

Climate and Spatial Variability: Vernal Pool Plant Abundance and Community Composition

by

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Climate Variability: Vernal Pool Plant Abundance and Community Composition

Thesis directed by Professor Sharon K. Collinge

Abstract

Vernal pools, also termed temporary wetlands, promote key ecosystem services such as floodwater retention and provide unique habitat for many organisms. Despite their ecological value, vernal pools are declining worldwide because of habitat loss and encroachment of non-native species. Because vernal pool obligate plant species are strongly influenced by variation in annual precipitation that fills the pools, climate change and alterations in precipitation regimes can drastically alter these fragile communities. To understand how annual variation in precipitation and temperature affect vernal pool plant community composition, I examined long-term vegetation data for constructed vernal pools on Travis Air Force Base in Solano Co. CA. I used native and non-native plant frequencies collected over a 10 year period to explore the dynamics between species frequency and climate variability. I further analyzed fine-scale site topography to explore the effects spatial variability on ponding. I identified key differences between native and non-native plant species' responses to climate variability and ponding. Overall, native species tend to respond positively to winter precipitation accumulations, but non-native species do not. Inundation appears to act as an ecological filter, preventing the establishment of non-native species. In addition, elevation seems to be a predictor of ponding—

lower elevation pools tend to have greater pool depths, which can enhance the effects of the inundation filter. Together, these findings will assist management efforts in understanding the climatic and spatial factors that influence vernal pool restoration practices.

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1. Introduction

Vernal pools are seasonal wetlands typical of Mediterranean climates (Keeley & Zedler, 1998; Deil, 2005; Collinge & Ray, 2009). In California, vernal pools typically experience three distinct seasonal phases. During the winter months, shallow depressions in the soil fill with precipitation and flood. The winter rains cue seeds to germinate and produce seedlings that grow and develop under inundation (Keeley, 1988; Collinge & Ray, 2009). Water evaporates from the pools in the spring and the predominately annual plants quickly develop, flower, and disperse their seeds prior to or during the summer-autumn dry phase (Collinge & Ray, 2009). The seeds remain in the seed bank throughout the dry months, a mechanism which facilitates propagule survival during unfavorable conditions (Zedler, 2003; Faist, Ferrenberg, & Collinge, 2013), and the vegetative life cycle begins anew with the onset of the winter rains.

Vernal pools provide an array of ecosystem services (McGreavy, Webler, & Calhoun, 2012). Vernal pools act as basins for retaining floodwaters, help recycle nutrients while sequestering toxins, and promote the renewal of ground water (Rhazi et al., 2012). Vernal pools are also home to and support a wide range of endemic flora and fauna. California's vernal pool communities are made up of over 60 endemic taxa of animals and plants—many of which are rare or in danger of extinction (Croel & Kneitel, 2011).

Despite their ecological value, vernal pools are declining across the globe (Rhazi et al., 2012). In the Central Valley of California in particular, 60-85% of the vernal pools have been destroyed (Rhazi et al., 2012). Two major threats linked to the degradation of vernal pools are well documented: habitat loss and species invasions. In recent years, agricultural development in the Central Valley has surpassed urbanization as the lead cause of vernal pool habitat loss. Much

of this development is due to agricultural shifts from traditional field crops like grains to higher priced crops produced in orchards and vineyards (Sleeter, 2008; AECOM, 2009). Of the remaining vernal pools, invasion by exotic species has resulted in significant declines in vernal pool native plant communities. Reports indicate that invasive plants have been observed encroaching into Central Valley vernal pools (Pollak & Kan, 1998; Collinge, Ray, & Gerhardt, 2011).

The third, often overlooked, factor that may contribute to shifts in vernal pool plant abundance and composition is changing climate variability. Plant species around the world are responding to climate variability by undergoing phenological shifts and range shifts. Despite these general trends, little is known about how plant species found within vernal pools respond to climate variability. Climate change is projected to result in temperature and precipitation shifts in the Central Valley (Hayhoe et al, 2004; Cayan et al., 2009). Water is a vital element to vernal pool communities and many vernal pools are entirely dependent upon precipitation as the sole source of water (Jokerst, 1990). Year to year precipitation fluctuations often result in different plant community compositions (Bauder, 2005). Because vernal pool plant communities depend upon inundation, climate change acts as a threat to their persistence (Pyke, 2005) and may increase the risk of extinction for many threatened or endangered vernal pool obligate plant species (Bauder, 2005). My aim in this study was to better understand how temporal climate variability and spatial variability affect the composition of vernal pool flora. I set out to answer the following two questions: 1) Do changes in annual temperature and precipitation affect the frequency of native and non-native species found in vernal pools? and 2) Does site specific topography affect ponding and contribute to changes in community composition within individual vernal pools in the research area?

2. Methods

2.1 Vernal Pool Study Site

In an effort to restore native plant communities and ecosystem function in degraded vernal pool communities, 256 experimental vernal pools were constructed on Travis Air Force Base (TAFB) near Fairfield, CA (38° 15' 00'' N, 122° 00' 00'' W, 6 m elevation) (Collinge & Ray, 2009). The constructed pools were designed to mimic naturally occurring vernal pools found on TAFB (Collinge & Ray, 2009). Despite the protected habitat on TAFB, native plant abundance has dropped dramatically over the last seven years and non-native species have encroached upon native species within the constructed vernal pools (Figs. 1 & 2; Collinge, Ray, & Marty, 2013). Data suggest that the decline in native plant abundance may be partially explained by extreme weather events in 2006 and 2007. Such extreme weather events may become more frequent and intense in the future.

