Title

Interannual Trends of Flowering Phenology and Native Species Richness in California Vernal Pools

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Publication Date

2022

UNIVERSITY OF CALIFORNIA, MERCED

Interannual Trends of Flowering Phenology and Native Species Richness in California Vernal Pools

A dissertation submitted in partial satisfaction of the requirements for the degree
Doctor of Philosophy

in

Environmental Systems

by

Brandon Hendrickson

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This dissertation is dedicated to the light of my world,

my wife,

Gabrielle Hendrickson.

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Acknowledgements

I thank my advisor, Jason Sexton, for providing me with amazing opportunities to work on such beautiful plants and believing in me to succeed. I thank my committee for all their feedback, guidance, and support when I needed it most. I thank the UC Merced undergraduates for all their hard work collecting data beside me in rain and heat.

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Education

2017	University of California, Santa Barbara B.S. Ecology, Evolution and Marine Biology
2022	University of California, Merced PhD Environmental Systems; Advisor: Jason Sexton

Publications

Shay JE, Pennington LK, Mandussi Montiel-Molina JA, Toews DJ, Hendrickson BT and Sexton JP. Rules of Plant Species Ranges: Applications for Conservation Strategies. *Front. Ecol. Evol.* (2021) 9:700962. doi: 10.3389/fevo.2021.700962

Mazer, S. J., **Hendrickson, B. T.**, Chellew, J., Kim, L., Liu, J., Shu J., Sharma, M. Divergence in pollen performance between *Clarkia* sister species with contrasting mating systems supports predictions of sexual selection. *Evolution* (2018) 72(3); 453-472.

Larsen, A. E., **Hendrickson, B. T.**, Dedeic, N., MacDonald, A. J. Taken as a Given: Evaluating the Accuracy of Remotely Sensed Crop Data in the USA. *Agricultural Systems* (2015) 141; 121-125.

Research Experience

August 2019 – Present **Research Lead**: School of Natural Sciences, University of California, Merced

In an experiment aimed at tracking trait plasticity in competitive environments, I have recorded the development and morphology of 5,000 *Mimulus guttatus* sporophytes spanning over 1,500 plots of varying density, genotype diversity, and nutrient concentrations. The experiment yielded multiple major findings concerning life history plasticity, flowering time, and fitness inequality.

August 2017 – Present **Research Lead and Undergraduate Mentor**: School of Natural Science, University of California, Merced

The project goals were to track the floral phenology and biodiversity of vernal pool and grassland plant species for monitoring community health, invasion, and interannual variability of abiotic and biotic dynamics. Over 4 years, I have recruited and trained 43 undergraduate researchers at UC Merced with monitoring phenology and recording biodiversity. In the process of training undergraduates, I have learned the identity 100+

plant species and developed an appreciation for the traits and environmental conditions that enable rapid expansion of invasive species into unoccupied locals.

February 2019 – Present **Research Assistant and Field Experiment Leader**: School of Natural Sciences, University of California, Merced & NSF-IOS

Performed a multiyear common garden experiment along an elevation gradient in Central California. I managed the site discovery, acquired landowner permission, planted over 12,000 *Mimulus guttatus* over 3 years and monitored survival, phenology, development, and fitness of each plant.

September 2013- May 2016 **Research Assistant**: Ecology, Evolution, and Marine Biology Department, University of California, Santa Barbara

Investigated the current literature on land sparing and land sharing farming practices, and reviewed the potential effects each practice has on human health, local economy, and biologic community. Examined the statistical robustness of USGS annual crop data, and proposed potential solutions to shortcomings in statistical methods and imaging practices.

March 2014- December 2018 **Research Assistant**; Ecology, Evolution, and Marine Biology Department, University of California, Santa Barbara

Principal Investigators: Dr. Susan Mazer and Dr. Manju Vesudevan; Conducted research on two California native wild flowers with contrasting mating systems, *Clarkia unguiculata and Clarkia exilis*, to test predictions on the evolution of pollen performance traits between mating systems. Lead the undergraduate research team through the Summer of 2015 to Fall 2016.

March 2015- July 2016 **Research Assistant**; Ecology, Evolution, and Marine Biology Department, University of California, Santa Barbara

Investigated sensory pathways and response in multi-sense single celled fungi. Establish phylogenetic relationship with single celled multi-sensed fungi and multicellular organisms. Performed PCR and genomic library assembly.

February 2016- July 2016 **Research Assistant**; Ecology, Evolution, and Marine Biology Department, University of California, Santa Barbara

Correlated phenology with live fuel moisture to detect subsequent fire risk by using four chaparral plants throughout the Southern California region. Managed data analysis using R.

June 2016- August 2016 **Summer Research Assistant**; Ecology, Behavior and Evolution Department, University of California, San Diego

Investigated optical flow information processing and memory updating of *Apis mellifera*. Gained valuable experience bee keeping, managing hive health and reproduction, as well as engineering the hives themselves.

March 2014- May 2015	**Laboratory Assistant**; Ecology, Evolution, and Marine Biology Department, University of California, Santa Barbara

Maintained and organized lab materials. Helped individuals with their projects. Performed radio-isotope dating.

Outreach

2020 – Present	**Court Appointed Special Advocate** Merced, CA
2020 – Present	**Youth 2 Youth Mentor and UC Merced Affiliate** Merced, CA
2018 – 2020	**Volunteer at Valley Children's Hospital** Madera, CA
2017 – 2019	**Educational Outreach Assistant for Local Merced High-Schools** Merced, CA
2013 – 2017	**Guardian Scholars Mentor** Santa Barbara, CA
2010 – 2013	**Volunteer at St. Joseph's Hospital** Santa Ana, CA

Fellowships

2015-2017	University of California, UC LEADS Research Scholarship
2018 Summer	University of California, Merced Summer Fellowship

Presentations

2021	University of Louisiana, Lafayette Biology Seminar
2016	UC LEADS Best Poster Presentation, Mathematics.
2016	UC LEADs Research Symposium; University of California, Davis.
2015	Undergraduate Research Colloquium; University of California, Santa Barbara
2015	UC LEADs Research Colloquium; University of California, Santa Barbara
2016	Undergraduate Research Conference; University of California, San Diego
2016	Southern California Conference for Undergraduate Research; University of California, Riverside

Skills

Genetics: DNA Extraction, RNA extraction, PCR, Genomic Library Assembly
Programming: R, Python, Bash/Command Line, Mathematica, JavaScript, Processing
Data Analysis: GIS, JMP, R & R markdown, Excel

Dissertation Abstract:

Nearly 90% of California's vernal pool habitat has been destroyed by human activity in the past 100 years. The University of California, Merced manages one of the largest actively protected vernal pool habitats in the state, the UC Merced Vernal Pools and Grassland Reserve (MVPGR), aimed at conserving rare native species and landscapes through research, teaching, and outreach. Because the reserve was only recently established, little is known about the interannual patterns of vernal pool plants occupying the region. Consequently, the phenological and demographic responses of the native species inhabiting the MVPGR to reduced precipitation, biological invasions, and cattle grazing has not been quantified. The goal of this dissertation is to investigate the composition, flowering time, and invasion intensity of vernal pool plant communities across multiple climate years. Chapter 1 focuses on two wildflowers native to California, *Limnanthes douglassi* ssp. *rosea* (meadowfoam) and *Trifolium variegatum* (whitetip clover),and quantifies each species' phenological response to variable precipitation and temperature across 7 years. Additionally, population size of both focal species in response to competition and eutrophication were assessed. I found that both meadowfoam and whitetip clover flower earlier in response to lower precipitation. Chapter 2 focuses on plant community responses to abiotic and biotic dynamics across zones within pools, which are established by soil texture and flooding gradients. Chapter 2 expands upon Chapter 1 by characterizing the community composition, invasion intensity, and interannual flowering trends of 42 plant species across three zones: pool bottom, edge and upland. I found a distinct plant community occupying each zone, and each zone responded uniquely to invasion and winter precipitation. The pool bottom plant community flowered earlier in response to lower winter precipitation, whereas native species in the upland plant community were negatively associated with non-native species richness. No correlations were found between precipitation and the floral phenology of upland species, and neither was there a correlation between non-native species richness and native biodiversity patterns in the pool bottom. The findings elucidate the sensitivities and ramifications of climate change, invasion, and eutrophication amongst 'zones of vegetation' on the UCMGVPR. Conserving the native species also requires community participation in the management and legislative process, and ideally the scientific process. Chapter 3 examines several recruitment and retention methods for a community science project involving UC Merced undergraduates and provides guidance on how to achieve a long lasting and high engagement project. I found that in-person presentations achieved a recruitment rate than email flyers. In addition, giving volunteers the freedom to decide the time and date they volunteer and providing periodic updates in the form of a newsletter can improve retention rate of volunteers at different stages.

Chapter 1: Mediterranean vernal pool plant phenology, competition, and eutrophication responses

ABSTRACT:

Vernal pools in the Mediterranean climate of California are surrounded by grasslands, and home to a variety of native wildflower species very different than their grassland counterparts. Vernal pool plants are small, colorful, and specialized to extremely dry summers and flooded conditions. These species germinate rapidly in response to the first rain and grow rapidly to take advantage of available water supplies. Recent changes to temperature and precipitation in the Central Valley are altering the hydrological patterns of vernal pools, and many species in other habitats have exhibited advanced flowering in response to reduced rainfall and warmer than average temperatures. The floral phenology of vernal pool plant species is little understood despite being a crucial developmental stage for producing seeds. In addition, interspecific interactions between plants and herbivores may be influenced by climate and may change in the future. The current study focuses on two vernal pool plants, *Limanthes douglassii* var. *rosea* (meadowfoam) and *Trifolium variegatum* (whitetip clover), and characterizes their phenology, between species interactions, and responses to eutrophication. We find that meadowfoam and whitetip clover flower significantly earlier in response to reduced rainfall, though we find that both species' flowering is delayed in response to warmer temperature. We also find that meadowfoam and whitetip clover interfere with each other's growth: meadowfoam produces fewer seeds when growing besides whitetip clover and whitetip clover produces fewer flowers when growing besides meadowfoam. Both species' populations were severely depressed during eutrophication and for several years after. Understanding the biotic and abiotic environmental drivers of vernal pool plant phenology and population dynamics will elucidate whether these species are susceptible to or at risk from recent climate change.

INTRODUCTION:

Vernal pools are endorheic, ephemeral wetlands of shallow depth defined by dramatic transitions from flooded to desiccating conditions (Smith and Verrill 1998; Solomeshch et al. 2007) that are inhabited by a charismatic assemblage of wildflowers with varying adaptations to these unique conditions (Zedler 1984; Bauder 1987; Bauder 2000; Emery et al. 2009). Following winter rains, submerged vernal pool specialists germinate and grow slowly while persisting as diminutive rosettes, then rapidly complete their life cycle as the pool dries (Keeley 1988; Bliss & Zedler 1997). Three ecologically distinct stages have been ascribed to mark the progression of plant phenology that parallels the hydrologic cycle: the aquatic stage – germination; the terrestrial stage – rapid reproduction; and the drought stage – dormant seed bank (Wiggins et al. 1980; Zedler 1987; Keeley & Zedler 1998). High interannual variability of precipitation and temperature is characteristic of Mediterranean climates, and consequently the length of time the aquatic, terrestrial or drought stages last (Gosejohan 2017). Phenological plasticity in fine-grained heterogenous habitats ensures that developmental transitions coincide with and are completed during ideal environmental conditions (Anderson et al. 2012). Additionally, directional selection for earlier flowering has been uncovered in many plant species (Anderson et al. 2011; Munguia-Rosas et al. 2011; Ehrlen & Munzbergova 2009). With current and impending climate change, it is more important than ever to understand the sensitivities and ramifications of phenology effects. Nevertheless, little is known about the abiotic factors underlying vernal pool phenology.

Vernal pool plant populations are adapted to the hydrologic regime of flooding and drying (Emery et al. 2009; Gosejohan et al. 2017), and therefore may express unique flowering patterns. Few studies have examined the climate variables that modify vernal pool species' floral schedules in-situ, but greenhouse experiments reveal that inundation length is associated with germination time, growth, and flowering time (*Lasthenia conugens*: Collinge et al. 2003). However, the natural interannual variability of first flowering and seeding dates in these systems has not been documented, and thus a baseline dataset is needed for long-term climate change studies. Given that vernal pool organisms rely heavily upon sufficient precipitation to annually flood vernal pools, hotter and dryer winters are likely to impact vernal pool communities severely (Stewart et al. 2004; Maurer 2007). Characterizing the interannual patterns and environmental determinants of vernal pool plant phenology will elucidate whether these communities are responding to or at risk from anthropogenic climate change.

Similar to recent range shifts (i.e., from lower to higher elevations) of populations tracking optimal thermal and hydrologic conditions (Kelly & Goulden 2008; Kopp & Cleland 2013), plant species in vernal pool habitats may shift their ranges towards lower elevation to track lower water levels. Anomalously unpredictable precipitation patterns in Mediterranean climates– particularly seasonal frequency and volume of rainfall events – are driving lower inundation lengths across vernal pool habitats (Shin & Kneitel 2019), a key element in determining community structure across many ephemeral aquatic habitats (Brendonck et al 2015; Shin & Kneitel 2019). It is hypothesized that vernal pools will serve as hydrological refugia in the face of lower precipitation (McLaughlin et al. 2017). Convergence of many plant species' ranges can impose more intense competition for scarce nutrients and water (Robertson 1895, Rathcke and Lacey 1985).

A common tool to manage invasion is the use of low intensity cattle grazing, which can release native plants from competition with exotic species (Dole 1988; Barry 1998). Pools with grazing also have longer inundation periods that effectively exclude invasive plants and permit native species to complete their life cycle prior to the drought phase (Marty 2005). Despite the reported benefits of cattle grazing, cattle waste can be an ecological contaminant causing algal blooms in the standing water of vernal pools (Smith et al. 1999) where cattle habitually congregate (Wallis de Vries and Shippers 1994; James et al. 2007). The resulting eutrophic condition can dramatically reduce ecosystem function and native biodiversity (Smith et al. 1999; Smith and Schindler 2009; Croel & Knietel 2011), with effects primarily at the pool bottom. Alternatively, vernal pools are often nitrogen-limited, and higher than average nitrogen deposition may improve plant growth. To fully characterize these processes, long-term observations of plant communities in eutrophic pools in natural environments are needed. Given that most to all remaining vernal pool habitats are grazed by cattle, understanding the effect of their excrement on native vernal pool plant communities is necessary for conserving species. Nevertheless, it is not ideal purposefully induce eutrophication given the potential negative effects on rare and endangered vernal pool species. Thus, observing the natural occurrence and effects of eutrophication on biodiversity is preferred.

