2017). Negative values indicate dryer than normal conditions and positive values indicate wetter than normal conditions (Fig. 2). The 12-month SPEI includes both the water availability of the current month and the influence of the past 11 months. For the statistical analysis of SPEI per se, we used one-month SPEI rather than 12-month SPEI to avoid correlations in the residuals.

Modeling the effects of weather variables on plant demography

We fit models with linear terms (the $x_{i,t,j}$ in Eq. 1) for site and a site by year interaction. The site by year terms allow for differences in responses between sites and for linear trends across time other than predicted by variation in weather. For better comparison between sites, we centered the year variable at 2004, which is 16 yr after data collection started at Sheep Corral Gulch in 1989 and the end of the first demographic year of the continuous time series at Haynes and Reservoir Creeks. The method for estimating FLMs of lagged weather data is described in detail by Teller et al. (2016). For each monitoring year, t, we calculated 30 time lags; each time lag aggregated the weather data over one month (e.g. average temperature, summed rainfall). This way we could evaluate how demographic rates in year t were influenced by weather up to 30 months back in time ($m = -1, -2, \ldots, -30$). We modeled the relationship between the annual demographic rates, $\log(\lambda_t)$, or the observed change in population size $\log(N_{t+1}/N_t)$, and each weather variable by fitting a smoothing spline (package mgcv 1.8-17 [Wood 2011]; cubic spline basis with $\gamma = 1.2$ and all other parameters set at the defaults).

[6] http://www.prism.oregonstate.edu/

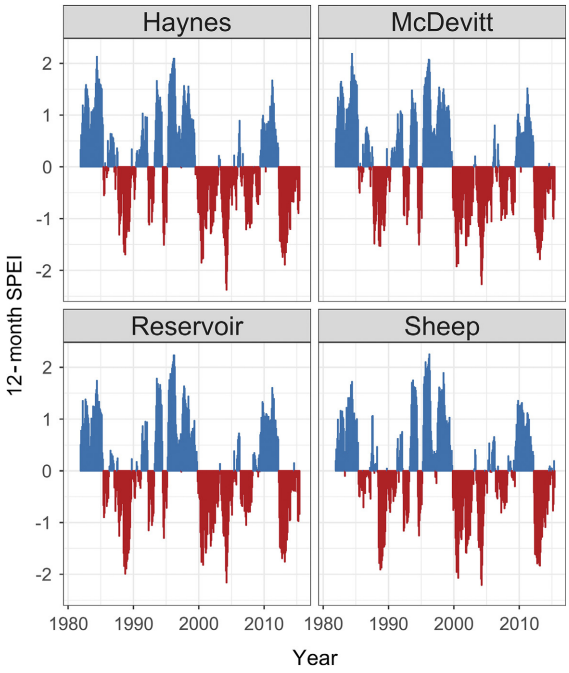

FIG. 2. Standardized multi-scalar drought index SPEI (standardized precipitation evapotranspiration index) per month at the four study cites from 1982 to 2015. Negative values (red) indicate dryer than normal conditions, and positive values (blue) indicate wetter than normal conditions. All four sites are getting more drought prone. Haynes Creek and McDevitt are in Idaho and Reservoir Creek and Sheep Corral Gulch are in Montana.

For each vital rate and $\log(\lambda_t)$, we fitted three models using monthly average temperature, monthly total precipitation, or one month SPEI. Models did not converge for the flowering to dormant transition, probably because there was no inter-annual variation at two sites. For the remaining 17 vital rates, we compared AIC values to identify the best environmental driver of variation (Appendix S2: Tables S1 and S2). We chose a priori to evaluate 30-month lags based on the observation of a two-period cycle in flowering. We evaluated the robustness of our conclusions to the specification of different time lags (6–36 months) of the models using SPEI (Appendix S3).