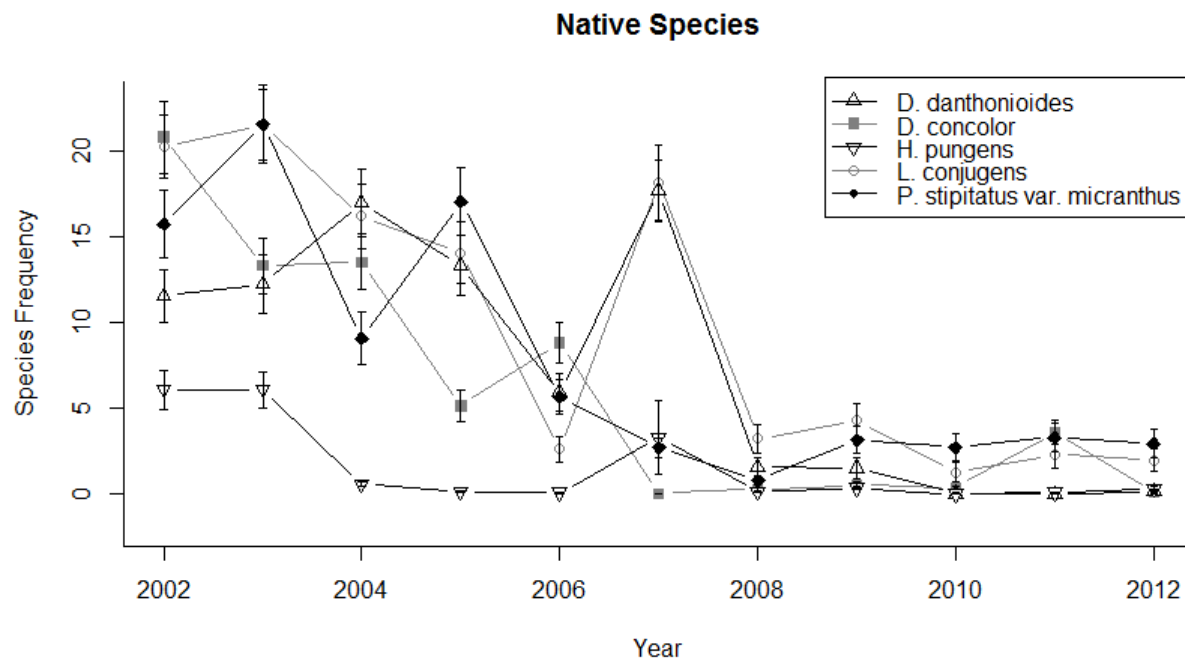


Fig. 1. Means frequency values and standard errors are presented for native focal species which showed distinct association to temperature and/or precipitation for the period 2002-2012.

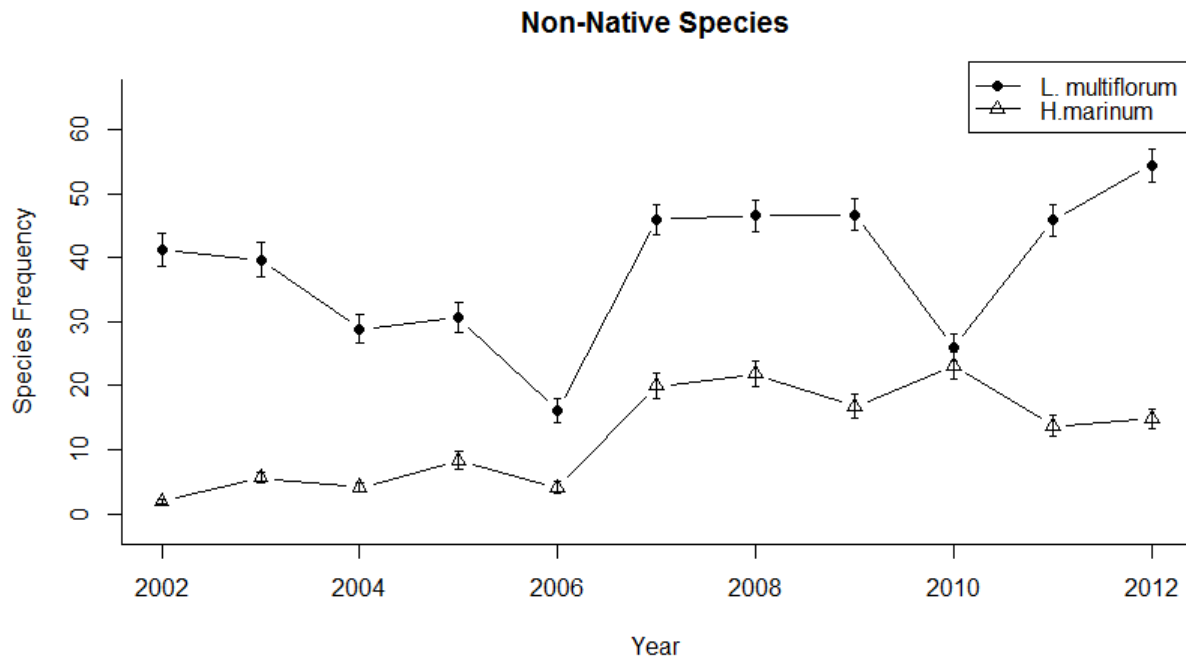


Fig. 2. Means frequency values and standard errors are presented for non-native focal species which showed distinct association to temperature and/or precipitation for the period 2002-2012.