Vernal pool obligates are narrowly specialized to ephemeral aquatic conditions, whereas more facultative species benefit from water retained within pools but are not dependent upon vernal pools to survive or reproduce (Barbour et al. 2005). *Limnanthes douglasii* (rosy meadowfoam) is an annual California endemic species adapted to clay soils and variable inundation periods; it is often observed flowering between the months of March and July (Hickman 1993; Calflora, https://www.calflora.org). Meadowfoam seeds are high in stable oils, resistant to oxidation, adapted for long periods of dormancy in vernal pool environments, and repurposed as an economically viable resource used for preserving cosmetics (Nyunt and Grabe 1987; Bosisio 1989; Purdy and Craig 1987). Rosy meadowfoam primarily occupies the flooded portions of a vernal pool, with populations presenting as isolated islands within the surrounding grassland habitat (Hickman 1993). This contrasts with the distribution of *Trifolium variegatum,* which inhabits a wide range of habitats, mainly wet meadows, from Alaska to Baja California (Čelakovský 1874; Hickman 1993). *Trifolium variegatum* (whitetip clover) flowers from March to July mainly along the dryer edges of vernal pools (Calflora, https://www.calflora.org). *Trifolium* species are nitrogen fixing (Fogg 1956), fulfilling a necessary ecosystem service for vernal pool habitats, which could be nitrogen limited (Rains et al. 2008). Prior species characterizations of these two species found variability in when and where these species grow within different pools, however, interannual observations have not been made. As such, the interannual variability of microhabitats inhabited by vernal pool populations of both meadowfoam and whitetip clover is not understood.

The goal of the project is to establish long-term monitoring of two native plants and to characterize their developmental and growth patterns within vernal pool environments. Community scientists, under my guidance collected the weekly abundance of meadowfoam and whitetip clover plants, flowers, seeds, and events of co-occurrence on the UC Merced Vernal Pools and Grassland Reserve (MVPGR). Across the 7 years observed, the data set has captured the wettest, as well as driest years among the last 30 years in Merced, as well as recorded several occasions of detrimental levels of algal growth. We asked three questions: 1. What environmental factors are most strongly associated with meadowfoam and whitetip clover floral phenology? 2. What influence does meadowfoam population abundance and phenology have on whitetip clover fitness, and vice versa? And 3. What are the short- and long-term consequences of eutrophic conditions on vernal pool plant growth, persistence, and recovery rate?

The project is a long-term natural observation experiment and has the advantage of monitoring multiple climatic events (e.g. El Nino, La Nina, Pacific Decadal oscillation) and within pool dynamics (i.e., eutrophication, stratification of vegetation, and competitive intensity) in a naturally occurring landscape representative of the Mediterranean climate vernal pool community. The findings of this study will elucidate the potential effects of climate variability on floral phenology, population growth, and persistence of meadowfoam and whitetip clover in vernal pool environments.

METHODS:

Study Site:

Located in the northern Central Valley of California, Merced is exposed to a Mediterranean climate marked by wet winters season followed by hot, dry summers (Mooney & Parson 1973; Walter 1979). The Merced landscape prior to the 1800's was characterized as a patchwork of riparian habitat formed by streams that cut through the gentle hills, and elevated alluvial terraces high in clay that were occupied by thousands of vernal pools (Warner & Hendrix 1984). The alluvial terraces were formed by oscillating cycles of geologic uplift and erosion, and consequently, soil types range in age, metal content, salt concentration, and clay concentration (Lettis 1982). Since then, construction and agricultural expansion has destroyed 66% (Kreissman 1991) to 85% (Holland 1978) of the original vernal pool habitat native to California. The San Joaquin Valley has witnessed a dramatic loss in its vernal pool species owing to a large tree nut industry that demands the removal of the thick clay layer that prevents almond growth but is necessary for vernal pools to form (King 1998). The UC Merced Vernal Pools and Grassland Reserve (MVPGR) is a 6,500-acre reserve owned by the University of California, and one of the largest complex of actively protected vernal pools. The MVPGR was established in 2014 with the aim of promoting active research on the plants, animals, and abiotic dynamics present in vernal pools habitats so as to better protect and conserve the ecosystem and its species.

Shortly after the establishment of the reserve in 2015, a cohort of undergraduate students worked with UC Merced Professor Jason Sexton to design a low-cost phenology survey of two vernal pool plants -- *Limnanthes douglassii* var. *rosea and Trifolium variegatum* -- aimed at characterizing each species' quantitative phenological and demographic response to climate change. Community scientists were recruited from UC Merced undergraduates. Three pools were chosen for long-term ecological observation; each contained populations of meadowfoam and whitetip clover, and they represented different pool sizes and soil texture. The number of pools observed was kept small so as to be tractable for weekly and annual observations by volunteers. However, even a few pools can generate much data within and among seasons (e.g. Collinge et al. 2013). Prior to any data collection, one week of training was required of volunteers, which included an introduction to meadowfoam and whitetip clover morphology, and floral and seed appearance. Volunteers were then monitored and provided assistance throughout the experiment to ensure high quality data collection.

Survey Methods:

Quadrats (10 cm by 10 cm) were placed every 20 cm along east-west and north-south transects spanning the length of a pool, covering the entire pool bottom, edge and approximately 3 meters into the upland. The placement of the quadrat alternated between sides of the transect every 20cm. When an obstruction prevented the placement of a quadrat, the quadrat was placed on the other side of the transect. The number of plants rooted in the quadrat, flowers, and seeds (described below) of both meadowfoam, and whitetip clover were recorded per quadrat.

The upland, edge and bottom of the pool were determined by soil type and flood depth (Crowe et al. 1994). Soil texture was assessed by hand, and the flood depth was recorded for each pool when water was present using a meter stick. The clay content of the soil was determined using the ribbon method (Thien 1979). The soil texture can then be determined using the results of the ribbon method and assessing sand grain size using touch. The upland is the region of each pool that never floods. The edge is distinguished as having high silt and sand content, while also being inundated. The bottom of the pool is high in clay, and regularly floods.

Scoring Phenophases:

The number of plants per quadrat was measured by counting the number of basal rooting stems belonging to meadowfoam and whitetip clover. The phenophase, flower, was determined for meadowfoam when the anthers and stigma were clearly visible, and the plant's petals were fully displayed (Walls et al. 2014; Stucky et al. 2018). Each meadowfoam flower forms an aggregate fruit containing 3-5 nutlets that take several days to weeks to ripen. Right before dehiscence, the nutlets become hard and whitish; when fully ripe a day or two later, the seeds will fall off the flower with a gentle breeze or the slightest touch. The number of 'near mature' meadowfoam fruits, not nutlets, were counted as the seeds were showing the early signs of dehiscence (Yost 2017.

Whitetip clover's flower head contains 20-50 separate flowers, which eventually form a small bean fruit. Not all individual flowers on a single head are open at once. A whitetip clover plant was considered flowering when any of the ~50 individual flowers was open. A single flower head was counted as one flower. The fruits, like meadowfoam, disperse using gravity, though require more jostling for seeds to dehisce. The number of whitetip clover seeds was measured as number of inflorescences per quadrat with active seed dehiscence.

In this study, we consider peak flowering date to be when the highest number of flowers was recorded in a pool. Peak abundance of flowers was determined by adding all flowers recorded along both east-west and north-south transects of a pool for a single sampling date. The time that flower density and abundance is highest is the period that effective population size of breeding adults is largest, which is ecologically relevant to a population's potential for outcrossing.

Climate Variables:

All climatic variables were sourced from Merced Station 148 (Lat. 37.314139, Lon. -120.3867) operated by the California Irrigation Management Information System (CIMIS, https://cimis.water.ca.gov). The station is 4 miles south of the reserve. Raw measurements from the CIMIS used in this study were monthly average temperature, monthly average total precipitation, monthly average dew point, daily average temperature and daily average dew point. Starting from January 2016 and ending on March 2022, daily and monthly climate variables were retrieved. Monthly precipitation was used to calculate accumulated precipitation for the water year (October 1st – September 31st) and the total accumulated winter precipitation (December 1st – February 28th). Additionally, monthly precipitation was used to calculate the accumulated precipitation for any combination of consecutive months between October to May. I designated winter in this study as the dates between December 1st to February 28th. Mean winter temperature was calculated by taking the average temperature of December to February. Winter temperature variability was calculated for each year by taking the variance of average daily temperatures from December 1st to February 28th. Similarly, winter dew point variability was calculated by taking the variance of average daily dewpoint during the winter months. The station is near a river, and the cooling and buffering of the water could cause the sensor to underestimate the daily average temperature and temperature variability found on the MVPGR. Precipitation totals are unlikely to differ greatly between the station and the reserve given the spatial proximity.

Algae Sampling and Determining Eutrophication:

Algae blooms in pools were identified visually and then every quadrat along the transects containing algae was recorded (Griggs et al. 2015). Samples of water with suspended plant matter were collected and viewed under a light microscope to verify the presence of algae. To distinguish between normal levels of algae growth and algae blooms, pools with over 90% of quadrats with algae recorded for a single sampling period were considered to have an algae bloom.

Analysis: Meadowfoam and whitetip clover abundance and range within pools

To determine if meadowfoam occupies different zones depending upon the pool, a two-way ANOVA models was produced with zone, pool, and the interaction as independent categorical variables. The continuous response is meadowfoam maximum plant abundance per quadrat. In this analysis, plant abundance is the highest number of plants recorded in a quadrat over a sampling season every 20 cm along the NS and EW transects. All two-way ANOVA models were produced using JMP Pro 16. Pairwise differences between pools and zones regarding mean plant density were conducted using post hoc Tukey Honest significant differences, also performed using JMP Pro 16.

Analysis; Phenological trends across pools and years:

To determine the interannual patterns of meadowfoam and whitetip clover first flowering date, peak flowering date and peak abundance, phenological variables were linearly regressed with year as the model predictor. Correlation estimates were calculated, and model significance was determined. Each linear regression was performed and plotted using the {sjPlot} package (Ludecke et al. 2021) from R version 4.0.03.

To determine if the phenology of meadowfoam and whitetip clover differed between pools, one way ANOVA models were produced. For each pool, least squared means of day to first flower, peak flowering time, and peak flower abundance of both focal species were calculated. All pairwise comparisons between the three pools and three years were conducted using post-hoc Tukey HSD. ANOVA and Tukey HSD tests were produced using the package {car} (Fox et al. 2022) from R version 3.0-13.

Analysis: Environmental covariates of rosy meadowfoam and whitetip clover floral schedules:

To determine the climatic covariates strongly associated with the flowering phenology of the two focal species, linear regressions of phenological response variables -- day to first flower, peak flower date, and peak abundance— with environmental predictors were performed for each species. A series of multiple regression models were produced to identify the significant environmental variables that explain most of the flowering time variation observed in meadowfoam and whitetip clover. One of two environmental variables that were found to be correlated with each other (r>0) were removed. The final set of environmental covariates for either meadowfoam or whitetip clover were used as predictors in a multiple regression of day to first flower and peak flowering time. Nonsignificant predictors were removed, and model fit (AICc) score was calculated. The model that produced the lowest AICc score was chosen to represent the environmental and phenological relationship.

To assess the effect of winter climatic conditions on the phenology of rosy meadowfoam and whitetip clover, multiple regression models were produced. Meadowfoam first flowering date, peak flowering date, and peak abundance are response variables with average winter temperature and winter precipitation as predictors. The model design was repeated for whitetip clover. Multiple regression models were produced using the {car} R package (Fox et al. 2022) version 3.0-13.

Analysis: Competition and Developmental Consequences:

Quadrats that contained both meadowfoam and whitetip clover were recorded. Quadrats that contained one species were designated low interspecific diversity, whereas quadrats that contained both species, were designated as having high interspecific diversity. To determine if meadowfoam and whitetip clover were competing within quadrats occupied by both taxa, the mean plant abundance and fecundity of plots with high and low interspecific diversity were compared. The mean number of meadowfoam plants, flowers, and seeds per quadrat was calculated for quadrats with whitetip clover present, and those without, and vice versa. One-way ANOVAs were performed to compare mean plant abundance, flower production and seed production between interspecific treatments for meadowfoam and whitetip clover. In quadrats containing both species, a significant reduction in either mean plant abundance, flower production and seed output (relative to quadrats with only one of the species) would signify negative interactions between the species.

To parameterize the effect each species had on the other species' fecundity, linear regression of meadowfoam flower production per quadrat and seed output per quadrat (fit separately) was fit against whitetip clover plant abundance per quadrat, and vice versa. Only quadrats with events of co-occurrence were used in the above analysis. A significant negative response would indicate that one species' fecundity is reduced in response to growing interspecific density. ANOVA and linear regressions were performed using R version 3.0-13 package {car} (Fox et al. 2022).

Analysis: Eutrophication effect on Vernal Pool Population Health:

The population sizes of meadowfoam and whitetip clover in pools that experienced eutrophication were further divided into three years: the year before eutrophication, the year during and the year following. To characterize the consequences of eutrophication and the lasting impact on population health, the mean number of plants, flowers, and seeds of meadowfoam and whitetip clover were compared between years – 1. the year during eutrophication, 2. the year prior and 3. the year following. Percent change of population abundance was calculated for three visually distinct zones occupied by both species to determine if the effect of cattle waste is concentrated within the pool basin.

RESULTS

Pool Characteristics:

The three pools differed in size and depth (Table 1.1). Both Pools 1 and 3 were of comparable surface area, both approximately 800m^2 when fully filled. Meadowfoam was observed flowering en masse within vernal pools (Fig. 1.1).