We visualized the effect of lagged weather variables on plant demography by plotting the estimated mean effect of the lagged weather data and the pointwise 95% confidence intervals. An AIC best-fit model is only relatively good, so we assessed the effect size of the lagged weather variables by considering both the overall F test of the spline term and whether pointwise 95% confidence intervals excluded zero for any lag. For brevity, we only display the results where the overall F tests for the smooth spline had $P < 0.01$ because P values for the smooth term in generalized additive models are only approximate and are likely too low (Wood 2017). Our preliminary analysis found that the pointwise 95% CI of splines with $P > 0.01$ usually included zero effect of weather variables at all lags. We focus on presenting the effect of SPEI on vital rates and $\log(\lambda_t)$ of *A. scaphoides* populations because SPEI integrates the effect of temperature and precipitation on the water demand of plants in a biologically appropriate way. Temperature and precipitation

are correlated (Appendix S2: Fig. S1), making direct statistical models of the interaction problematic.

Finally, we tested the ability of the model to make predictions on independent data by refitting the model of $\log(\lambda_t)$ and SPEI to a subset of data with the response in each year left out in turn, resulting in 25 models. Each of the 25 models was used to predict the response at all sites for the year left out. We repeated the cross-validation with a model where the spline term is set to zero to evaluate the relative contributions of the spline and linear terms in the model. These independent predictions were compared with the observed responses using a simple linear regression, where the expected value of the intercept is 0 and of the slope is 1.

Simulating the effect of bootstrapped SPEI data

This procedure served as a post-hoc semi-parametric power analysis for evaluating the detectability of a weather signal on *A. scaphoides* demography. We used bootstrapping to generate random SPEI sequences that kept the statistical properties of the historical SPEI sequence during the demographic *A. scaphoides* study and maintained the spatial correlation structure between all four sites (see Appendix S4 for details of bootstrap procedure). The advantage of using bootstrapped SPEI data is that it preserves the temporal relationship between temperature and rainfall. Then we used the results of the linear smooth spline analysis to give us annual means and standard deviations of the population growth rate, $\log(\lambda_t)$, associated with the bootstrapped SPEI sequence. We simulated the effect of bootstrapped SPEI data 1,000 times and calculated the probability of detecting a significant effect as the proportion of runs with $P < 0.01$. The analysis was repeated with three different standard deviations in the presence and absence of correlations in weather conditions between sites. We used the standard deviation from the linear smooth spline analysis ($\sigma = 0.25$) with larger values ($\sigma = 0.5, 0.8$) mimicking an environment with larger environmental variation.

Software

All analysis was performed in the open source software R (version 3.4.0; R Development Core Team 2017). Code and data available from the Dryad Digital Repository (see *Data Availability*).

Results

Effects of weather variables on Astragalus scaphoides

For each site, we calculated the 12-month SPEI indices and plotted the deviations from the average; the weather pattern was extremely similar between sites (Fig. 2). In the following, we refer to the "monitoring year" as the period from the July census in the previous year ($t - 1$) to the July census in the current year (t). The monitoring year starts at a lag of -12.

Vital rates.—FLMs indicated that 8 out of 17 vital rates considered showed significant effects of one or more weather variables (mean temperature, total precipitation or SPEI; overall F test, $P < 0.01$, Appendix S2*:* Table S1). In four cases, SPEI was the AIC best model for that vital rate and the other two weather variables were either not significant or had $\Delta AIC > 3$. In three cases, mean temperature or total precipitation were the AIC best models, but the SPEI model in all three cases had $P < 0.01$ and $\Delta AIC < 1$. In the final case, survival of flowering plants, only mean temperature had $P < 0.01$.

For small, large, and flowering plants, flowering in year t was highest if winter/spring of year t was wet (positive effect of SPEI over lags 0 to -5, 0 to -7, and 0 to -6, respectively), but also if the preceding year was dry (negative effect of SPEI over lags -13 to -16 [small], and -16 to -22 [flowering]; Fig. 3a–c) although this negative effect had confidence intervals including zero for large plants. Recruitment in year t was highest with wet springs in year t (positive effect of SPEI over lags 0 to -6, and 0 to -4), and had a tendency (only significant for large recruits) to be higher following dry years in $t - 1$ (negative effect of SPEI over lags -13 to -18, Fig. 3d, e). Survival of vegetative plants from $t - 1$ to t was highest if summer of year $t - 1$ was dry (negative effect of SPEI over time lags -11 to -15 [small], and -13 to -15 [large]; Fig. 3f, g). For large vegetative plants, survival was also negatively affected by SPEI two years in the past (over time lags -24 to -26, Fig. 3g). Mean temperature positively affected flowering plant survival during $t - 2$ (over time lags -17 to 28), and negatively during the spring of year t (over time lags 0 to -5, Fig. 3h). Drought conditions two years in the past had no significant effect on any other vital rate (Fig. 3).