2.2 Field Data Collection

I examined plant species frequency data collected for native and non-native plant species found within the constructed vernal pools on TAFB from 2002-2012. Every spring during peak flowering, permanent plots within the constructed pools and naturally occurring pools were measured for species occurrence and frequency. A 0.5 x 0.5 m grid frame divided into 100 cells was positioned over each of the marked plots and the frequency (the total number of cells out of 100 in which a species is present) of all the occurring species was recorded within the area of the grid (Collinge & Ray, 2009).

I initially selected 12 focal species for my study. These focal species were the six native and six non-native species that were present in the greatest number of constructed pools over the duration of the study. However, one of the native species selected, *Eryngium vaseyii*, is a perennial whereas all of the other focal species are annuals. Because perennial and annual plants have different life histories, which affect population dynamics and the timing of observed responses to abiotic influences, the *E. vaseyi* data was not utilized in this study. Thus I focused my analyses on five rather than six native plant species (Table 1). I compiled frequency data for all eleven focal species. I then calculated annual arithmetic mean frequency values for the focal plant species by averaging the frequency of each species across all 256 pools for each year.

| | Species Name | Family | Type | Common Name |
|---------------------------|---|---------------|-------------|----------------------------|
| Native Species | <i>Deschampsia danthonioides</i> | Poaceae | Grass | Annual hairgrass |
| | <i>Downingia concolor</i> | Campanulaceae | Forb | Maroonspot calicoflower |
| | <i>Hemizonia pungens</i> | Asteraceae | Forb | Common spikeweed |
| | <i>Lasthenia conjugens</i> | Asteraceae | Forb | Contra Costa goldfields |
| | <i>Plagiobothrys stipitatus</i> var. <i>micranthus</i> | Boraginaceae | Forb | Stalked popcornflower |
| Non-native Species | <i>Bromus hordeaceus</i> | Poaceae | Grass | Soft brome |
| | <i>Erodium botrys</i> | Geraniaceae | Forb | Longbeak stork's bill |
| | <i>Hordeum marinum</i> | Poaceae | Grass | Mediterranean barley |
| | <i>Lolium multiflorum</i> | Poaceae | Grass | Italian ryegrass |
| | <i>Vicia villosa</i> | Fabaceae | Forb | Winter vetch |
| | <i>Vulpia bromoides</i> | Poaceae | Grass | Brome fescue |

Table 1. A summary of the eleven focal species used in this study (Collinge, Ray, & Marty, 2013; plants.usda.gov).

2.3 Growing Season Data

I initially used the entire annual growing season (October-March) abiotic data to examine the effects of the abiotic factors on the annual focal species frequency data. This process proved ineffective and I turned to an earlier greenhouse study, (Gerhardt & Collinge, 2007) that examined the effects of inundation on vernal pool plant communities, to help identify key annual growing season time intervals that were most appropriate to use for this study. The results from the greenhouse study suggested that inundation affects the different life stages of the vernal pool vegetative communities. Two stages were particularly affected: 1) plant development and survival and 2) plant growth and reproduction. The first half of the growing season is characteristic of vegetative development and survival for the study site, whereas plants typically grow and reproduce during the second half of the growing season. Thus, I divided the growing season data into early growing season (October-December) and late growing season (January-March). In doing so, I was able to explore the effects of ponding stages and seasonal temperature patterns on the life cycle of the 11 focal species. Specifically, I explored the effects of precipitation and temperature on the germination and early survival of the perennial focal species by concentrating specific analyses on early season data. I explored the effects of temperature and precipitation on pool drying and the growth and reproduction of adult focal species by devoting specific analyses to the late growing season.

2.4 Temperature and Precipitation Data Collection

I examined species frequencies in relation to temperature and precipitation values using data collected over the course of my study to gain a better understanding of how annual variation in precipitation and temperature affect the frequency of the focal species. I collected monthly

precipitation totals and temperature values for Fairfield, CA between the years 2002-2012 from the Western Regional Climate Center (<http://www.wrcc.dri.edu>), located approximately 11.28 km from the study area. Both inundation and temperature are key factors that prompt developmental responses in many vernal pool plant species. To address temperature effects I used growing degree days (GDD) data to help gauge key developmental events in the plants' lifecycles. GDD may be understood as the amount of thermal energy that is available to an organism for growth and development. A GDD value is the mean number of degrees that exceed a base temperature within a 24 hour period. However, the temperature accumulation of a single day does not typically affect plant development. Rather it is the accumulation of warming days over a period of time that acts on development. Thus, the GDD data were summed for each annual growing season. I selected a base temperature of 10.0° C for my analyses. I selected 10.0°C as my base temperature because the mean temperature at which most of the annual vegetation in the constructed vernal pools begins to germinate in December is about 9.44°C.

2.5 Temperature and Precipitation Statistical Analyses

I performed multiple regression analyses using the computing environment R (version 3.0.2). Frequency data for each of the focal species were individually modeled by early growing season precipitation totals and GDD totals as well as late growing season precipitation totals and GDD totals. These linear regression models were then simplified by stepwise deletion. I began with the most complicated model and successively removed variables with the highest p-value until all of the predictors were significant ($\alpha = 0.05$).

Because my samples sizes were limited and the distribution of the dependent variable was not normal, I performed additional analyses to see if transformations for normality were warranted. Log transformations normalized the data and they were incorporated into the same

linear models that were previously used to test the non-parametric data. These models were also simplified by stepwise deletion, until all of the predictors were significant. Once all of the predictors were significant, I removed the transformation from the dependent variables, to explore its effects on the raw data, and calculated the explanatory power for each model. I compared the R^2 values of the previously transformed model to the untransformed model to determine which model was a better fit for the data. In addition, I also checked to ensure the normality of the residuals for each of the models that carried the higher explanatory power.