The location of meadowfoam within the three observation pools did vary considerably. The two ANOVA of meadowfoam abundance per quadrat compared across zones and pools was significant for all predictors (ANOVA F = 49.03, $p < 0.0001$, df = 8); zone (F = 132.83, $p < 0.0001$, df = 2), pool (F = 4.64, p = 0.0097, df = 2), zone x pool (F = 21.79, $p < 0.0001$, df = 4). Meadowfoam populations were significantly higher in the bottom (least squares mean = 2.38) than the upland (least squares mean = 0.39; Contrast with pool bottom, F = 218.53, $p < 0.0001$) and edge (least squares mean = 1.19; Contrast with pool bottom, F = 112.56, $p < 0.0001$). Additionally, meadowfoam plant abundance in Pool 3 (least square mean = 1.72) was significantly higher than Pool 1 (least square mean = 1.28; Contrast with Pool 3, F = 8.97, p = 0.0028). Within Pool 1, meadowfoam plant abundance was highest both in the bottom and edge (Table 1.2). In Pool 2 and 3, meadowfoam plant abundance was highest solely in the pool bottom (Table 2).

Maximum whitetip clover abundance per quadrat was significantly different between pools (F = 8.93, $p < 0.0001$, df = 2), among zones within pools (F = 92.22, p = 0.0001, df = 2), and among the same zones between pools (F = 41.71, $p < 0.0001$, df = 4). Pool 3 had the highest whitetip clover abundance (least squares mean = 1.97), which was significantly higher than Pool 2 (least square mean = 1.52; Contrast with Pool 3, F = 17.4, $p < 0.0001$) and Pool 1 (least square mean = 0.62, F = 182.11, $p < 0.0001$). Whitetip clover plant abundance was highest in the edge (least squares mean = 1.6), then the upland (least square mean = 1.27; Contrast with Upland, F = 7.3, p = 0.0069) and lowest in the pool bottom (least square mean = 1.22; Contrast with edge, F = 17.39, p < 0.0001). Maximum whitetip clover plant abundance in Pool 3 was highest in pool bottom, and lowest in the upland, whereas maximum whitetip clover plant abundance in Pool 1 was highest in the upland and lowest in the bottom. Pool 2 had highest whitetip clover abundance along the edge. Ultimately, the zone that whitetip clover maximum abundance per quadrat is highest varied considerably between pools (Table 1.2).

Flowering Phenology:

First flowering dates of both meadowfoam and whitetip clover were observed between April and February on the vernal pool reserve. Across the entire seven-year observation period, the first flowering date of both species had a range of 59 days (Fig. 1.2). Between 2016 to 2022, there was a significant advancement to the first flowering dates of both meadowfoam (slope = -6.48, std error = 1.37, p < 0.0001; Table 1.3) and whitetip clover (slope = -5.39, std error = 1.85, p 0.009; Table 3). The peak flowering date of meadowfoam was advancing, on average, by 4.62 days per year and 4.93 days per year for whitetip clover (Table 1.4). There was no significant difference between pools regarding day to first flower and peak flowering date in either meadowfoam or whitetip clover (Table 1.5).

To determine if the winter climate influenced meadowfoam and whitetip clover day of first flowering or peak flowering dates, multiple regression was run with winter precipitation and winter temperature as predictors. Meadowfoam day to first flower was significantly associated with both average winter temperature (slope = 8.43, std error = 3.92, p = 0.0485) and winter precipitation (slope = 0.12, std error = 0.02, p < 0.0001), whereas whitetip clover day of first flower was only associated with winter precipitation (slope = 0.1, std error = 0.04, p = 0.0182) (Table 1.3). Meadowfoam peak flowering date was not correlated with any winter climate factors, though whitetip clover peak flowering date was significantly correlated with both average winter temperature (slope = 14.81, std error = 5.9, p = 0.0241) and winter precipitation (slope = 0.07, std error = 0.03, p = 0.0331) (Table 1.4). Average winter temperature is positively correlated with peak whitetip clover date, and meadowfoam day to first flower.

The environmental covariates strongly associated with each focal species' day to first flower and peak day of flower are shown in Table 1.6. For meadowfoam, the three most significantly associated environmental covariates with first flowering time were winter precipitation, winter dew point variance and February dew point variance. Whitetip clover day to first flower was most significantly associated with average January temperature, December precipitation, winter dew point variance and February dew point variance.

To determine the set of environmental covariates that explain the most variation observed in meadowfoam flowering time, I took the significant environmental covariates one-way linear regressions with meadowfoam day of first flower and removed variables that were correlated. The four environmental covariates that were correlated with meadowfoam day of first flower used in the first multiple regressions were average January temperature, winter precipitation, annual dew point, and winter dew point variance (Table 1.7). A stepwise series of multiple regression models reveal that the best fit model (AICc = 108.48) was when the predictors of meadowfoam flowering time were annual dew point, winter precipitation, and average January temperature. For whitetip clover day of first flowering multiple regression models, the set of independent variables were average January temperature, December precipitation, annual dew point, annual temperature variance, and February dew point variance. The initial model using all predictors mentioned above produced the lowest AICc score, and removal of any predictor resulted in a decreased model fit (Table 1.8). All variables were significantly associated with meadowfoam day of first flower, and the R^2 was 0.966.

Intra-pool Species Ranges and Interspecific Competitive Dynamics:

Over a seven-year sampling period of three observation pools, the two species were observed together in the same quadrat 544 times out of 5927 observations. Mean whitetip clover abundance per quadrat increases from 2.45 plants when alone to 2.70 plants when cooccurring with meadowfoam (ANOVA: F = 8.5194, p = 0.0036, df = 1; Table 9; Fig. 1.3). On the other hand, mean meadowfoam abundance per quadrat is reduced from 2.54 when alone to 2.31 when growing in quadrats that contain whitetip clover (ANOVA: F = 6.64, p = 0.01, df = 1). The number of whitetip clover flowers in quadrats with meadowfoam were significant fewer than in plots without meadowfoam (ANOVA: F = 6.12, p = 0.0135, df = 1).

A second set of analyses were conducted to determine the effect interspecific density has on each species' flower production and seed production. In quadrats occupied by both taxa, whitetip clover plant abundance significantly reduces meadowfoam fruit production (slope = -0.27, std error = 0.07, $p < 0.0001$; Table 1.10), though whitetip clover abundance had no effect on meadowfoam flower production (slope = 0.11, std error = 0.08, p = 0.1768; Table 1.10). Alternatively, meadowfoam significantly reduces whitetip clover flower production (slope = - 0.07, std error = 0.03, p = 0.0229; Table 1.10) while showing little negative influence on whitetip clover seed set (slope = 0.004, std error = 0.04, p = 0.9289; Table 1.10).

Eutrophication

High algal growth occurred twice – in Pool 1 in 2019 and in Pool 2 in 2020 – during a 5-year period when algae growth was documented. In Pool 1, the meadowfoam population was reduced by 93.4% and the whitetip clover population was completely extirpated in the pool bottom. Along the pool edge and upland of Pool 1, whitetip clover populations were reduced by 99.2% and 37.4%, respectively, whereas the meadowfoam population grew in both the edge and upland (Table 1.11). Similarly in Pool 2, the meadowfoam and whitetip clover populations were severely reduced in the pool bottom. In contrast to Pool 1, both meadowfoam and whitetip clover populations dropped by 36.8% and 66.4% along the pool edge, respectively. In the upland of Pool 2, whitetip clover populations were negatively affected during the algae bloom.

The year following algae growth, bottom-dwelling meadowfoam populations in Pool 1 remained depressed while swiftly recovering to pre-algal levels in Pool 2 (Table 1.11). In both Pools 1 and 2, meadowfoam populations increased along the edge by 241% and 223.7%, respectively, from pre-algal bloom conditions. Whitetip clover populations were lower post-algae than pre-algae across most zones other than the bottom of Pool 1. When comparing post-algae bloom population sizes of both species to population abundance during algal growth, there were increases across all zones, and thus recovery was clearly witnessed. However, post-algae meadowfoam populations in Pool 1 were nearly 1/3 of pre-algae conditions, compared to 18.8% in Pool 2.

DISCUSSION:

Vernal pool environments are representative of the harsh climate endemic to the California Central Valley; inclement winters of freezing temperatures and concentrated rainfall rapidly followed by sweltering summers devoid of precipitation. Vernal pools flood for several months and rapidly dry in the spring, which enables the establishment of semi-aquatically adapted plants that track highly unpredictable precipitation events with finely tuned phenological transitions. Interannual variability of precipitation in Mediterranean climates has been linked to variable germination dates (Fernandez-Zamudio et al. 2018), and we find that unpredictable hydrology also translates into variable floral start dates and peak flowering dates. In addition, the findings of this study suggest that precipitation year has a large effect on floral phenology, eutrophication, interspecific relationships, and consequently, population sizes.

Plant floral phenology is strongly associated with external environmental cues, called "zeitgebers" (Wigge et al. 2005; Amasino 2010). Depending upon the species and habitat, the environmental 'zeitgeber' may be day length, water concentration or temperature. Aquatic plants occupying temporary ponds germinate rapidly in response to precipitation regardless of the season, which ensures high seed production during periods of available water supply (Fernandez-Zamudio et al. 2018). Similar to temporary ponds, the seeds of plants inhabiting California vernal pools germinate after the first rain (Collinge et al. 2013), though plant floral phenology is more diverse (Bliss and Zedler 1997). Over a 2-year study period, winter annuals ranging from forbes to grasses in Mediterranean climates flowered earlier in response to reduced rainfall (Kigel et al 2013), whereas no phenological pattern to climate variables was observed from geophytes or perennial grasses. Munson and Long (2016) confirmed these findings with a larger data set, discovering that warmer than average temperatures promote advanced flowering of annual C3 species and delayed flowering of perennial C4 species (Munson & Long 2016). In this study, meadowfoam and whitetip clover, two C3 annual forbes, both flowered earlier in response to reduced rainfall and later in response to warmer temperature. Although no prior investigation into the phenology of vernal pool meadowfoam and whitetip clover exists, both vernal pool specialists, *Downingia bella* and *D. cuspidata*, have earlier flowering when desiccation is earlier in the year (Martin & Lathrop 1986). This complements the findings for both whitetip clover and meadowfoam, which had delayed flowering when water was available later into the season.

Nevertheless, another vernal pool specialist, Lasthenia cojugens, germinates and initiates flowering earlier under higher water concentrations (Collinge et al. 2003). Research into the floral patterns of more vernal pool plant species is required to determine if flowering time of vernal pool plants have common zeitgebers and responses.

The climate of the Central Valley in the past 30 years is trending towards warmer winter and spring seasons (Dettinger & Cayan 1995). The increase in evaporation rate is uncompensated by any change to precipitation patterns (Stewart et al. 2004; Maurer 2007), and future projections suggest that the precipitation regime will shift towards more infrequent, and larger storms (Stewart et al. 2004). Shifts towards warmer winter and spring season have been followed by considerable advancement of flowering time in many annual flowering species (Lesica & Kittelson 2010; Abu-Asab et al. 2001; Primack et al. 2004). Sensitive groups are annuals in temperate climates including, but not limited to, Mediterranean grasses, California native wildflowers, and aquatic macrophytes. Across the 7-year study period, the first flowering date of meadowfoam has advanced by ~30 days from the beginning of the study. In the most recent three years, meadowfoam flowering time was in February, which is two months before the normal bloom date found amongst Jepson herbarium records and a month before all field observations within the Calflora data base. Vernal pool plants thrive under rapidly ephemeral aquatic conditions. While prior specialization to disturbance regimes enables swift adaptation to climate change in some plant species, climate change threatens to disrupt hydrologic cycles of vernal pools and remove the disturbance regimes that maintains native species abundance. These results suggest that current climate warming is causing rapid acceleration of flowering time. Longer phenological surveys will confirm tease phenological trends in response to climate change from the natural flowering time variability common in these two focal species.

The two focal species in this study occupied regions of the pool corresponding to previous species characterizations. Whitetip clover, *Trifolium variegatum*, is a member of the trifolio variegate-lasthenietum glaberrimae vernal pool syntaxon described by Barbour et al. 2005, primarily inhabiting the pool edge. Whitetip clover populations recorded in this study were found with high abundance along the edge, and also within the shallow bottoms of Pools 2 and 3. This interzonal range parallels findings by Bliss and Zedler (1997), in which they found that whitetip clover will also occupy shallow pools. No mention was made concerning the edaphic association of whitetip clover populations in prior analyses; however, the findings of this study suggest that lower clay content pools may harbor higher whitetip clover plant populations. Meadowfoam was found occupying the bottom of the pool, which coincides with other species within Genus *Limnanthes*. Meadowfoam and whitetip clover were often observed together in Pool 2 and 3, which contradicts the species associations, or syntaxons, previously defined by Bliss and Zedler (1997). In their investigation, *T. variegatum* and *L. douglassii* var. *rosea* were within two syntaxons characterized by substantially different tolerances to inundation, and thus the two species are thought to co-flower but not necessarily co-occur. Nevertheless, the immense variety of vernal pools, gradients and climates does create opportunity for guilds to rearrange. More investigations of climate years, soil types and community compositions are required in the Central Valley to characterize the pool distributions of whitetip clover, meadowfoam and the microhabitats inhabited by both.

Cattle consume invasive grass species and provide a necessary ecological service historically facilitated by extinct grazers. In addition, the high nitrogen content in their manure bolsters algae growth and potentially leads to eutrophic conditions. Croel and Kneitel (2011) constructed experimental mesocosms with varying nitrogen concentrations, and after 10 weeks of flooding and algae growth, species richness and plant cover were reduced by 54% and 87%, respectively. In another mesocosm experiment with varying nitrogen additions, Kneitel and Lessin (2010) found that vascular plant cover was reduced from 80% in the control mesocosm to 40% in the high nutrient, high algae cover treatment. I find that meadowfoam and whitetip clover populations are reduced dramatically (90% to 100%) during algae growth in natural pools, complementing and exceeding previous findings. In addition, when natural pools were filled for nearly 10 weeks, a length comparable to the inundation regime utilized within experimental mesocosms, population sizes of both meadowfoam and whitetip clover did not recover the year following. However, the meadowfoam population within pool two, which was only flooded for 4 weeks, recovered rapidly the following year after eutrophication, potentially explained by the inundation length and storage effects of the seed bank (Collinge et al. 2013). On the other hand, whitetip clover populations remained low in Pool 1 and Pool 2, which corresponds with the negative population growth of cultivated whitetip clover fields in response to supplemental nitrogen additions of manure and synthetic fertilizers. The novelty of the present research is that eutrophication is shown to have long lasting consequences for affected species, suppressing growth for multiple years and across multiple zones. Further research is required to test the soil for anaerobic metabolites, nutrient concentrations, or pathogenic microbes that restrict reestablishment of meadowfoam into the pool bottom and of whitetip clover in general.