Our conclusions are robust to the specification of the number of lags to include. In most cases with significant smooth splines, the models with 30 time lags had either the lowest AIC or were similar to the lowest AIC value (difference to smallest ≤ 2; Appendix S3). Even in those cases where the difference in AIC was larger for the models with 30-month lags, the qualitative predictions of models with different time lags were the same (same sign and trend with time during overlapping lags).

Asymptotic growth rates, log(λ_t).—We repeated the analysis with $\log(\lambda_t)$, i.e., the leading eigenvalue of the matrix composed of vital rates for each year, as the response variable. Although $\log(\lambda_t)$ does not reflect the observed changes in population size, it integrates variation in all vital rates in a biologically meaningful way (Fig. 3I). $\text{Log}(\lambda_t)$ was highest if winter/spring of year t was wet (positive effect of SPEI over time lags 0 to -5) but also if the preceding year was dry (negative effect of SPEI over time lags -12 to -19). Overall, growth rates from $t - 1$ to t are highest in years when year $t - 1$ was dry but spring of t was wet. The net effect of wet conditions in year t is greater than the net effect of dry conditions in year $t - 1$. Therefore, increasing drought likely reduces population growth rates of *A. scaphoides*, in spite of both positive and negative effects on different vital rates and at different times of year. For comparison we also calculated the effect of SPEI on the observed population growth rate, $\log(N_t/N_{t-1})$, where N_t specified the total population size in year t (Appendix S5). Interestingly, only the positive effect of SPEI over time lags 0 to -6 was significant for the observed population growth rate although the sign of the signals is consistent with the $\log(\lambda_t)$ analysis.