2.6 Topographic Data Collection

I investigated whether fine scale site topography affects the accumulation of water in pools and thus the frequency of native and non-native plant species found within the constructed vernal pools. I used a 2010 Topcon AT-B4 automatic surveying level (accuracy ± 2 mm) to measure the difference in elevation between pools. I systematically moved the survey rod to each of the constructed pools and measured its elevation by placing the rod on a permanent seed plot marker. Because soil type also affects water permeability I used soil samples collected from a previous study (Gerhardt, 2003; Gerhardt & Collinge, 2003) to explore the effects of soil composition on water depth within pools. Finally, I compiled pool depth readings from 2009-2012. From these data I extracted the maximum depth value for each pool. I then took the arithmetic mean of each value to produce an overall maximum pool depth value for each pool.

2.7 Topographic Statistical Analyses

Regression analyses were used to address the relationship between elevation and the mean maximum pool depth values. I performed three individual linear regressions analyses, rather than a single multiple regression analysis, to explore the effects of soil type on mean maximum pool depth values because there was a correlation between soil types. The three

models explored mean maximum pool water depth by % sand, % silt, and % clay individually. AIC values and Akaike weights were obtained to determine if elevation or soil type is a better predictor for maximum pool water depth.

3. Results

3.1 Temperature and Precipitation Analyses

3.1.1 Native Species

In general the native focal species responded positively to early precipitation totals. I found a statistically significant relationship between annual frequencies of *D. concolor*, *H. pungens*, *L. conjugens*, and *P. stipitatus* var. *micranthus* and early precipitation accumulations (Table 2). As early season precipitation totals increased, species frequency values increased. I also found a statistically significant relationship between *H. pungens* and *L. conjugens* frequency and late season precipitation totals (Table 2). In this case, precipitation in the late growing season was associated with decreased species frequency values. There were no significant relationships between native species frequencies and early season GDD totals. However, I found a positive relationship between late growing season GDD accumulations and *D. danthonioides*, *L. conjugens* and *P. stipitatus* var. *micranthus* mean frequencies (Table 2). Late season GDD totals were positively associated with species frequency totals (Table 2).

| Species Name | Early Precip. Coefficient | Late Precip. Coefficient | Early GDD Coefficient | Late GDD Coefficient | Overall Adj. R ² | Overall F-Statistic | Overall P-value |
|--------------------------------------|---------------------------|--------------------------|-----------------------|----------------------|-----------------------------|---------------------------|-----------------|
| <i>D. danthonioides</i> | NS | NS | NS | 0.065 (P=0.003) | 0.610 | F _{1,9} = 16.610 | 0.003** |
| <i>D. concolor</i> | 0.911 (P=0.027) | NS | NS | NS | 0.374 | F _{1,9} = 6.961 | 0.027* |
| <i>H. pungens</i> | 0.244 (P=0.006) | -0.503 (P=0.000) | NS | NS | 0.805 | F _{2,8} = 21.590 | 0.001** |
| <i>L. conjugens</i> | 0.670 (P=0.021) | -0.942 (P=0.021) | NS | 0.058 (P=0.005) | 0.805 | F _{3,7} = 14.730 | 0.002** |
| <i>P. stipitatus var. micranthus</i> | 0.944 (P=0.009) | NS | NS | 0.043 (P=0.030) | 0.600 | F _{2,8} = 8.528 | 0.010* |
| <i>B. hordeaceus</i> | NS | NS | NS | NS | 0.211 | F _{1,9} = 3.680 | 0.087 |
| <i>E. botrys</i> | NS | NS | NS | NS | 0.020 | F _{1,9} = 1.204 | 0.301 |
| <i>H. marinum</i> | -1.0196 (P=0.021) | NS | NS | NS | 0.407 | F _{1,9} = 7.866 | 0.021* |
| <i>L. multiflorum</i> | -1.102 (P=0.045) | -1.69 (P=0.024) | NS | NS | 0.568 | F _{1,8} = 7.560 | 0.014* |
| <i>V. villosa</i> | NS | NS | NS | NS | -0.067 | F _{1,9} = 0.373 | 0.556 |
| <i>V. bromoides</i> | NS | NS | NS | NS | 0.022 | F _{1,9} = 1.229 | 0.296 |

Table 2. Summary of the results from the multiple regression analyses performed on mean species frequency values in relation to early and late season precipitation and temperature totals. Coefficients for independent variable that have a significant effect on the dependent variable are highlighted with associated individual p-value in parenthesis. Predictor variables with a non-significant effect on the dependent variable are marked with: NS. The significance levels for the overall p-values are: * P<0.05, ** P<0.01, ***P<0.001.

3.1.2 Non-native Species

There was a statistically significant negative relationship between *H. marinum* and *L. multiflorum* frequencies and early season precipitation totals (Table 2). There was also a statistically significant negative relationship between *L. multiflorum* and late season precipitation totals. There were no significant associations between non-native species frequency values and GDD totals for either early or late growing seasons (Table 2).