We conducted this study in three vernal pools in one county of California. The geographic distribution of vernal pools in California ranges from San Diego to Humboldt counties. There are 17 vernal pool regions in California, and 8 vernal pool series with a different geologic origins, impermeable substrata, and assemblage of indicator species. I studied the claypan vernal pools in the San Joaquin Valley region, with *Limnanthes douglassii rosea*, *Lasthenia fremontii*, and *Trifolium variegatum* as indicator species. In comparison, the mesa vernal pools of San Diego County can be identified from the presence of *Navarretia fossalis* and *Pogogyne abramsii* populations. Flowering induction by climate is known to be modulated by soil type, and in addition, species can exhibit novel phenological responses to different community compositions (Wolf et al. 2017). As such, the restricted geographic scope of this study limits the generalities that can be made about vernal pool wide phenological responses to climate and sensitivities to climate change. Another limitation of this study is that nutrient concentrations were not measured in “eutrophic” pools. It is generally believed that algae crust directly impacts plant growth by occluding the sun, however, it is necessary to collect nitrogen, oxygen and phosphorous to validate the cause of algal blooms and progression of eutrophication in promoting dead zones.

Overall, our study demonstrates that the day of first flowering and peak flowering of two vernal pool associates native to California exhibits high interannual variation in response to precipitation. This suggests that vernal pool wildflowers may be susceptible to climate change disruption. However, a larger data set is required to create a baseline of their phenology. So far, the establishment of this continuous phenological survey on the UC reserve is a good start. Future observations of within pool dynamics, interspecific interactions, and climate years will be needed to parse out the influence of climate change on plant phenology from the normal variability expressed in vernal pool habitats.

TABLES

Table 1.1 Characteristics of three vernal pools on the UC Merced Grassland and Vernal Pool reserve. Size indicates the circular area in m^2). Max depth was measured with a yard stick, and the value reported is the maximum depth of water measured during peak flooding across the 7 sampled years (2016-2022).

Pool	*Size (m^2)*	*Max Depth (m)*
1	843.88	0.47
2	372.34	0.24
3	871.35	0.31

Table 1.2 Mean maximum plant abundance per quadrat of meadowfoam and whitetip clover across three zones of three different pools. ANOVA of meadowfoam plant abundance per quadrat was significant between zones in Pool 1 (F = 16.01 $p < 0.0001$, df = 2), Pool 2 (F = 65.92, $p < 0.0001$, df = 2), and Pool 3 (F = 74.08, $p < 0.0001$, df = 2). In addition, ANOVA of whitetip clover plant abundance per quadrat was significant between zones in Pool 1 (F = 39.42, $p < 0.0001$, df = 2), Pool 2 (F = 14.22, $p < 0.0001$, df = 2), and Pool 3 (F = 37.56, $p < 0.0001$, df = 2). Post-hoc Tukey HSD levels are reported, with significant differences between zones within a zone denoted by a different letter (ie. A, B, and C).

Pool	*Zone*	*Mean Meadowfoam Plant Abundance/Quadrat*	*Tukey HSD Levels*	*Mean Whitetip Clover Abundance per quadrat*	*Tukey HSD Levels*
1	Bottom	1.80	A	0.18	C
	Edge	1.49	A	0.59	B
	Upland	0.55	B	1.21	A
2	Bottom	3.87	A	1.39	B
	Edge	1.04	B	2.63	A
	Upland	0.15	B	1.58	B
3	Bottom	3.15	A	3.32	A
	Edge	1.34	B	2.18	B
	Upland	0.69	C	1.39	C

Table 1.3 Relationship between day to first flower and two sets of predictor variables for two focal species (meadowfoam and white tip clover) on the MVPGR. Four separate models are shown, two for each of the focal species: a model with just Year as a predictor and a model with Average Winter Temperature and Winter Precipitation as predictors. For each model, the fitted estimate and the p-value of the predictor is indicated. Significant variables (p<0.05) are bolded. Overall model statistics are shown at the bottom: the sample size (Observations, typically n=21 due to 7 years of observations across 3 pools) and the overall R^2 and adjusted R^2 for the model. Sample sizes for the models with climate variables are lower due to a lack of winter precipitation records in 2018.

	Meadowfoam Day to First Flower		**Meadowfoam Day to First Flower**		**Whitetip Clover Day To First Flower**		**Whitetip Clover Day To First Flower**	
Predictors	*Estimate*	*p*	*Estimate*	*p*	*Estimate*	*p*	*Estimate*	*p*
Intercept	13144.95	**<0.001**	-26.40	0.432	10967.04	**0.009**	54.82	0.354
Year	-6.48	**<0.001**			-5.39	**0.009**		
Average Winter Temperature			8.43	**0.048**			-0.09	0.990
Winter Precipitation			0.12	**<0.001**			0.10	**0.018**
Observations	21		18		21		18	
R^2 / R^2 adjusted	0.539 / 0.514		0.673 / 0.630		0.308 / 0.271		0.328 / 0.238	

Table 1.4 Relationship between peak flowering time and two sets of predictor variables for two focal species (meadowfoam and white tip clover) on the MVPGR. Four separate models are shown, two for each of the focal species: a model with just Year as a predictor and a model with Average Winter Temperature and Winter Precipitation as predictors. For each model, the fitted estimate and the p-value of the predictor is indicated. Significant variables ($p<0.05$) are bolded. Overall model statistics are shown at the bottom: the sample size (Observations, typically n=21 due to 7 years of observations across 3 pools) and the overall R^2 and adjusted R^2 for the model. Sample sizes for the models with climate variables are lower due to a lack of winter precipitation records in 2018.

	Peak Flowering Date Meadowfoam		**Peak Flowering Date Meadowfoam**		**Peak Flowering Day Whitetip Clover**		**Peak Flowering Day Whitetip Clover**	
Predictors	*Estimate*	*p*	*Estimate*	*p*	*Estimate*	*p*	*Estimate*	*p*
Intercept	9409.00	**0.003**	15.14	0.779	9151.80	**0.005**	-46.87	0.356
Year	-4.62	**0.004**			-4.49	**0.005**		
Average Winter Temperature			6.41	0.328			14.81	**0.024**
Winter Precipitation			0.07	0.080			0.08	**0.033**
Observations	21		18		21		18	
R^2 / R^2 adjusted	0.367 / 0.334		0.209 / 0.104		0.345 / 0.311		0.398 / 0.317	

Table 1.5 Least squares mean of each focal species' annual phenology schedule and peak abundance for Pools 1, 2 and 3. Day to first flower and day to peak flower are presented as Julian Date. Peak abundance is measured as number of individuals. Post-hoc Tukey HSD levels are reported; significant differences between pools regarding day to first flower, day to peak flower, and peak abundance are denoted by different letters. ANOVA reveals that there are no significant differences between pools regarding meadowfoam day to first flower (F = 0.0452, p = 0.96, d = 2), day to peak flower (F = 0.11, p = 0.89, d = 2), and peak abundance (F = 1.18, p = 0.33, d = 2). There is no significant differences between pools in respect to whitetip clover day to first flower (F = 0.0479, p = 0.95, d = 2) and day to peak flower (F = 0.09, p = 0.92, d = 2), whereas pools are significantly different in respect to whitetip clover peak abundance (F = 17.54, p < 0.0001, d = 2).

		Meadowfoam		*Whitetip Clover*	
	Pool	LSM	TukeyHSD Levels	LSM	TukeyHSD Levels
Day to First Flower					
	1	67.85	A	77.86	A
	2	69.86	A	77.86	A
	3	70.86	A	80.86	A
Day to Peak Flower					
	1	89.17	A	91.83	A
	2	85.67	A	96.33	A
	3	87.17	A	96.33	A
Peak Abundance					
	1	101	A	17.77	B
	2	150	A	72	B
	3	185.67	A	129.5	A

Table 1.6 Pearson correlation coefficients and degree of significance between environmental covariates and day of first flower and peak flowering date for both focal species. * = p < 0.05, ** = p < 0.005, *** = p < 0.0005.

	Meadowfoam Day of First Flower	*Meadowfoam Day of Peak Flower*	*Whitetip Clover Day of First Flower*	*Whitetip Clover Day of Peak Flower*
Average Annual Temperature	0.43	-0.83***	0.37	-0.64**
Average Winter Temperature	-0.22	-0.7**	-0.36	-0.38
Average January Temperature	0.52*	0.7**	0.58**	0.4
Average February Temperature	-0.06	-0.73**	-0.45*	-0.62**
Average March Temperature	0.19	-0.29	-0.2	-0.05
Annual Precipitation	0.24	-0.08	0.26	-0.8
Winter Precipitation	0.75***	0.07	0.57*	0.03
October Precipitation	0.4	0.3	-0.4	0.22
November Precipitation	0.17	0.45	0.57*	0.29
December Precipitation	-0.41	-0.67**	-0.58**	-0.14
January Precipitation	0.29	-0.18	0.11	-0.41
February Precipitation	0.16	0.01	0.38	0.01

Table 1.6 cont.

	Meadowfoam Day of First Flower	*Meadowfoam Day of Peak Flower*	*Whitetip Clover Day of First Flower*	*Whitetip Clover Day of Peak Flower*
March Precipitation	-0.03	0.1	-0.12	0.05
October to November Precipitation	-0.09	0.48*	0.3	0.30
October to December Precipitation	-0.52*	-0.36	-0.4	-0.06
October to January Precipitation	-0.03	-0.34	-0.12	-0.37
October to February Precipitation	0.05	-0.21	0.1	-0.23
October to March Precipitation	-0.09	-0.17	-0.06	-0.20
January to February Precipitation	0.27	-0.1	0.27	-0.24
Janurary to March Precipitation	0.03	-0.07	0.01	-0.22
February to March Precipitation	0.01	0.06	0.21	0.03
Annual Dew Point	-0.57*	-0.82***	-0.62**	-0.40

Table 1.6 cont.

	Meadowfoam Day of First Flower	*Meadowfoam Day of Peak Flower*	*Whitetip Clover Day of First Flower*	*Whitetip Clover Day of Peak Flower*
Winter Dew Point	-0.4	-0.72**	-0.49*	-0.51*
January Dew Point	0.5*	0.45	0.45*	0.51*
February Dew Point	-0.06	-0.51*	-0.25	-0.6*
March Dew Point	0.46	0.1	0.14	0.26
Annual Temperature Variance	-0.16	-0.54*	-0.49*	-0.62**
Winter Temperature Variance	0.47*	-0.07	0.36	0.12
February Temperature Variance	0.27	0.37	0.54*	0.6*
Annual Dew Point Variance	-0.12	-0.11	0.15	0.11
Winter Dew Point Variance	0.89***	0.48*	0.82***	0.58*
February Dew Point Variance	0.81***	0.57*	0.87***	0.6*

Table 1.7 Stepwise series of multiple regression models using environmental covariates with the highest significance with meadowfoam day to first flower. Two correlated variables (r > 0.5) were reduced to one variable by filtering out the other. The Year 2018 did not have winter precipitation recorded at the Merced station operated by California Irrigation Management and Information System. Annual dew point is not yet available for the Year 2022, thus reducing the 'Observations' down from n=18 to n=15 when the variable is included.

	Meadowfoam Day to First Flower		**Meadowfoam Day to First Flower**		**Meadowfoam Day to First Flower**		**Meadowfoam Day to First Flower**	
Predictors	*Estimate*	*p*	*Estimate*	*p*	*Estimate*	*p*	*Estimate*	*p*
Intercept	-484.24	**0.015**	-437.01	**0.005**	89.99	0.389	-9.74	0.661
Average January Temp	27.09	**0.004**	25.85	**0.002**			6.67	**0.025**
Winter Precipitation	0.22	**0.035**	0.18	**<0.001**	0.01	0.896	0.11	**<0.001**
Annual Dew Point	36.65	**0.044**	30.80	**0.005**	-8.29	0.609		
Winter Dew Point Variance	-1.90	0.661			4.22	0.480		
Observations	15		15		15		18	
R^2 / R^2 adjusted	0.787 / 0.701		0.782 / 0.723		0.481 / 0.340		0.697 / 0.657	
AICc	114.016		108.486		121.508		132.071	

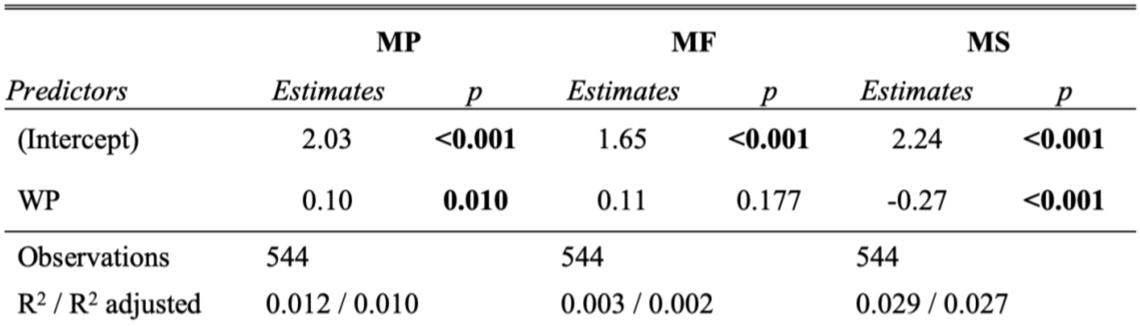
Table 1.8 Stepwise series of multiple regression models using environmental covariates with the highest significance with whitetip clover day to first flower. The year 2018 did not have winter precipitation recorded at the Merced station operated by the California Irrigation Management and Information System. There were 18 days to first flower observations of whitetip clover from 3 pools over 6 years.