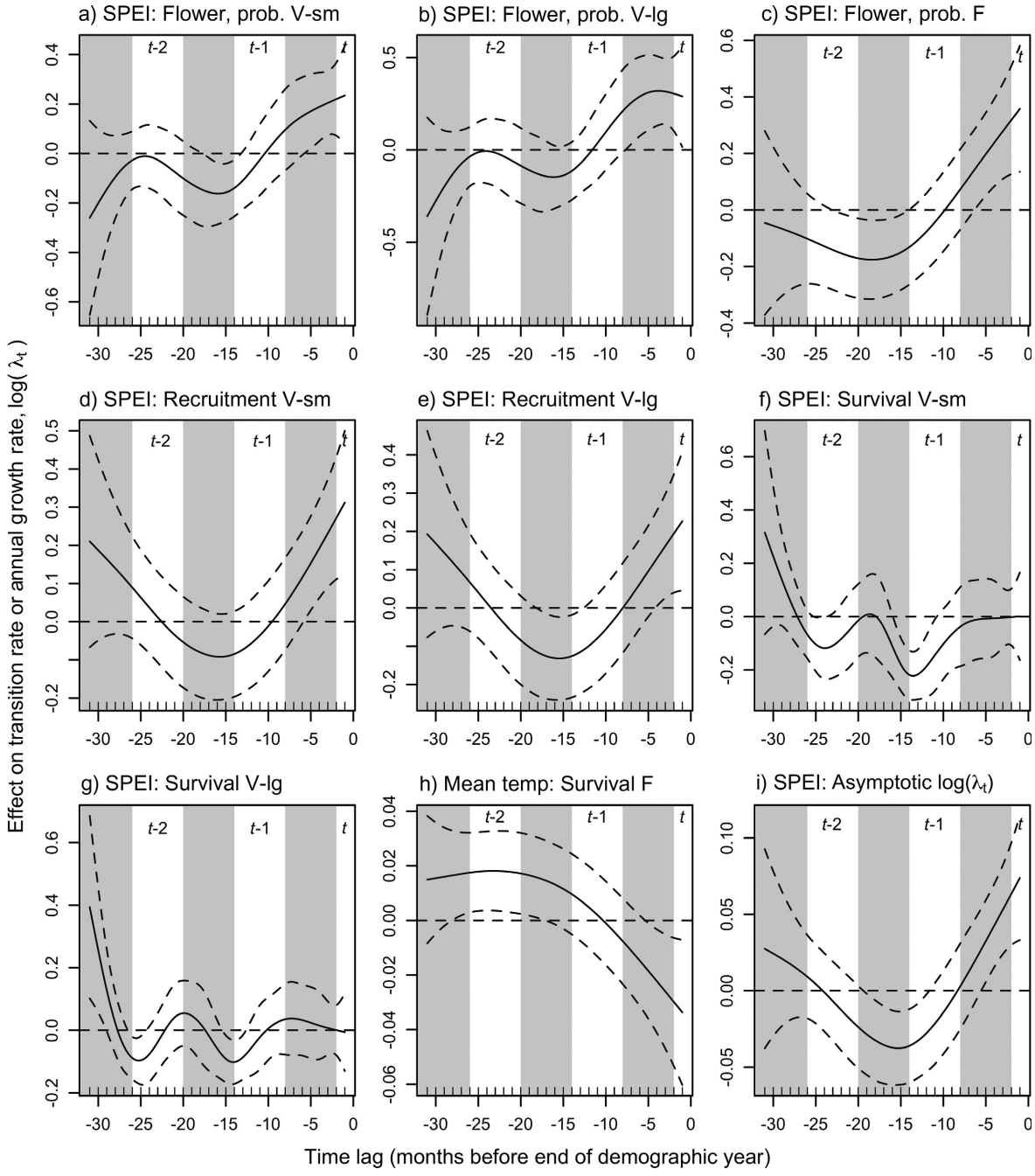

FIG. 3. Effect of past (a–g, i) SPEI or (h) mean temperature (temp) on vital rates and population growth rate, $\log(\lambda_t)$, of *A. scaphoides* during the demographic transitions between July in year $t - 1$ and t. The x-axes show time in the past at a resolution of months. The gray and white stripes indicate winter/spring and summer/fall periods, respectively. The horizontal line indicates no effect, and the solid line indicates the average effect. There is a significant effect of SPEI or mean temperature during those time periods where the 95% confidence intervals (dashed lines) do not overlap with the horizontal line.

Test of independent predictions.—The independent predictions generated from the leave-one-year-out cross validation including the spline term were significantly related to the observed response ($F_{1,72} = 17.7$, $P = 7.2 \times 10^{-5}$, $R^2 = 0.2$). The intercept of the validation model is not significantly different from zero (0.02 ± 0.034 [mean $\pm$ SE], $t = 0.561$, $P = 0.576$), and although the slope is less than 1 the difference is not significant (0.72 ± 0.171, $t = 1.63$, $P = 0.11$). In contrast, when the spline term was set to zero, the independent predictions generated from the leave-one-year-out cross validation were no longer significantly related to the observed response ($F_{1,72} = 3.6$, $P = 0.06$, $R^2 = 0.05$).

Utility of space for time substitution for detecting weather signal on plant demography

We compared the fits of $\log(\lambda_t)$ to FLMs of SPEI on the full data set to models fitted to subsets of data that reduced

the number of sites, the length of the monitoring period, or both (Table 1), and to bootstrapped SPEI data (Table 2). For brevity, we only display the P values and considered a weather signal to be significant if $P < 0.01$. Including all data led to the strongest relationship (Fig. 3I and Table 1; $P = 0.0001$). Including only the two longest time series (25 yr × 2 sites) weakened the effect slightly (Table 1; $P = 0.0006$). Next, we included only the first 20 yr and the last 20 yr for the two longest monitored sites in the analysis, which further weakened the effect but still led to a significant ($P < 0.01$) relationship in the same direction. Finally, we included the last 10 yr of all four sites (2004–2014) in the analysis, which included the same number of years (10 yr × 4 sites) as subsampling the two longest sites. This last analysis no longer detected a significant effect of SPEI on $\log(\lambda_t)$.