3.2 Topographic Effects on Pool Depths

There were significant relationships between elevation and soil type in relation to ponding (Table 3) where maximum pool water depths were positively associated with clay and silt concentrations and negatively associated with sand concentrations. There was also a significant relationship between elevation and % clay, % sand, and % silt found in the soil (Table 3). As elevation increased concentrations of clay and silt found in pool basins decreased, while concentrations of sand increased. Maximum pool depth was also negatively associated with pool elevation (Table 3). In comparing the four models which explored the effects of clay, sand, silt, and elevation on ponding, elevation was a better predictor of maximum pool depth than were concentrations of clay, sand, or silt (Table 4).

| Dependent Variable | Independent Variable | Coefficient | Adj. R ² | F-Statistic | P-value |
|--------------------|----------------------|-------------|---------------------|----------------------------|-----------|
| Pool Depth | % Clay | 0.235 | 0.134 | F _{1,59} = 10.27 | 0.002** |
| Pool Depth | % Sand | -0.206 | 0.124 | F _{1,59} = 9.517 | 0.003** |
| Pool Depth | % Silt | 0.033 | -0.016 | F _{1,59} = 0.079 | 0.780 |
| Pool Depth | Elevation | -1.906 | 0.264 | F _{1,59} =22.520 | <0.001*** |
| % Clay | Elevation | -1.841 | 0.081 | F _{1,59} =6.286 | 0.015* |
| % Sand | Elevation | 3.726 | 0.311 | F _{1,59} = 28.030 | <0.001*** |
| % Silt | Elevation | -1.86 | 0.205 | F _{1,59} =16.430 | <0.001*** |

Table 3. Summary of the topographic regression analyses. The first four rows describe the effects of soil composition and elevation on mean maximum pool ponding depths. The last three rows describe the relationship between elevation and soil composition. The significance levels are: * P<0.05, ** P<0.01, ***P<0.001.

| Dependent Variable | Independent Variable | AICc | dAICc | df | Akaike Weight |
|--------------------|----------------------|-------|-------|----|---------------|
| Pool Depth | Elevation | 181.6 | 0.0 | 3 | 0.686 |
| Pool Depth | % Clay | 183.9 | 2.3 | 3 | 0.215 |
| Pool Depth | % Sand | 185.5 | 3.9 | 3 | 0.099 |
| Pool Depth | % Silt | 198.2 | 16.6 | 3 | <0.001 |

Table 4. AIC results for the topographic regression models in relation to mean maximum pool depth.

4. Discussion

I identified key trends among native and non-native plant species found in constructed vernal pools in response to climate variability and site-specific topography. In general, native forbs responded positively to early precipitation totals. As early season precipitation totals increased, native species frequency values tended to increase, while late season precipitation totals tended to be negatively associated with native species frequency values (Fig. 3). These trends are explained by examining the timing of the three key phases associated with ponding, or the process by which vernal pools become filled with precipitation. The first stage of ponding is marked by the moistening of the soil. Precipitation is the primary trigger of seed germination in most vernal pool plant species and the first rains that moisten the soil typically initiate the germination process (Bliss & Zedler, 1998). Greenhouse experiments conducted using vernal pool plant species indicate that moist soil is adequate for germination; furthermore, in these experiments, most species did not require inundation to cue germination (Bliss & Zedler, 1998). Thus, the positive associations between species mean frequency values and increased precipitation in the early growing season that I observed in this study could be explained by the initiation of germination.

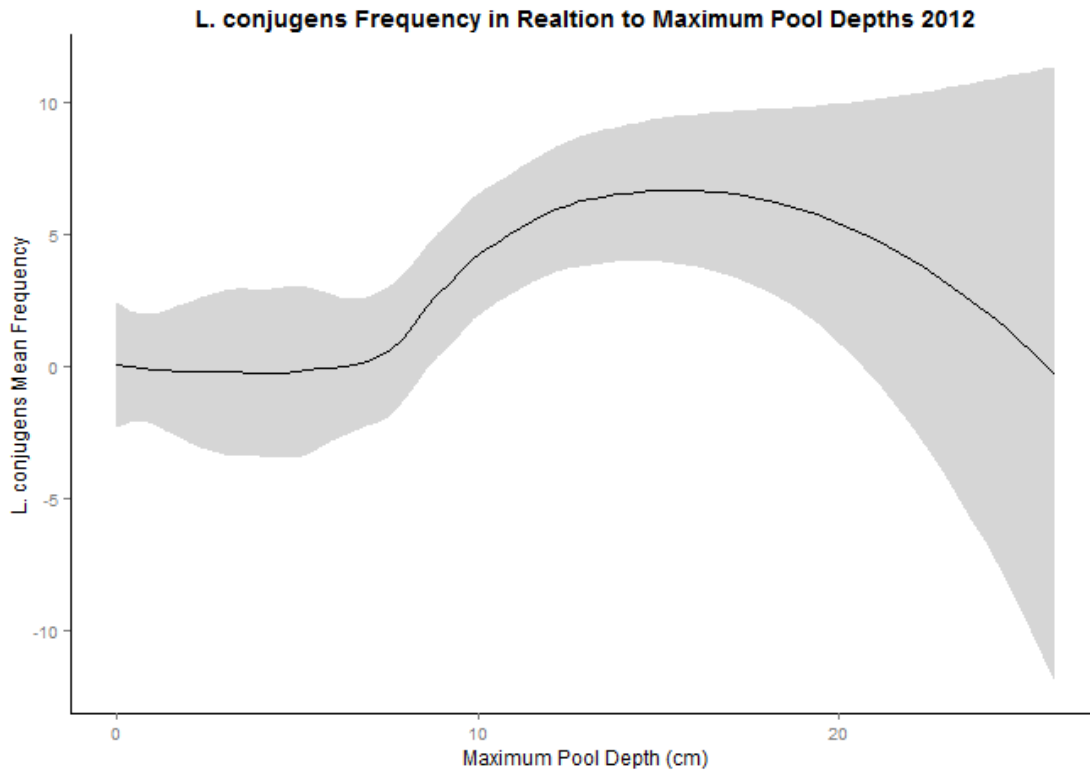


Fig. 3 A smoothed trend line with standard error bands shows how *L. conjugens* frequency values fluctuate with precipitation accumulation. This figure uses a native focal species to demonstrate that native forbs tend to respond positively to deeper inundation levels compared to non-native grasses.