	Whitetip Clover Day To First Flower		**Whitetip Clover Day To First Flower**		**Whitetip Clover Day To First Flower**		**Whitetip Clover Day To First Flower**	
Predictors	*Estimate*	*p*	*Estimate*	*p*	*Estimate*	*p*	*Estimate*	*p*
Intercept	9626.30	**0.001**	1333.87	**<0.001**	835.56	0.057	164.31	**0.009**
Average January Temp	-389.71	**0.001**	-48.28	**<0.001**	-28.21	0.140		
Dec Precip	2.49	**0.001**	0.18	0.159			-0.15	0.274
Annual Dew Point	-565.70	**0.001**	-69.15	**<0.001**	-37.90	0.082	0.75	0.924
Annual temp Variance	-31.18	**<0.001**	-5.94	**<0.001**	-4.52	**0.013**	-2.36	**<0.001**
February Dew Point Variance	-23.74	**0.002**			1.36	0.305	3.30	**<0.001**
Observations	18		18		18		18	
R^2 / R^2 adjusted	0.966 / 0.952		0.925 / 0.902		0.919 / 0.894		0.912 / 0.885	
AICc	119.261		128.094		129.427		130.847	

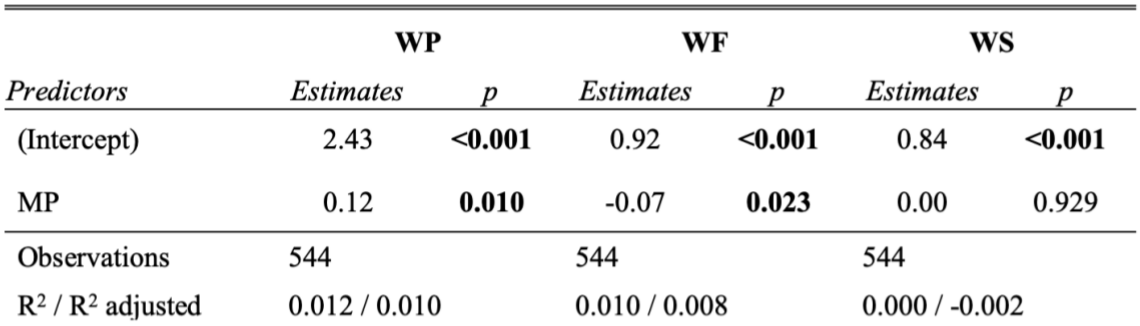
Table 1.9 Mean plant abundance, flower number, and seed pods recorded for plots of only meadowfoam and whitetip clover (co-occurrence = 0) and when the two species were observed together (co-occurrence = 1). Interspecific treatments are when a focal species is found alone in a quadrat or with the other species within a quadrat. Instances where mean abundance of plants, flowers and seeds were statistically different between interspecific treatments are bolded.

Co-occurrence	*Mean Plant Abundance*	*Mean Flower Number*	*Mean Fruit Count*
0			
Meadowfoam	**2.55***	1.74	1.58
Whitetip Clover	**2.45***	**0.95***	0.94
1			
Meadowfoam	**2.24***	1.82	1.56
Whitetip Clover	**2.70***	**0.75***	0.85

Table 1.10 Effect of meadowfoam or whitetip clover plant abundance on the other focal species' plant, flower, and seed abundance per quadrat in quadrats containing both species. Interspecific affects between meadowfoam and whitetip clover on plant, flower, and seed abundance. (Top) Meadowfoam plant abundance (MP), flower production (MF), and seed number (MS) response to higher whitetip clover plant abundance per quadrat (WP). (Bottom) Whitetip clover plant abundance (WP), flower productions (WF), and seed numbers (WS) to higher meadowfoam plant abundance per quadrats (MP).



	MP		**MF**		**MS**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
(Intercept)	2.03	**<0.001**	1.65	**<0.001**	2.24	**<0.001**
WP	0.10	**0.010**	0.11	0.177	-0.27	**<0.001**
Observations	544		544		544	
R^2 / R^2 adjusted	0.012 / 0.010		0.003 / 0.002		0.029 / 0.027	



	WP		**WF**		**WS**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
(Intercept)	2.43	**<0.001**	0.92	**<0.001**	0.84	**<0.001**
MP	0.12	**0.010**	-0.07	**0.023**	0.00	0.929
Observations	544		544		544	
R^2 / R^2 adjusted	0.012 / 0.010		0.010 / 0.008		0.000 / -0.002	

Table 1.11 Abundance of meadowfoam (top) and whitetip clover (bottom) plants within Pools 1 and 2 during, before and after algal blooms were observed. Abundance was measured as the highest number of meadowfoam, and whitetip clover plants observed on a sampling date along the transects in either the upland, edge, or bottom. Algal blooms occurred in Pool 1 during 2019, and in Pool 2 during 2020. Algae was measured weekly when present, and pools that obtained an algae cover of > 90% were designated as having an algae bloom. Percent change from the pre-algae levels is reported beside the plant count for that season.

Pool	*Zone*	*Pre-Algae Bloom*	*During*	*Post-Algae Bloom*
Meadowfoam				
1	Bottom	560	37 (-93.4%)	172 (-69.3%)
	Edge	39	52 (+33.3%)	133 (+241%)
	Upland	2	10 (+400%)	4 (+100%)
2	Bottom	915	49 (-94.5%)	1087 (+18.8%)
	Edge	38	24 (-36.8%)	123 (+223.7%)
	Upland	7	0	0
Whitetip Clover				
1	Bottom	27	0 (-100%)	32 (+18.5%)
	Edge	120	1 (-99.2%)	16 (-86.7%)
	Upland	179	112 (-37.4%)	159 (-11.2%)
2	Bottom	208	21 (-89.9%)	94 (-54.8%)
	Edge	247	83 (-66.4%)	193 (-28%)
	Upland	54	38 (-29.6%)	37 (-31.5%)

FIGURES

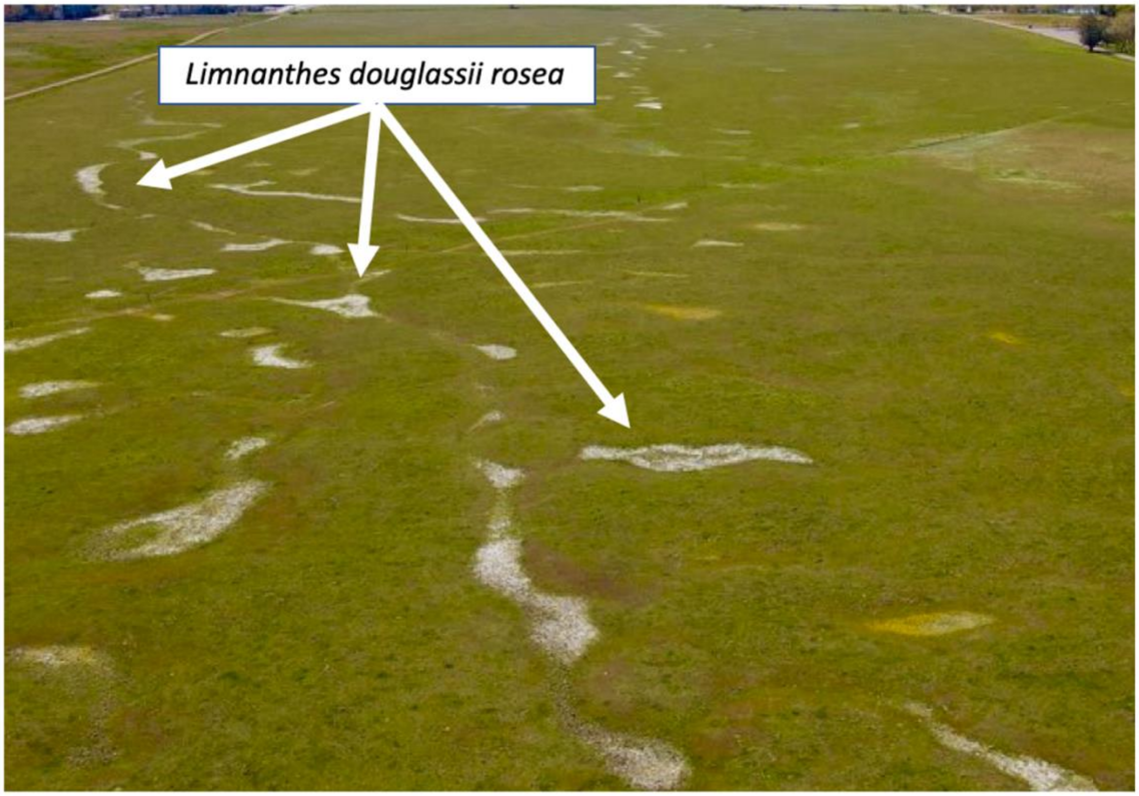


Figure 1.1 Aerial photo of vernal pools on the MVPGR on March 19th, 2021, with dense populations of meadowfoam plants in bloom (white flowers). Meadowfoam is a dominant species in vernal pools during the early season, and the initiation of its bloom indicates the beginning of the flowering season for the entire vernal pool habitat.

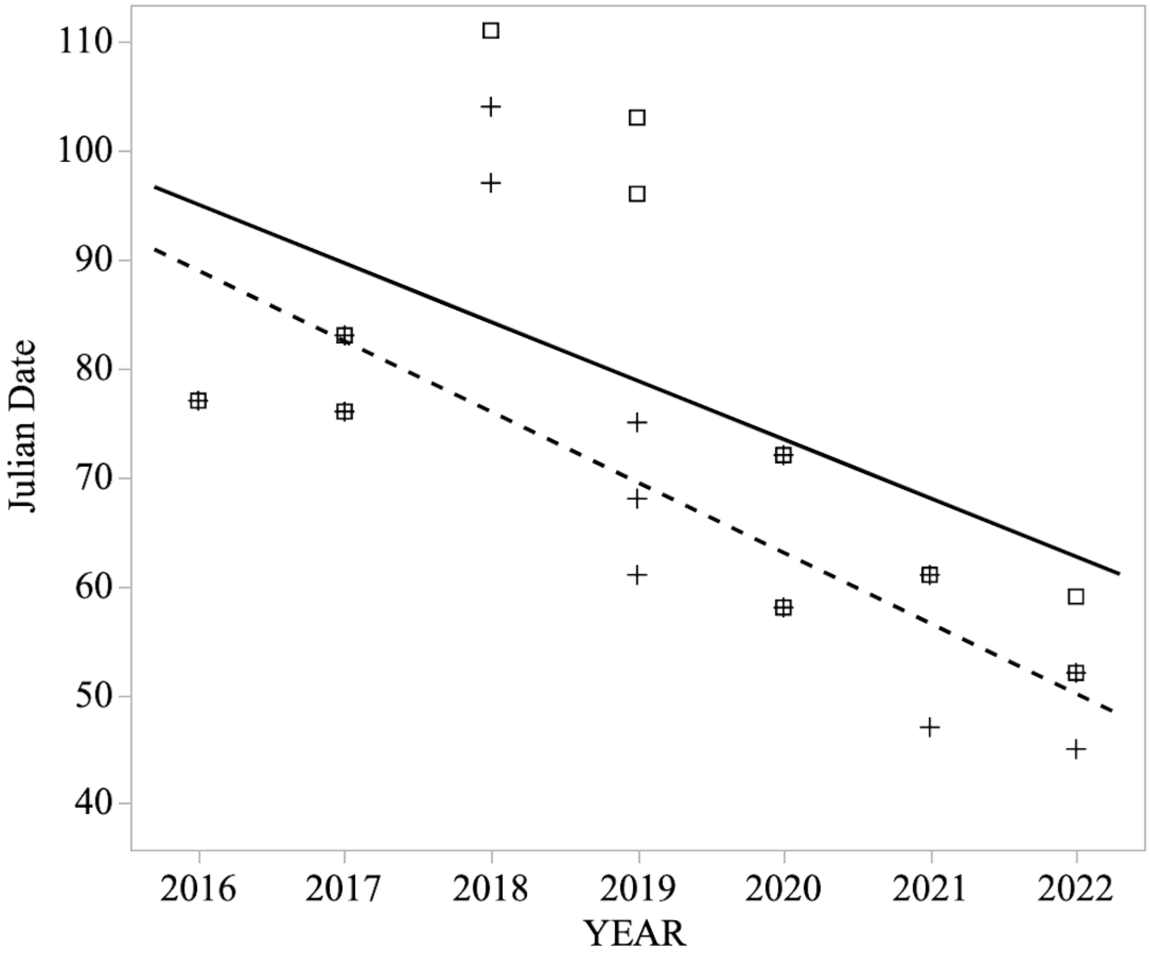


Figure 1.2 Day of first flower of both focal species across a seven-year sampling period. Day of first flowering of whitetip clover (squares) and meadowfoam (crosses) from 2016 – 2022. Day of first flower is measured as Julian date (January 1st = 1). Best fit line from linear regression is plotted for meadowfoam (dashed line) and whitetip clover (solid line).
Whitetip clover linear regression results are: R^2 = 0.27, slope = -5.39, p = 0.009.
Meadowfoam linear regression results are: R^2 = 0.51, slope = -6.48, p = 0.0002.

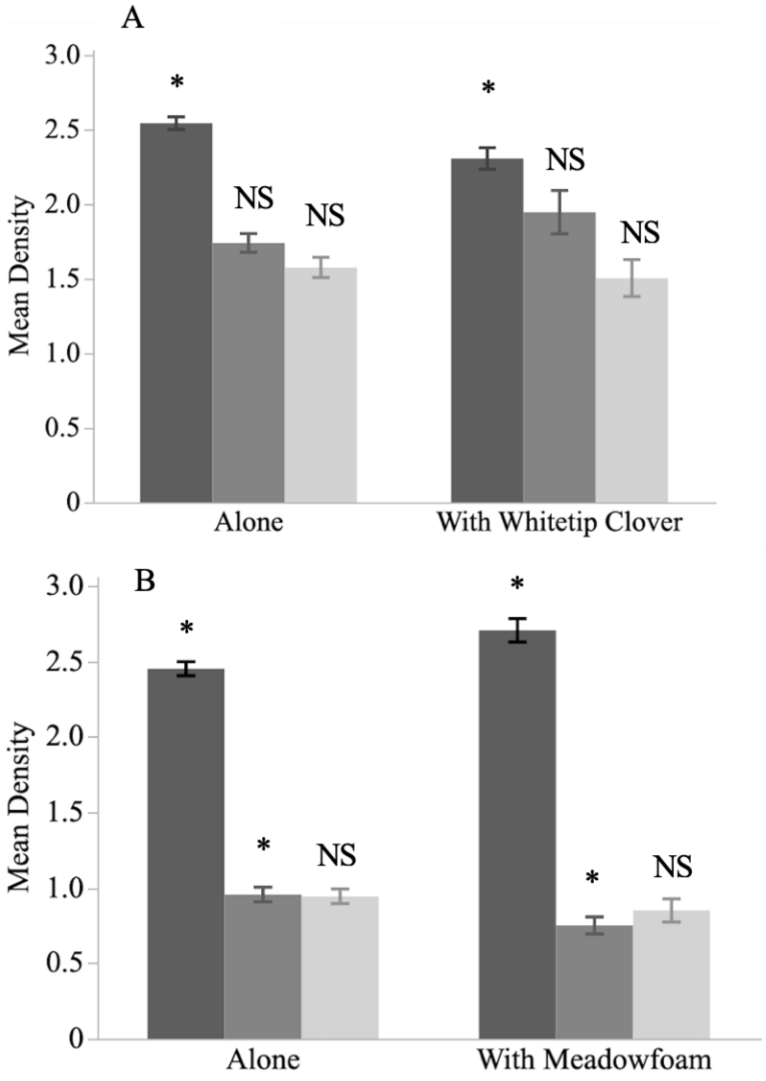


Figure 1.3 Bar graph of mean (A) meadowfoam or (B) whitetip clover plant, flower and seed density in quadrats found alone and quadrats with the other focal species. (A) Bar graphs of mean meadowfoam plant (dark grey), flower (grey) and seed density (light grey) in plots found alone and plots found with whitetip clover. Significant differences of meadowfoam plant density between interspecific treatments (ie. ‘Alone’ or ‘With Whitetip Clover’) is depicted with an ‘*’, whereas nonsignificant differences of flower and seed density between interspecific treatments are depicted using ‘NS’. (B) Bar graphs of mean whitetip clover plant (dark grey), flower (grey), and seed density (light grey) in plots found alone and plots found with meadowfoam.