Next, we performed a post-hoc semi-parametric power analysis by fitting FLMs to bootstrapped SPEI data. We simulated the effect of SPEI on $\log(\lambda_t)$ by drawing values from normal distributions with three different SDs (SD = 0.25, 0.5, and 0.8, Table 2). When using the standard deviation derived from the empirical data (SD = 0.25), our analysis virtually always detected a significant SPEI signal (99–100%). In contrast, when increasing the SD to 0.8 we detected a significant weather signal in only 44–66% of the runs. Correlation in weather between sites and using a shorter time period for bootstrapping decreased detection ability. Overall, our analysis confirmed that using a shorter time period reduced the detectability of the SPEI signal (bootstrapping from 2001 to 2014 vs. 1981–2014), and that including correlation of weather variables between sites decreases the power to detect effects of SPEI, presumably because correlation reduced the variation in SPEI values included in the analysis. If sites were not correlated and bootstrapping was based on a long time series (1981–2014), the power of simulating four sites for 10 yr was comparable to simulating two sites for 20 yr because the variation in SPEI included in both analyses was similar. Reducing the time period from which we bootstrapped the data decreased detectability of the SPEI signal highlighting the need for including a sufficiently large range of weather data to detect weather signals.

Table 1. Effect of monitoring window on detecting weather signals on asymptotic growth rate $\log(\lambda_t)$ using the smooth spline method proposed by Teller et al. (2016).

No. sites	No. observations	Sites	Transition period	P for smooth term
4	70			0.0001
		Devitt, Sheep	1989–2014	
		Haynes, Reservoir	2004–2014	
2	50	Devitt, Sheep	1989–2014	0.0006
2	40	Devitt, Sheep	1994–2014	0.0041
2	40	Devitt, Sheep	1989–2009	0.0028
4	40	Devitt, Sheep, Haynes, Reservoir	2004–2014	0.1767

Note: The sites are McDevitt Creek (Devitt), Sheep Corral Gulch (Sheep), Haynes Creek (Haynes), and Reservoir Creek (Reservoir).

Discussion

Immediate and delayed effects of weather variables on Astragalus scaphoides

Abiotic drivers are key determinates of plant population viability, but there are few studies quantifying their demographic effects (Crone et al. 2011, 2013, Dalgleish et al. 2011, Chu et al. 2016, Dahlgren et al. 2016). This study demonstrates clear associations between drought measured as SPEI and plant demography when using long-term demographic and climate data (≥20 years from two sites). As hypothesized, our analysis shows that wet conditions early in the current growing season promoted flowering and recruitment of *A. scaphoides* (Fig. 3). We also detected hypothesized delayed effects: wet conditions in the previous spring reduced flowering and survival of vegetative plants (Fig. 3). The negative effect of wet spring conditions extends back two years for the survival of large vegetative plants. We did not find immediate or delayed effects of drought on growth, presumably because the monitoring data distinguished only between small and large vegetative plants and flowering plants were not differentiated by size. Detecting an effect on growth likely requires a larger number of size classes representing the size distribution of plants.

Our results are consistent with resource allocation by flowering plants affecting transitions from the flowering stage. We hypothesized that the larger proportion of the population flowering in wet years reduced pollen limitation (Crone et al. 2009) and the resulting high fruit production depleted the pool of NSC stores in flowering individuals (Crone et al. 2009). The low NSC pool in the following year reduced the

Table 2. Results from bootstrapped standardized precipitation evapotranspiration index (SPEI; standardized drought index) sequences to evaluate the effect of monitoring window on detecting the effect of SPEI on asymptotic growth rate $\log(\lambda)$ using the smooth spline method proposed by Teller et al. (2016).