Increased precipitation in the early growing season also promotes the onset of inundation, the second phase of ponding, in which water begins to accumulate in pools. In fact, early ponding acts as an ecological filter, preventing the establishment of non-native species. Greenhouse experiments show that inundation acts as an abiotic pressure which prevents the establishment of non-native species that are not adapted for development under water (Bliss & Zedler, 1998; Gerhardt & Collinge, 2003; Gerhardt & Collinge, 2007). Although native seedlings are capable of growing and developing under the inundation of water they do not appear to depend on inundation for survival (Bliss & Zedler, 1998).

Additionally, pool depths tend to increase as elevation decreases. Lower elevations potentially receive greater amounts of water due to runoff and underground seepage/flow. Lower elevation pools are often composed of higher concentrations of clay. Clay soils are much more impermeable to water than are other soil types, resulting in greater water retention. The lowest elevation pools are potentially composed of higher amounts of clay due to the different soil horizon types. It is often the case that clay soil is found below the organic and decaying organic layers. The excavation of the constructed pools resulted in the removal of some of the upper organic layers, perhaps resulting in pools that are higher in clay concentrations. Soil horizons extend across the research area and some of the upper layers may be less prevalent at lower elevations. When pools were constructed at lower elevations higher concentrations of clay may have been exposed due to less prevalent upper layers. Thus it is likely that lower elevations tend to promote increased ponding and may enhance the effects of the inundation filter.

Finally, the ponding cycle is terminated once ponding water begins to evaporate and the pools become dry. The drying phase is a crucial turning point in the lifecycle of most vernal pool

native plant species. It is during this phase that the majority of native species undergo a metamorphosis in which flat foliage begins to supplant fleshy, cylindrical foliage (Keeley & Zedler, 1998). This event may correspond to the negative association observed between late season precipitation totals and some vernal pool native forbs. The species examined are perennials and would likely incur an ecological advantage if their adult lifecycles were spent in soil that is not inundated. Because of the short growing season, these annual plants are limited to a narrow window of opportunity to produce propagules. Dry soils also help ensure that newly produced seeds are stored in the seed bank until conditions are suitable for germination in subsequent growing seasons (Faist, Ferrenberg, & Collinge, 2013).

My results also suggest that increased rainfall hinders the viability of some non-native grasses (Fig. 4). As precipitation totals increase, *H. marinum* and *L. multiflorum* mean frequency values decrease. Similarly, *L. multiflorum* appears to respond negatively to late season precipitation accumulations. As discussed above, increased water accumulations within vernal pools acts as an ecological filter which prevents non-native species from establishing and proliferating (Gerhardt & Collinge, 2007). However, count data indicates that *L. multiflorum* has thoroughly spread, become established, and often dominates the vegetative communities found in vernal pools (Collinge, Ray, & Gerhardt, 2011). In this case, *L. multiflorum* has bypassed the inundation filter and has invaded many constructed vernal pools in the research area.