LITERATURE CITED

Abu-Asab, M., Peterson, P.M., Shetler, S.G., & Orli, S. S (2001) Earlier plant flowering in spring as a response to global warming in the Washington, DC, area. Biodiversity and conservation, 10(4), 597-612.

Amasino, R. (2010) Seasonal and developmental timing of flowering. Plant Journal, 61(6), 1001-1013.

Anderson, J. T., Lee, C. R., & Mitchell-Olds, T. (2011) Life-history QTLs and natural selection on flowering time in Boechera stricta, a perennial relative of Arabidopsis. Evolution 65, 771–787.

Anderson, J. T., Inouye, D. W., McKinney, A. M., Colautti, R. I., & Michell-Olds, T. (2012) Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. Proceedings of The Royal Society, 279, 3843-3852.

Barbour, M. G., Solomeshch, A. I., Holland R. F., Witham C. W., Macdonald R. L., Cilliers, C. C., Molina, J. A., Buck, J. J., & Hillman J. M. (2005) Vernal pool vegetation of California, communities of long-inundated deep habitats. Phytocoenologia, 35, 177-200.

Barry, S. (1998) Managing the Sacramento Valley vernal pool landscape to sustain the native flora. .In, C.W. Witham, E.T. Bauder, D. Belk, W.R. Ferren Jr., and R. Ornduff (Eds.). Ecology, Conservation, and Management of Vernal Pool Ecosystems – Proceedings from a 1996 Conference. California Native Plant Society, Sacramento, California. 1998.

Bauder, E.T. (1987) Species assortment along a small-scale gradient in San Diego vernal pools. Dissertation. University of California, Davis and San Diego State University.
Bauder, E.T. (2000) Inundation effects on small-scale distributions in San Diego, California vernal pools. Aquatic Ecology, 34,43-61.

Bliss, S.A., & Zedler, P. (1997) The germination process in vernal pools: sensitivity to environmental condition and effects on community structure. Oecologia, 113: 67-73.
Bosisio, M. (1989) Meadowfoam: pretty flowers, pretty possibilities. Agricultural Research USDA Research Service, 37(2), 10-11.

Brendonck, L., Jocque, M., Tuytens, K., Timms, B., & Vanschoenwinkel, B. (2015) Hydrological stability drives both local and regional diversity patterns in rock pool metacommunities. Oikos, 124, 741-749.

California, State of. CIMIS, https://cimis.water.ca.gov

Čelakovský, L. (1874) Ueber den Aufbau der Gattung Trifolium.Österreichische Botanische Zeitschrift, 24(2), 37-45.

Collinge, S. K., Wise, C. A., & Weaver, B. (2003) Germination, Early Growth and Flowering of Vernal pool annual in response to soil moisture and salinity. Madrono, 50(2):83-93.

Collinge, S.K., Ray, C., & Marty, J.T. (2013). A long-term comparison of hydrology and plant community composition in constructed versus naturally occurring vernal pools. Restoration Ecology, 21(6), 704-712.

Croel, R. C., Kneitel, J. M. (2011) Cattle waste reduces plant diversity in vernal pool mesocosms. Aquatic Botany, 95, 140-145.

Crowe, E. A., Busacca, A. J., Reganold, J. P., & Zamora, B. A. (1994) Vegetation zones and soil characteristics in vernal pools in the Channeled Scabland of eastern Washington. Great Basin Naturalist, 54(3).

Dettinger, M.D., & Cayan, D.R. (1995) Large-scale atmospheric forcing of recent trends toward early snowmelt in California. Journal of Climatology, 8, 606-623.

Dole, J. (1988) Results of a Field Survey for the Butte County Meadowfoam in the Vicinity of the City of Chico, California. City of Chico, Chico, CA.

Ehrle´n, J. & Mu¨nzbergova´, Z. (2009) Timing of flowering: Opposed selection on different fitness components and trait covariation. American Naturalist ,173, 819–830. Emery, N.C., Stanton, M. L., & Rice, K.J. (2009) Factors driving distribution limits in an annual plant community. The New Phytologist, 181, 734-747.

“Explore.” Calflora, https://www.calflora.org/.

Fernandez-Zamudio, R., Garcia-Murillo, P., & Diaz-Paniagua, C. (2018) Effect of the filling season on aquatic plants in Mediterranean temporary ponds. Journal of Plant Ecology, 11(3), 502-510.

Fogg, G.E. (1956) Nitrogen Fixation by Photosynthetic Organisms. Annual Review of Plant Physiology, 7, 51-70.

Fox, J., & Weisberg, S. (2019) car: Companion to Applied Regression. R package, version 3.0-13.

Gosejohan, M. C., Weisberg, P. J., & Merriam, K. E. (2017) Hydrologic Influences on Plant Community Structure in Vernal Pools of Northeastern California. Wetlands, 37(2), 257-268.

Griggs, A.N., Selckmann, G. M., Cummins, J., & Buchanan, C. (2015) Methods for estimating filamentous algae cover in streams and rivers of the Shenandoah River Basin. Report for U.S. EPA Region 3.

Hickman, J. C., ed. (1993). The Jepson Manual: higher plants of California. University of California Press, Berkeley and Los Angeles, California.

Holland, R. F. (1978) The geographic and edaphic distribution of vernal pools in the Great Central Valley, California. California Native Plant Society special publication.

James, E., Kleinman, P., Veith, T., Stedman, R., & Sharpley, A. (2007) Phosphorous contributions from pastured dairy cattle to streams of the Cannonsville Watershed, New York. Journal of Soil and Water Conservation. 62, 40-47.

Keeley, J.E. (1988) Anaerobiosis as a stimulus to germination in two vernal pool grasses. American Journal of Botany,75, 1086-1089.

Keeley, J.E., & Zedler, P.H. (1998) Characterization and global distribution of vernal pools. .In: Witham, C.W., Bauder, E.T., Belk, D., Ferren Jr., W.R., Ornduff, R. (Eds.), Ecology, Conservation, and Management of Vernal Pool ecosystems – Proceed- ings from a 1996 conference. California,California Native Plant Society, Sacramento, pp. 1–14.

Kelly, A. E., & Goulden, M. L (2008) Rapid Shifts in plant distribution with recent climate change. PNAS. 105(33), 11823-11826.

Kigel, J., Konsens, I., Rosen, N., & Rotem, G. (2013) Relationships between flowering time and rainfall gradients across Mediterranean-Desert Transects. Israel Journal of Ecology and Evolution, 57(1), 91-109.

King, J.L. (1998) Loss of diversity as a consequence of Habitat Destruction in California Vernal Pools. 119-123 in C.W. Witham, E. T. Bauder, D. Belk, W.R. Ferren, & R. Ornduff ed Ecology, Conservation and Management of Vernal pool Ecosystems – Proceedings from a 1996 Conference, California Native Plant Society, Sacramento, CA.

Kneitel, J.M., & Lessin, C.L. (2010) Ecosystem-phase innteractions: aquatic eutrophication decreases terrestrial plant diversity in California vernal pools. Oecologia, 163(2), 461-469.

Kopp, C. W., & Cleland, E. E. (2013) Shifts in plant species elevational range limits and abundances observed over nearly five decades in a western North America mountain range. Journal of Vegetation Science, 25(1), 135-146.

Kreissman, B. 1991. pg. 81. California: An Environmental Atlas and Guide. Bear Klaw Press, CA.

Lesica, P., & Kittelson, P.M. (2010) Precipitation and temperature are associated with advanced flowering phenology in a semi-arid grassland. Journal of Arid Environments, 74(9), 1013-1017.

Lettis, W.R. 1982. Late Cenozoic stratigraphy and structure of the western margin of the central San Joaquin Valley, California. Report USGS.

Ludecke, D., Bartel, A., Schwemmer, C., Powell, C., Djalovski, A., & Titz, J. (2021) sjPlot: Data Visualization for Statistics in Social Science. R package, version 2.8.10.

Martin, B.D., & Lathrop, E. (1986). Niche Partitioning of Downingia bella and D. cuspidata (Campanulaceae) in the Vernal Pools of the Santa Rosa Plateau Preserve, California. Madrono, 33(4), 284-299.

Marty, J. T. (2005) Effect of cattle grazing on diversity in ephemeral wetlands. Conservation Biology, 19, 1626-1632.

Maurer, E.P. (2007) Uncertainty in hydrologic impacts of climate change in the Sierra Nevada, California, under two emissions scenarios. Climate Change, 82, 309–325.

McLaughlin, B., Ackerly, D. D., Klos, P. Z., Natali, J., Dawson, T. E., & Thompson, S. E. (2017) Hydrologic refugia, plants, and climate change. Global Change Biology, 23(8), 2941-2961.

Mooney, H. A., & Parsons, D. J. (1973) Structure and function in the California chaparral – an example from San Dimas, In F. di Castri and H. A. Mooney [ed.] Mediterranean type ecosystems, origin and structure. Springer-Verlag Heidelberg.

Munguı´a-Rosas, M., Ollerton, J., Parra-Tabla, V., & De-Nova, J. (2011) Meta-analysis of phenotypic selection on flowering phenology suggests that early flowering plants are favoured. Ecology Letters, 14, 511–521.

Munson, S. M., & Long, A. L. (2016) Climate drives shifts in grass reproductive phenology across the western USA. New Phytologist, 213(4). 1945-1955.

Nyunt, S., Grabe, D.F. (1987) Induction of secondary dormancy in seeds of meadowfoam (Limnanthes alba Benth.). Journal of Seed Technology 11(2), 103-110.

Primack, D., Imbres, C., Primack, R.B., Miller-Rushing, A.J., & Del Tredici, P. (2004) Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. American Journal of Botany, 91, 1260–1264.

Purdy, R.H., & Craig, C.D. (1987) Meadowfoam: new source of long-chain fatty acids. American Oil Chemical Society, 64(11), 1493-1494, 1496-1497.

Rains, M.C., Dahlgren, R. A., Fogg, G. E., Harter, T., & Williamson, R. J. (2008). Geological Control of Physical and Chemical Hydrology in Vernal Pools, Central Valley, California. Wetlands, 28, 347-362.

Rathcke, B., & Lacey, E.P. (1985) Phenological patterns of terrestrial plants. Annual Review of Ecology and Systematics, 16, 179-214.

Robertson, C. (1895) The philosophy of flower seasons, and the phaenological relations of the entomophilous flora and the anthophilous insect fauna. American Naturalist 29:97–117.

Shin, H.R., Kneitel, J.M. (2019). Warming interacts with inundation timing to influence the species composition of California vernal pool communities. Hydrobiologia, 843, 93-105.

Smith, V.H., & Schindler, D.W. (2009) Eutrophication science: where do we go from here? Trends Ecology and Evolution, 24, 24, 201–207.

Smith, V.H., Tilman, G.D., & Nekola, J.C. (1999) Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environmental Pollution, 100, 179-196.

Stewart, I.T., Cayan, D.R., & Dettinger, M.D. (2004) Changes in snowmelt runoff timing in western North America under a “business as usual” climate change scenario. Climate Change, 62(1-3), 217-232.

Stucky, B.J., Guralnick, R., Deck, J., Denny, E.G., Bolmgren, K., & Walls, R. (2018). The plant phenology ontology: A new informatics resource for large-scale integration of plant phenology data. Frontiers Plant Science, 9(517).

Smith D.W., & Verrill, W.L. (1998) Vernal pool-soil-landform relationships in the Central Valley, California. In: Witham CW, Bauder ET, Belk D, Ferren Jr WR, OrnduffR (eds) Ecology, conservation, and management ofv ernal pool ecosystems. proceedings from a 1996 conference. California Native Plant Society, Sacramento, pp. 15–23.

Solomeshch, A.I., Barbour, M.G., & Holland, R.F. (2007) Vernal pools. In: Barbour MG, Keeler-Wolf T, Schoenherr AA (eds) Terrestrial vegetation of California. University of California Press, Berkeley, pp. 394–424.

Thien (1979) A flow diagram for teaching texture-by-feel analysis. Journal of Agronomic Education, 8, 54-55.

Wallis de Vries, M.F., & Schippers, P. (1994) Foraging in a landscape mosaic: selection for energy and minerals in free-ranging cattle. Oecologia ,100, 107–117.

Walls, R.L., Deck, J., Guralnick, R., Baskauf, S., Beaman, R., & Blum, S. (2014). Semantics in support of biodiversity knowledge discovery: an introduction to the Biological Collections Ontology and related ontologies. PLOS One, 9.

Walter, H. (1979). Vegetation of the earth and ecological systems of the geo-biosphere. 2nd Edition. Springer-Verlag, New York.

Warner, R. E., & Hendrix, K. M. ed (1984) California Riparian Systems: Ecology, Conservation, and Productive Management. Berkeley, University of California Press.

Wigge, P.A., Kim, M.C., Jaeger, K.E., Busch, W., Schmid, M., Lohmann, J.U., & Weigel, D. (2005). Integration of spatial and temporal information during floral induction in Arabidopsis. Science, 309(5737), 1056-1059.