Bootstrapping source period	No. simulated years	No. sites	Correlation between sites	Proportion of runs with $P < 0.01$		
				SD = 0.25	SD = 0.5	SD = 0.8
1981–2014	20	2	Yes	1	0.931	0.592
1981–2014	20	2	No	1	0.963	0.657
1981–2014	10	4	Yes	1	0.884	0.568
1981–2014	10	4	No	1	0.927	0.614
2001–2014	10	4	Yes	0.993	0.790	0.439
2001–2014	10	4	No	0.994	0.865	0.518

Note: SD denotes the magnitude of environmental variation.

flowering probability as has been proposed for other systems (Chapin et al. 1990, Wyka 2000), which is consistent with the results of this study (Fig. 3C). For many perennial plant species the amount of stored resources has a direct effect on next year's regrowth (Landa et al. 1992) and plant size is positively correlated with survival (e.g., Ellner and Rees 2006, Tenhumberg et al. 2008, 2015). Thus, the low NSC pool should have also reduced the survival probability of flowering plants. In fact, the negative effect of fruit production on survival has been demonstrated by Crone et al. (2009). Although we did not find a significant effect of SPEI on the survival of flowering plants, the effect of mean temperature on flowering plant survival shows a consistent pattern (compare Fig. 3C, H). Higher mean temperatures mean lower SPEI values, so the effect of mean temperature has the opposite sign to the SPEI effect. It would be informative to examine possible trade-offs between survival and flowering because life history trade-offs can lead to negative autocorrelation in time (Buckley et al. 2010), which can have important implications for population persistence (e.g., Pike et al. 2004, Tuljapurkar and Haridas 2006, Eager et al. 2017).

Alternatively, the effect of drought on plant vital rates could be explained by intensified intraspecific competition for scarce resources. We found that wet years had a positive effect on recruitment, which is one of the most vulnerable transitions in the life cycle of plants (Harper 1977). High recruitment in wet years should increase population size in the following year, which may trigger density-dependent regulation of plant vital rates. For instance, density dependence can affect survival even at low densities provided the environment is stressful (Dahlgren et al. 2014). A similar effect could operate via interspecific competition if other members of the plant community are positively affected by wet conditions, leading to increased competition the following year. If population regulation is not immediate, the positive effect of wet years on population size may carry over to more than one year, which would explain the longer lasting signal of SPEI on survival. Competition might also affect plant growth in our system, but detecting such an effect would require higher size resolution than was available in our study.

One way to integrate the effect of drought on all vital rates is to calculate the annual asymptotic growth rates, log (λ_t). Annual asymptotic growth rate log(λ_t) may differ from the annual population growth rate observed in the field because observed change in population size is affected by both the vital rates and the relative proportion of individuals in each life history stage (e.g., Caswell 2001, Tenhumberg et al. 2009, Tenhumberg 2010). For *A. scaphoides*, the effect of drought on log(λ_t) was similar to that of flowering and recruitment (Fig. 3): log(λ_t) was highest if conditions in the growing season were wet and the conditions in the previous year were dry. Overall, increasing drought should reduce population growth rates of *A. scaphoides* because the magnitude of the positive effects during the year t generally exceeded the negative effects of SPEI during the year $t - 1$. Our observed temporal effect of drought on vital rates and population growth implies that temporal autocorrelation in SPEI could be an important determinant of *A. scaphoides* demography. Based on our results, we would expect larger variation in vital rates and log(λ_t) if wet years are more likely to be followed by dry years (negative autocorrelation), while their variation should be dampened if wet years are more likely followed by wet years (positive autocorrelation). Dampened variation in vital rates and log(λ_t) generally promotes population persistence. However, in our study, SPEI was not significantly autocorrelated in time (Appendix S2: Fig. S2), suggesting that temporal autocorrelations in vital rates might be driven by environmental factors other than temperature and precipitation. For instance, an analysis of 50 terrestrial plant species (Buckley et al. 2010) found that vital rates and log(λ_t) were negatively correlated in time. The correlation was mostly due to survival of stages other than seedlings, which might be mostly influenced by fire and herbivory (Buckley et al. 2010).