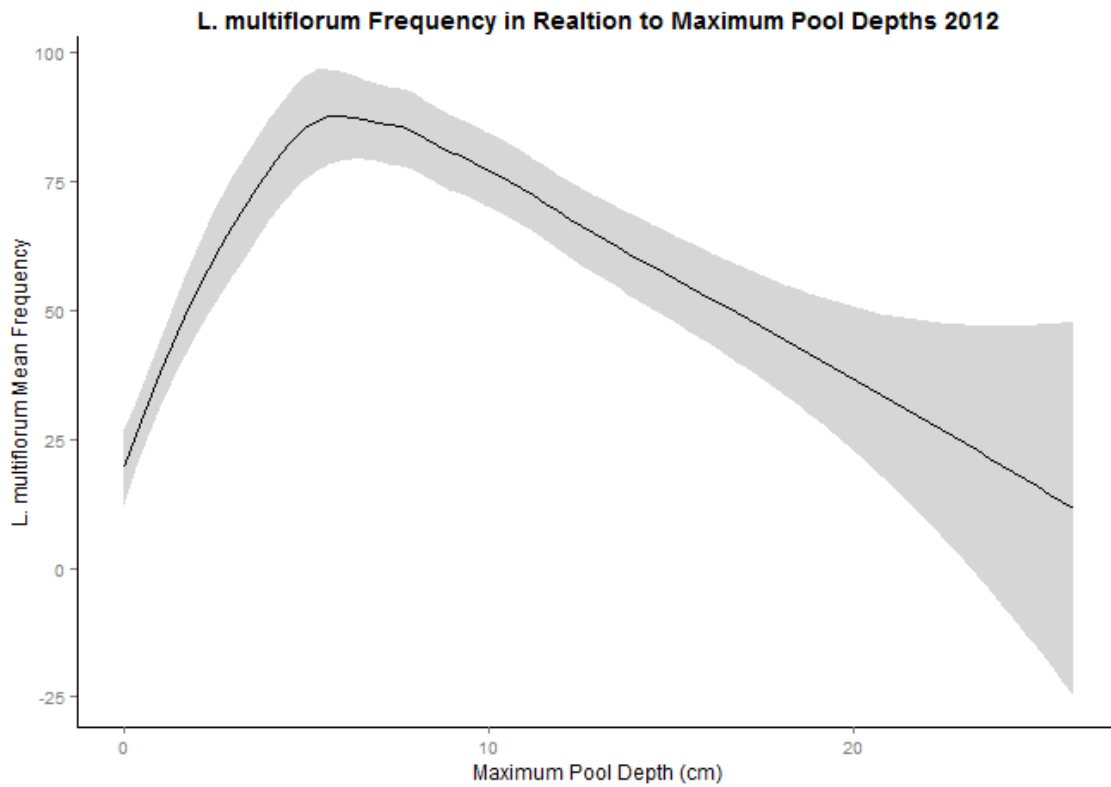


Fig. 4 A smoothed trend line with standard error bands shows how *L. multiflorum* frequency values fluctuate with precipitation accumulation. This figure uses a non-native focal species to demonstrate that non-native grasses tend to respond negatively to deeper inundation levels compared to native forbs.

The invasion of *L. multiflorum* in constructed pools may be explained by examining frequency data and precipitation data collected over time and identifying the point at which *L. multiflorum* frequency jumps from relatively low to high values. These data reveal an overall decline in the mean frequency values of *L. multiflorum* from 2002-2006. *L. multiflorum* frequency values plummeted in 2006, reaching their lowest recorded levels through the 10 year period. Frequency data collected for other non-native species as well as native plant species also indicate a sharp decrease during the 2006 growing season (Figs. 1,2, & 5). The 2006 growing season was marked by extremely high precipitation with a total accumulation of nearly 25 centimeters greater than the average for the duration of this study (Fig. 6).

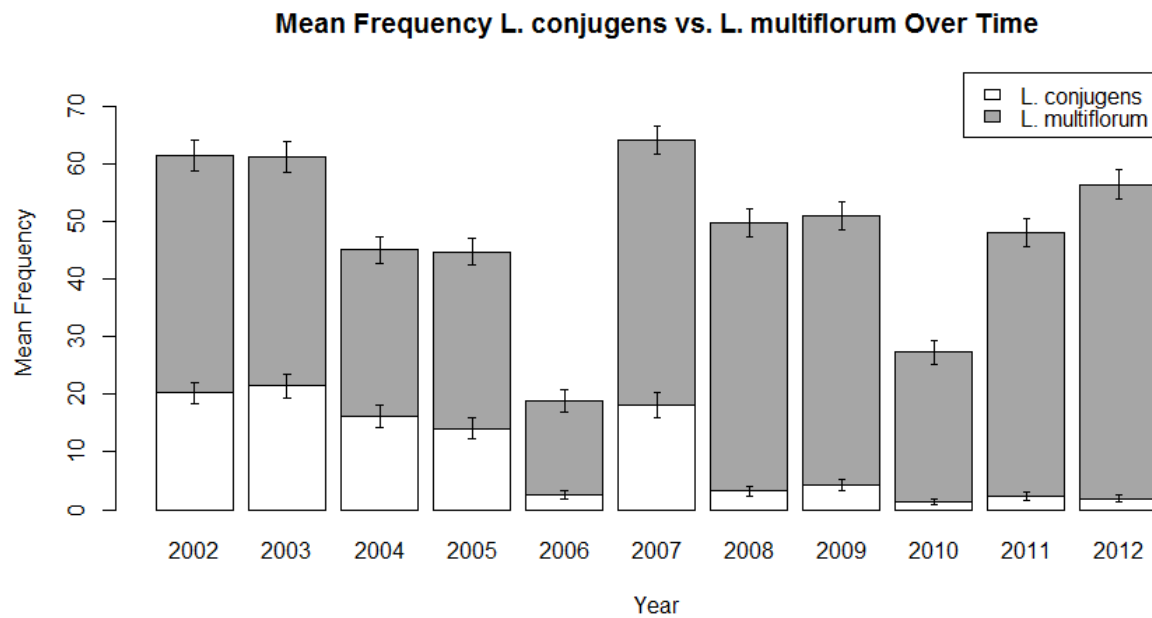


Fig. 5. Mean frequency values for *L. conjugens* and *L. multiflorum*, 2002-2012. *L. conjugens* is an endemic and vernal pool obligate plant species currently listed as endangered. *L. multiflorum* is a non-native plant species that has invaded many of the constructed vernal pools on the research site.