Wiggins, G. B., Mackay, R. J., & Smith, I. M. (1980) Evolutionary and ecological strategies of animals in annual temporary pools. Archiv fur Hydrobiologie, Supplement ,58: 97–206

Wolf, A.A., Zavaleta, E.S., & Selmants, P.C. (2017) Flowering phenology shifts in response to biodiversity loss. PNAS, 114(13), 3463-3468.

Yost, J.M., Sweeney, P.W., Gilbert, E., Nelson, G., Guralnick, R., Gallinat, A.S., Ellwood, E.R., Rossington, N., Willis, C.G, Blum, S.D., Walls, R.L., Haston, E.M., Denslow, M.W., Zohner, C.M., Morris, A.B., Stucky, B.J., Carter, R., Baxter, D.G., Blomgren, K., Denny, E.G., Dean, E., Pearson, K.D., Davis, C.C., Mishler, B.D., Soltis, P.S., & Mazer, S.J. (2017) Digitization protocol for scoring reproductive phenology from herbarium specimens of seed plants. Applications in Plant Sciences, 6(2).

Zedler, P.H. (1984) Micro-distribution of vernal pool plants of the Kearny mesa, San Diego County. In: Jain S, Moyle P (eds) Vernal pools and intermittent streams. Institute of Ecology Publication No. 28. University of California, Davis, pp. 185–197.

Zedler, P.H. (1987) The ecology of southern California vernal pools: a community profile. US. Fish Wildlife Service.

Chapter 2: Invasion and Climate Stress Gradients along Zones of Vegetation in Vernal Pool Habitats

Abstract:

The slope of a vernal pool is marked by both inundation and soil texture gradients that promote the stratification of plant communities. The assemblage of plants that occupy a similar zone are likely to respond to environmental conditions similarly, however, this has not been explicitly tested. Over a three-year period, the plant community that emerged along abiotic gradients was recorded and monitored for interannual responses to climate and invasion. We confirmed three distinct zones of vegetation based on flowering occurrences during spring floristic censuses: the upland community, the edge community, and the bottom community. The upland community is dominated by non-native grasses that are negatively associated with native biodiversity. Non-native species are largely absent from the pool bottom, and when present, are not associated with any reduction in native biodiversity. On the other hand, we find that contemporary drought is associated with advanced flowering of vernal pool bottom communities only. The zone-specific associations with invasion and climate variation suggest nuanced conservation strategies for different plant groups within a vernal pool.

INTRODUCTION

Vernal pools are pond-like depressions dispersed throughout Mediterranean-climate regions of California that cyclically fill with water and gradually dry through evaporation (Keeley & Zedler 1998; Smith and Verrill 1998; Deil 2005; Solomeshsch et al 2007). As water fills and evaporates, an inundation gradient is established along the slope of a pool. Inundation acts as an abiotic filter excluding invasive plant species while being beneficial for semi-aquatic plants further in the pool (Keeley & Zedler 1998; Gerhardt & Collinge 2007). Groups of species with similar adaptations to inundation and soil texture promotes fine grained spatiotemporal community distributions along the microtopographic elevation gradient of a pool, presenting as zones of vegetation (Bliss and Zedler 1998; Bauder 2000; Emery et al. 2009) (Fig. 1). The community of pool bottom species that require long inundation periods may respond differently to lower seasonal precipitation than plants in the upland, though no study has examined this effect. In addition, the assemblage of species that compose a distinct zone of vegetation are highly variable between vernal pool regions of California (Bauder 2000, Barbour et al. 2007). As such, the number of invasive species in distinct zones of vegetation are different between Southern, Northern, Coastal and Valley regions of California. Conservation of vernal pool species requires the identification of species and assessment of climate change and invasion risk to native species. The goal of this study is to preliminarily identify the plant communities composing different zones of vegetation on the recently established UC Merced Vernal Pools and Grassland Reserve (MVPGR) and determine the climate and invasion risk to each zone to help develop conservation strategies.

The distribution of invasive species abundance is low at the pool bottom, moderately suppressed along pool edges and highest in the surrounding grassland

(Holland and Jain 1981; Ferren et al 1998; Pollak and Kan 1998; Bauder 2000). The upland plant community is dominated by invasive grasses (Holland & Jain 1988; Bauder 2000), whereas communities at the pool edge and bottom are primarily composed of highly specialized endemic wildflower species, many of which are federally listed as endangered or threatened species (Holland & Jain 1981; Zedler 2003; Emery et al. 2009; Faist & Collinge 2015). Consequently, native species at the pool bottom are generally insulated from direct competition with introduced species (Gerhardt & Collinge 2003, 2007; Barbour et al. 2007). Invasive grasses restricted to the upland region deposit a dense mat of thatch that suppresses light, alters fire severity and disrupts the hydrologic regime (Evans and Young 1970; Barry 1995; Davies and Nafus 2013), which can then directly and indirectly interfere with growth of plants in the vernal pool edge and bottom communities. In addition, invasive species pose a direct threat to native biodiversity in the upland grassland (Harrison et al. 2001) and means to manage invasion include the use of low intensity cattle grazing (Evans and Young 1970; Barry 1995), which can release native plants from competition with exotic species (Dole 1988; Barry 1998; Marty 2005). Nevertheless, the current richness of non-native species on MVPGR is not currently known, and the interannual and within pool dynamics of non-native species have not been described.

Over the last 30 years, a large percentage of angiosperm species spanning every major biome has advanced its flowering time relative to historic averages (Abu-Asab et al. 2001; Cayan et al. 2001; Fitter & Fitter 2002; Primack et al. 2004; Miller-Rushing et al. 2007), with the largest shifts occurring for spring wildflowers native to temperate zone habitats. Rising winter and spring temperatures (Cayan et al. 2009) and shorter spring seasons (Bradshaw & Holzapfel 2006) have been implicated as causal factors driving the observed trends. The phenology of vernal pool specialists occupying the pool bottom is driven by precipitation (Chapter 1), whereas phenological responses of Mediterranean grasses are more diverse (Cleland et al. 2006). Both vernal pool associates and vernal pool obligates have flowered significantly earlier (~8 days/year) in response to lower precipitation and warmer-than-average temperature (Chapter 1). In addition, invasive and native grasses in grassland habitats show a slower response to recent warming trends, suggesting the magnitude of phenological advancement is variable across zones of vegetation within a Mediterranean climate vernal pool. The temporal structure between zones of vegetation, and the environmental covariates driving interannual variation of bloom dates exhibited across zones, are not currently known.

In this study I ask three questions, 1. Do plant communities along inundation and clay gradients significantly differ in species richness, similarity and degree of invasion?, 2. Do non-native species negatively impact native biodiversity throughout different zones of the vernal pool, 3. Do plant communities within vernal pool basins respond phenologically to reduced precipitation and warming, and is this zone-dependent? The findings of this observational report are intended to motivate targeted research and conservation of specific zones.

METHODS

Study Site:

The site chosen for the study is the 6,500-acre UC Merced Vernal Pools and Grassland Reserve (MVPGR) located next to the University of California, Merced campus and affiliated with the University of California Natural Reserve System. Along the western base of the Sierra Nevada, the MVPGR is situated on an annually flooded alluvial terrace landscape containing several hundred vernal pools. Oscillating cycles of erosion and uplift has resulted in a rich diversity of topographic features and soil outcrops throughout the reserve (Harden 1987; Howard 1979). Major soil series present on the reserve are Corning and Redding, and outcrop ages range from Late Cenozoic to Pleistocene (Marchand & Allwardt 1981). Hundreds of vernal pool and grassland plant species, 83 bird species, 13 mammal species, and 6 shrimp species are found on the UC Merced reserve (https://vernalpools.ucmerced.edu/). Three vernal pools were selected for long-term ecological observations of interannual biodiversity trends in response to altered inundation gradients and climatic trends. The pools varied by size, depth, microtopographic variation and soil texture (Table 1). The species observed in the study is the assemblage of flowering plants within and outside of a pool that could be observed between the months of February and May.

Field observations were conducted between the hours of 11am to 2pm, with one hour of species identification for each of the three pools. Observations were conducted by recording all flowering species observed while surveying in a walking, relevé fashion (Westoff & Van Der Maarel 1978). All flowering plants were identified to the species level, and several species-specific characteristics were then compiled from online databases (Calflora, https://www.calflora.org) such as native status, pollination syndrome, flower color, historic flowering dates, and life history. The California Irrigation and Management Information System (CIMIS, https://cimis.water.ca.gov) Station in Merced was used to collect daily and annual temperature, humidity, precipitation, and dew point over the entire study period and water year (October – September). The station is 4 miles south of the reserve. Raw measurements from the CIMIS used in this study were monthly average temperature, monthly average total precipitation, monthly average dew point, daily average temperature and daily average dew point. I designated winter in this study the dates between December 1st to February 28th. Mean winter temperature was calculated by taking the average temperature of December to February. Monthly precipitation was used to calculate accumulated precipitation for the water year (October 1st – September 31st) and the total accumulated winter precipitation (December 1st – February 28th).

Identifying Zones of Vegetation and Species and Recording Phenology:

Within a pool, zones were initially distinguished using hydrologic and edaphic characteristics (Crowe et al. 1994). A small handful of soil was collected every meter along a NS and EW transect spanning a pool. The soil was visually and texturally inspected for the presence of sand grains and silt. The soil was dampened, and clay content was estimated using the ribbon method (Thien 1979). Using both the tactile/visual assessment and the estimated clay content, a soil type was determined (Salley et al. 2018; Richer-de-Forges et al. 2022). The region with highest clay content was designated as the pool bottom. The region with some flooding, but a relatively low clay content was designated as the pool edge. Finally, the region with no observed flooding and low clay content was designated as the upland. The three regions were visually different as well: the pool bottom contained noticeable hoofprints from cattle, the upland had tall grasses, and the edge had small plants on loamy soils.

North-South and East-West transects were laid across the vernal pool, spanning all relevant zones and approximately 2 meters into the upland. The final transect length was recorded, and the positions were marked with a pile of rocks so the transects could be redrawn week after week. First flowering date, end flowering date, and zone of habitation were recorded for all species.

To test for distinct zones of vegetation, Sorenson's index of similarity (SIS) was calculated and compared within and between each zone. 'Within-zone' similarity was compared to 'between-zone' similarity to verify that within zone similarity was higher than between zone similarity (Clausnitzer et al. 2003) and validate the independent inference of zone boundaries. Within zone SIS epresents the average similarity of plant communities found in the same zone, but in different years or different pools. Between zone SIS represents the average similarity of plant communities found in different zones, either in the same pool in a different year or in different pools. For example, the pool bottom 'within-zone' similarity was calculated by taking the community of plants within the pool bottom of a single pool and comparing it to the community of plants within the bottom of a different pool or the community of plants within the same pool for a different year. The mean 'within-zone' similarity was the average of all similarity scores obtained by comparing each pool bottom community to another pool bottom community. 'Between-zone' similarity of the bottom to the edge community, as well as the bottom to the upland community, were calculated by taking the plant community within the bottom of a pool and comparing it to the edge and upland community, respectively. Therefore, there were two 'between-zone' comparisons for the pool bottom, and an average 'bottom to edge' SIS score and an average 'bottom to upland SIS score. The 'within-zone' similarity score of the pool bottom was compared to both 'between-zone' comparisons (ie. bottom-to-edge & bottom-to-upland). The same procedure of SIS calculation is followed for the edge and upland zones.

Biodiversity measurements were limited to a binary, presence-absence detection of species in flower for each week of observation. Alpha diversity of a single zone was reported as the average number of species of that zone across three pools and three years. Annual alpha diversity is the mean number of all species observed in a zone throughout a single sampling season. When calculating alpha diversity for different zones within a pool, each species within a pool was considered "present" only in the zone in which it attained its highest abundance.

The day of first flower for each species was recorded as the first date flowering was detected for that species. For plants with aggregate flowers, the species was recorded as flowering if any number of flowers were open on an inflorescence. A species was considered flowering if at least one individual within a pool was flowering. Species phenology was monitored weekly. Within a zone, day to first flower of all species was used to calculate the mean day of first flower for that ‘zone of vegetation.’

Analysis: Zones of Vegetation

Some species were observed flowering in multiple zones, and in 2019 and 2020, a $1m^2$ quadrat was placed along both NS and EW transects. Abundance of each species was counted and the zone with maximal abundance was recorded. To determine if the collection of species within zones of similar hydrology and clay content constitute a separate ‘zone of vegetation’, I compared the mean ‘within-zone’ SIS score of the upland, edge, and bottom zones with their respective ‘between-zone’ SIS scores using Dunnett’s comparison of means. I held ‘within-zone’ as the control, and then I directly compared the mean ‘within-zone’ SIS score to each mean ‘between-zone’ similarity score. A significantly larger ‘within-zone’ than ‘between zone’ SIS score would indicate that the plant community found in the same zone is quantitatively more similar than to the plant community found in a different zone. This would then mean that each zone initially demarcated by abiotic factors (ie. clay and water concentrations) is also biotically similar.

Analysis: Biodiversity differences between zones and pools

To determine if pools were significantly different regarding species richness, including native and non-native species abundance, I performed one-way ANOVA comparisons between pools. I then conducted all pairwise comparisons between pools using Tukey honest significant difference tests. Statistical tests were conducted using JMP Pro 16.

To determine if different ‘zones of vegetation’ harbor significantly different numbers of native and non-native species, I performed one way ANOVA comparisons between zones. I also compared the alpha diversity between zones using ANOVA. I further performed all pairwise comparisons using Tukey honest significant difference tests. Additionally, I compared the same zone of vegetation between different pools using one-way ANOVA to detect if different pools had significantly different upland, edge, and bottom communities. Statistical tests were conducted using JMP Pro 16.

Analysis: Non-native Plant impact on native species richness within zones

To determine if native species are negatively impacted by non-native species richness regardless of winter climatic conditions, I designed multiple regressions for each zone with native species richness as the response variable and non-native species richness, winter precipitation, and winter temperature as independent predictor variables. There are nine total observations of non-native and native species richness for each zone (3 pools X 3 years). Native species richness per zone was the total number of native species recorded throughout the sampling season within a zone of a single pool. Similarly, non-native species richness is the total number of non-native species recorded throughout a sampling season within a zone of a single pool. Non-native and native species identifies were found using the Calflora database. All multiple regressions were performed using the R version 3.0-13 package {car} (Fox et al. 2022).