These effects of past environmental conditions on present performance could be ecological carryover effects. O'Connor et al. (2014) defined a carryover effect as "... any situation in which an individual's previous history and experience explains their current performance in a given situation." In the present case, the hypothesis that increased moisture leads to increasing fruit production, which reduces survival, growth and flowering in the subsequent year is a carryover effect. The individual's past state (flowering and fruiting) affects performance in the current demographic year. The hypothesis that interspecific competition increases the year following a wet spring is not a carryover effect, because it is the current biotic environment that leads to the negative effects on survival, growth and flowering, not the individual's past state or the direct experience of increased rainfall.

Utility of space for time substitution for detecting weather signal on plant demography

Understanding how population viability changes over time is central to basic and applied ecology. Because long time series are rare, ecologists often use spatial variation to infer temporal variation (space-for-time substitution; Pickett 1989). As an example, space for time substitution has been used to reconstruct long-term temporal dynamics such as succession (reviewed by Walker et al. 2010), changes in biodiversity (Blois et al. 2013), community responses to climate change (reviewed by Fukami and Wardle 2005), and soil development (Matamala et al. 2008, Walker et al. 2010).

In this paper, we explored the utility of space for time substitution by analyzing subsets of our *A. scaphoides* monitoring data and by performing post-hoc semi-parametric power analyses with bootstrapped SPEI data. Our analysis suggests that space for time substitution did not work for detecting the effect of SPEI on log(λ_t). We detected a very strong signal when using only the two sites with the longest time series (25 yr at Mc Devitt and 25 yr at Sheep Corral Gulch, $P = 0.0006$); adding the other two sites (10 yr at Haynes Creek and 10 yr Reservoir Creek) only marginally improved signal detectability as indicated by a slightly lower P value. Using only 20 yr of the two sites with the longest time series, each was still sufficient for detecting a significant SPEI signal; it did not matter if we used the first or last 20 yr of the time series. In contrast, when using the last 10 yr of all four sites, we no longer detected a significant SPEI effect on log (λ) even though the total number of years included in the analysis was the same (4 sites $\times$ 10 yr = 2 sites $\times$ 20 yr). It

is possible that the weather between sites was too highly correlated so that adding more sites did not increase the range of SPEI values included in the analysis, even though the Montana and Idaho sites are located on opposite sides of the continental divide. In contrast, adding more years did increase the range of observed SPEI values because the sites became drier over the 25-yr period (Fig. 1). In agreement with these results, the power to detect a SPEI signal slightly decreased if sites were correlated and if only the weather from the last 10 monitoring years were included in the bootstrapping procedure (Table 2). We suspect that space-for-time substitution may be suitable in cases, such as successional studies, where the range of environmental variation is known and can be sampled across a number of separate sites. In contrast, if the range of temporal variation is not known a priori, space-for-time substitution runs the risk of not sampling relevant environmental variation. Other reasons why space for time substitution can be inaccurate include using sites that do not share similar environmental conditions and histories (Pickett 1989, Fukami and Wardle 2005, Jongejans and De Kroon 2005, Walker et al. 2010), if sites differ in their spatiotemporal dynamics (Hammond and Kolasa 2014), if variation between sites does not represent the temporal auto-correlation through time of single sites (Tyre et al. 2000), or if genotypes vary among sites (Huenneke 1991).

Conclusions

FLM analysis is a powerful method to detect weather signals on plant vital rates and annual population growth rates, $\log(\lambda_t)$. *A. scaphoides* populations do best if dry conditions in one growing season are followed by wet conditions in the following growing season. This pattern may be explained by wet years triggering density-dependent regulation and influencing resource allocation of plants. It also illustrates a complex relationship between environmental drivers and plant vital rates (specifically negative and positive effects over different time periods) and the use of integrated (population) models to resolve the net effects. However, our analysis confirms that FLM requires long-term time series data for capturing sufficiently large variation in weather variables. How many years are required for capturing a weather signal probably depends on the natural variation in precipitation and temperature as well as the sensitivity of a species to that variation. Substituting space for time (2004–2014) was not suitable for this system because variation in weather variables between sites was too small compared to variation over the entire time series (1989–2014).

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2163/suppinfo

Data Availability

Data associated with this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.f2mp4.