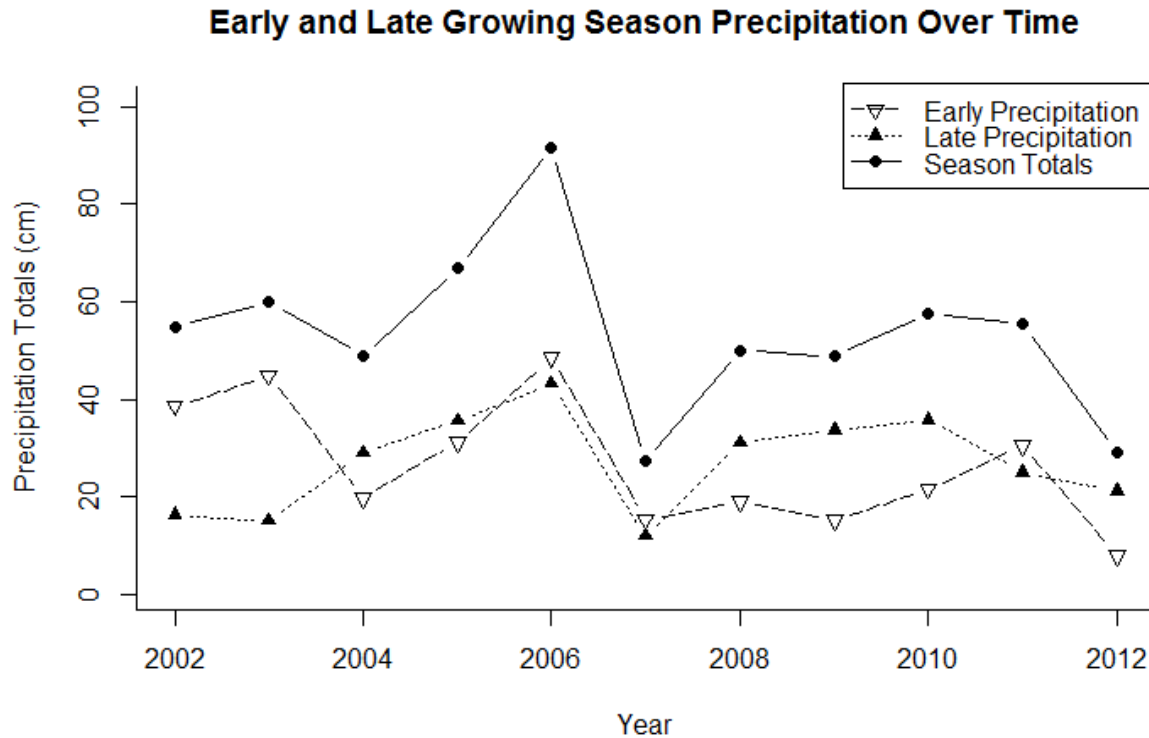


Fig. 6. Early season (October-December) and late season (January-March) precipitation totals are plotted over time. Overall season totals (October-March) are also included.

This observation coincides with the data obtained from the regression analyses in relation to early and late season precipitation totals. In this case, extremely high precipitation totals accumulated across both the early and late 2006 growing season. The extreme amount of rain that fell in 2006 likely resulted in abnormally high precipitation accumulations in the late growing season which untimely lead to delayed drying. My analyses indicate that native and non-native species frequencies are negatively associated with increased late season precipitation totals. Thus the intense 2006 precipitation event likely hindered the development of native and non-native species. The 2007 growing season, on the other hand, was marked by extremely low precipitation accumulations. Although both native and non-native species frequency values rebounded during the 2007 growing season compared to the 2006 growing season, non-native species frequency tended to be greater than the native species frequency values for this particular year. It can be surmised that the extremely low 2007 precipitation event helped the non-native species bypass the inundation ecological filter that normally occurs during average precipitation events. The frequency data also suggests that once a non-native species is able to circumvent the inundation filter it tends to establish rapidly, which coincides with greenhouse experiments (Gerhardt & Collinge, 2007). This rapid establishment in turn hinders the viability of native species.

Given the increased climate variability that is predicted for the future, many vernal pools may be exposed to altered precipitation and temperature patterns. Most climate change projections agree that average annual temperatures are expected to increase across California with significant warming events in the spring and summer months (Hayhoe et al., 2004; Cayan et al., 2009). There is more variability in precipitation projections for the Central Valley; many projections infer dryer winter months, yet fewer projections suggest increased winter

precipitation averages (Hayhoe et al, 2004; Cayan et al., 2009). In light of the current climate projections two growing season climate scenarios may be offered to assist vernal pool management efforts: 1) hotter and dryer growing seasons or 2) hotter and wetter growing seasons. Under the first scenario, dry conditions in the early growing season would likely have adverse effects on native plant frequencies; native species are dependent upon wet early seasons to trigger seed germination and establish the inundation filter. On the other hand, a dry late growing season may promote vegetative development if sufficient amounts of precipitation were present in the early growing season. Increased temperatures in the dry growing season may cause the pools to dry too rapidly and hinder native development. Under the second scenario, wetter early growing seasons are likely to benefit native species while wetter late seasons are likely to hinder native species development. Increases temperatures under this scenario, however, may catalyze the drying phase and benefit native species development. Many native vernal pool species have adapted mechanisms that allow them to thrive in typical Mediterranean climates—mechanisms which are usually absent from non-native species. The typical climate patterns associated with Mediterranean climates may give way to novel climate patterns. Given these annual uncertainties, vernal pool community composition may change and threatened and endangered vernal pool native species may diminish. However, this study identifies key trends that may help land managers identify the ideal timing of restoration efforts and determine optimal vernal pool restoration locations where native species are more likely to survive.

5. Conclusion

The current understanding of vernal pool plant species reaction to climate variability is limited within the scientific community. I have identified key trends between native and non-

native plant species found in constructed vernal pools in response to climate variability. My analyses reveal an overall trend for native focal species: a positive response to precipitation accumulations, especially in the early growing season. No such trend was found among the non-native focal species. Inundation acts as an ecological filter preventing the establishment of non-native species. Greenhouse experiments concur with these results, suggesting that inundation exerts an abiotic pressure that acts to prevent the establishment of non-native species in the pools. Lower elevation pools promote ponding and may be more amenable to native species. As climate change intensifies, precipitation shifts will likely affect vernal pool hydrology and potentially reshape plant community structure. However, this study may help inform land managers of the appropriate timing of vernal pool restoration efforts in relation to the timing of precipitation events and ideal pool location in relation to site specific topography.

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