Analysis: Phenological associations with climate

Multiple regression models of day of first flowering were created for each zone using average winter temperature and winter precipitation as explanatory variables. The response variable was the mean ‘day of first flower’ for each zone, calculated by averaging the first flowering dates of every species found within a zone per year. Significant covariates were determined using a 95% confidence threshold, and the slope estimate of the model was also calculated. Multiple regression models were produced using the {car} package (Fox et al. 2022) in R version 3.0-13.

RESULTS

Zones of Vegetation:

All species observed throughout the study period are listed in Table 2. A total of 43 flowering species were observed within any of the three pools (33 species in Pool 1; 32 species in Pool 2; and 38 species found in Pool 3). Nine species occupied only one pool out of three, with 6 out of 9 being native species. Ten out of the 12 non-native species observed were found flowering in all three pools, with eight flowering in all three. Annual species make up 77% of the native plants observed, versus 83% of the exotic species and five are non-native grasses. Sorenson’s index of similarity was significantly higher for ‘within-zone’ comparisons of upland, edge, and bottom communities than any ‘between-zone’ comparison (Table 3). This indicates that all zones represent distinctive vegetative communities.

Zone Alpha:

Pools differed significantly in alpha diversity. Alpha diversity was significantly different between Pool 3 (Mean = 29.6) and Pool 2 (Mean = 22) (Tukey HSD: $p = 0.0105$). The average number of non-native species across the three pools was relatively equal (ANOVA: $F = 3.1667$, $p = 0.1151$; Mean Exotic Species Richness: Pool 1 = 8, Pool 2 = 7.25, Pool 3 = 8.75), however, a direct comparison of non-native species richness between pool 2 and 3 was significantly different (Tukey HSD: $p = 0.0465$). Similarly, Pool 3 contained significantly more native species (Mean = 21 native species) than Pool 2 (Mean = 14.33 species; Tukey HSD $p = 0.0061$), but not *significantly* more species than Pool 1 (Mean = 17.33; Tukey HSD $p = 0.0630$).

Average alpha diversity in the upland (Mean = 10.77) was statistically higher than both the edge (Mean = 6.55, Tukey HSD: $p < 0.0001$) and bottom zones (Mean = 6.67, Tukey HSD $p < 0.0001$). The upland regions contained significantly more non-native species (Mean = 7.44) than the pool bottom (Mean = 0.77, Tukey HSD $p < 0.0001$) and edge communities (Mean = 1.22, Tukey HSD: $p < 0.0001$), but there was no statistical difference between zones regarding native species richness (ANOVA: $F = 0.5435$, $p = 0.5877$).

Within the upland region, there was no difference between pools regarding alpha diversity (ANOVA: F = 1.1566, p = 0.3762, df = 2), native species richness (ANOVA: F = 3, p = 0.125, df = 2), or non-native species richness (ANOVA: F = 0.4062, p = 0.6832, df = 2). Similarly, pool bottom communities did not differ in alpha diversity (ANOVA: F = 2.25, p = 0.1866, df = 2), native species richness (ANOVA: F = 3.125, p = 0.1175, df = 2), and non-native species richness (ANOVA: F = 2.33, p = 0.178, df = 2). In contrast to the upland and pool bottom regions, the edge zone of Pool 3 contained significantly more species (Mean = 7.66) than both Pool 1 (Mean = 6, Tukey HSD: p = 0.022) and Pool 2 (Mean = 6, Tukey HSD: p = 0.022). This is because the number of non-native species in the upland of Pool 3 was significantly higher (Mean = 2) than either Pool 1 (Mean = 0.66, Tukey HSD: p = 0.0027) or Pool 2 (Mean = 1, Tukey HSD: p = 0.0104), whereas and richness of native species occupying the edge was similar across pools (ANOVA: F = 1.5, p = 0.2963). All zones of vegetation did not exhibit any annual increase or decrease to native and non-native species, proportion of non-native species, or average annual alpha diversity.

Exotic Species Associations with Native Plant Richness Across Zones:

Native biodiversity, measured as native species richness, was significantly correlated with the proportion of non-native species in the upland (slope = -14.23, std error = 0.93, p = 0.0001; Table 4), but not in the edge or bottom zones. Additionally, the number of non-native species was negatively associated with native richness in the upland (slope = -1.17; std error = 0.22, p = 0.007; Table 5, Fig 2). Native species richness was not correlated with non-native species richness in either the pool edge or bottom zones when controlling for winter temperature and precipitation (Table 6).

Floral Phenology Across Zones and Environmental Covariates:

The average first flowering dates of thirty-three species that were observed for more than one year varied across species (Fig. 3). First flowering dates of plant communities were significantly different between zones (ANOVA: F = 5.6446, p = 0.0041, df = 2), with the bottom community flowering earliest (Mean = 73.15), followed by the edge (Mean = 75.44) and upland communities (Mean = 83.91).

Floral phenology of bottom communities was significantly advanced in response to reduced precipitation (slope = 0.38, std error = 0.15, p = 0.016; Table 6), and edge plants also express a similar advancement in response to precipitation patterns (slope = 0.26, std error = 0.17, p = 0.128; Table 6). Upland species exhibit no significant phenological response to either winter precipitation or winter temperature (Table 6).

DISCUSSION

The goals of this project were to identify the flowering species that compose zones of vegetation on the UC Merced Vernal Pools and Grassland Reserve (MVPGR). In addition, I set out to quantify the associations of climate on phenology and invasion on native biodiversity across zones of vegetation. The response or lack of response of each zone of vegetation to invasion and climate highlights the necessity for zone specific strategies to preserving vernal pool landscapes.

I find that community diversity is hypervariable between pools, yet relatively stable between years and zones. Between pool differences can arise because of priority effects, abiotic filtering or dispersal limitation, and Collinge & Ray (2009) found evidence for all three. Other studies find that the distribution of species within pools parallels several gradients – inundation length, salinity, soil texture, soil conductivity, etc. (Linhart 1976; Holland & Jain 1988; Holland & Dains 1990; Bliss & Zedler 1997)– indicating that local adaptation to abiotic conditions may be key for establishing community structure within and between pools (Gosejohan et al 2017). I find that alpha diversity did not exhibit any response to climate factors, suggesting that annual variation of community composition and plant diversity is driven largely by local, within pool abiotic dynamics. Additionally, Faist & Collinge (2015) discovered that a species' seedbank coincides with above ground sporophyte distributions. In a separate study, Faist et al. (2013) found that the above ground community does change, though the storage effects exhibited by the seed bank acts a reservoir for native and rare species. These findings taken together potentially explain the low variability of species composition within zones of a pool over several years. Currently, no studies have examined the zonal dependence of dispersal limitation, storage effects, and priority effects in establishing stratified plant communities. If limitations to species establishment exists at the resolution of zones, conservational efforts to restore vernal pools may require assisted migration and plant removal programs to aid some sensitive plant species into their preferred microhabitat.

Exotic species are not normally competitive with native species or disruptive to abiotic and biotic cycles when introduced to a new range (Richardson et al. 2000; Hettinger 2001; Blackburn et al. 2011), and only 1% - 10% become invasive (di Castri 1989; Williamson and Fitter 1996). In certain contexts, invasive animals and plants can provide ecosystem services not initially present in the new range (Schlaepfer et al. 2011; Bertness & Coverdale 2013). However, with some exceptions, species introduced to vernal pool habitats are high biomass grasses unpalatable to grazing livestock that deposit dense thatch layers known to interfere with hydrology (Facelli & Pickett 1991), fire severity, and native species growth. I find that these non-native species are concentrated in the upland habitat. The zonal distribution of non-native species in this study supports the sporophyte (Holland & Jain 1988; Bauder 2000) and seed bank distribution (Faist & Collinge 2015) of non-native species of prior observations which has been attributed to the inundation gradient within pools (Faist & Collinge 2015). The species of most concern on the MVPGR are *Taeniatherum caput-medusae*, *Festuca perennis*, *Bromus hordeaceus*, *Bromus diandrus*, and *Aegilops triuncialis*. While the species are harmful to native biodiversity and thus invasive, several exotic species are naturalized and/or poor competitors, such as *Festuca octoflora*, *Aira caryophyllea*, and *Briza minor*. Many of the non-native plants observed throughout the study period were found occupying every pool, suggesting a wide distribution throughout the upland and high dispersal rates. Introduced species' ranges throughout the United States are increasing by 700,00 ha per year (Babbitt 1998), with many non-native species on the MVPGR having high dispersal rates (Erodium: Stamp 1989; Medusa Head: Davies 2008; Foxtail Barley: Cords 1960). While there is no current comparison of dispersal rate amongst vernal pool species, non-native plants in other habitats often exhibit far larger dispersal kernels than native species (Kota 2005; Sperry et al. 2021). Such noxious plants with high dispersal rates and low herbivory pressure by cattle creates a challenging situation for conservation managers to effectively control invasion within vernal pool habitats.

My observational investigation of non-native species on the MVPGR, along with several other observational and experimental studies, has found negative correlations of non-native species on native species richness in the grassland zone of vernal pool habitats (Gerhardt & Collinge 2003; Marty 2005). On the other hand, edge and bottom communities were found to be unaffected by non-native species presence and richness. However, without abundance observations and transplant experiments, the direct and indirect consequences of non-native plant species cannot be determined. Additionally, this is currently a regularly grazed ecosystem, which may heavily influence native-non-native interactions (Marty 2005). There is evidence in vernal pool environments that abiotic constraints, not negative interspecific interactions, limit the invasibility of highly flooded pool bottoms by exotic grasses (Gerhardt & Collinge 2007). Additionally, priority effects within vernal pools are modulated by abiotic gradients (Collinge & Ray 2009), highlighting how the abiotic context of vernal pool environments is determinant of biotic interactions and invasibility. While edge and bottom plant communities appear unaffected by non-native plant species, lower annual precipitation, and thus lower inundation, can lift the abiotic constraint currently limiting invasion into pool edges and bottoms. Rising temperatures in the Central Valley (Dettinger & Cayan 1995; Stewart et al. 2004) paired with unchanging or reduced precipitation (Stewart et al. 2004; Maurer 2007) can lead to earlier drying of vernal pool substrate (Berghuijs et al. 2014). More recent investigations of climate impacts on pool hydrology show that inundation period is shorter, resulting in a decline of vernal pool specialists (Montrone et al. 2019). Loss of native species biodiversity can cause a reduction and loss of ecosystem services (Cardinale et al. 2012; Delgado-Baquerizo et al. 2015). This poses a problem for the conservation of grassland natives and vernal pool habitats in the future.

Species richness did not exhibit any significant annual change in response to climate, however, the timing of species emergence and phenological patterns were strongly influenced by winter temperature and precipitation. Phenological advancement of spring blooming wildflowers has been observed in semi-arid grasslands (Lesica & Kittelson 2010: 32 species, Mean Advancement 0.61days/year), humid temperate forests (Abu-Asab et al. 2001: 89 species, range of advancement -3.2 to -46 days over 30 years), and temperate forests (Miller-Rushing & Primack 2008: 33 species, Mean advancement of 2.93 days per 1 C rise, and). Few studies have found a significant correlation of first flowering dates with changing annual precipitation (Sparks & Carey 1995; Thorhallsdottir 1998; Abu-Asab et al. 2001), with the exception of 9 semi-arid wildflower species that exhibited significant advancement with declining December plus January precipitation (Lesica & Kittelson 2010). I found that the mean day to first flower of the entire plant community was advanced by approximately 8 days when accumulated winter precipitation dropped from 350mm to 200mm. Specific to vernal pool habitats, water supply is a major determinant of community structure, and our findings suggest that zones of vegetation express phenological shifts in response to water supply. In this study, pool bottom and edge plant communities have been observed flowering 11 days earlier in response to a decrease of 150mm winter precipitation, whereas upland species are observed flowering later by a mean of 1 day. Our results suggest the possibility that upland plant wildflowers and those occupying the vernal pool basin respond uniquely to precipitation patterns, with vernal pool specialists exhibiting high interannual phenological variability in correspondence with unpredictable precipitation events.

There are several limitations of the current study that restrict the resolution of the findings. First, the study findings are observational, rather than mechanistic. There were no controls on temperature or invasion, such as artificial heating or non-native species removal. Consequently, the findings of community phenology and biodiversity are associations with recorded climate and species observations. Experimental manipulations will be required to determine the causal abiotic factors driving phenology of bottom plants and biotic factors reducing native biodiversity in the upland community. The second limitation is that there were no transplant experiments. The response of each species to invasion and climate could not be teased apart. Nevertheless, findings of the current study highlight the importance of considering different zones of vegetation as distinct units that respond uniquely to climate and invasion, however, more research will be required to determine how best to preserve each species within its community.

TABLES

Table 2.1 Characteristics of three focal pools on the MVPGR. Indicated are the over circular size (Size) and the maximum depth of water recorded for each pool (Depth). Also indicated are characteristics of the three zones within each pool: a measure of soil wetness (Mean Ribbon Length), soil texture, and the average percent of the north-south and east-west transect that covers the pool bottom and edge (Percent of Pool).

Pool	*Size (m^2)*	*Depth (m)*	*Zone*	*Mean Ribbon Length (mm)*	*Soil Texture*	*Percent of Pool*
1	843	0.47m				
			Upland	15	SL	
			Edge	22	LSCL	26.29%
			Bottom	82	MC	74%
2	372	0.24m				
			Upland	17	SL	
			Edge	27	SCL	34.73%
			Bottom	76	LMC	65.27%
3	871	0.31m				
			Upland	20	L	
			Edge	38	CL	15.28%
			Bottom	73	LMC	84.72%

Table 2.2 All flowering species observed during the sampling season (February – May). The common name, genus and species name are provided alongside the historical range of each species' bloom dates. The range of zones each species occupies is provided (Zone Range), as well as the zone with highest observed abundance (Zone). Native status and life history are also displayed. Historic bloom dates, life history and native status were collected from Calflora.
L = Pool bottom, M = pool edge, U = pool upland.
N = native & I = invasive
P = perennial & A = annual

Zone	*Zone Range*	*Common Name*	*Genus*	*Species*	*Calflora (Beginning - End)*	*N/I*	*P/A*
M	M - L	Alkali Checkerbloom	Sidalcea	hirsuta	A-My	N	A
U	U - M	Blow Wives	Achyrachaena	mollis	A-My	N	A
U	U	Bluedicks	Dichelostemma	capitatum	F-A	N	P
L	M - L	Brass Buttons	Cotula	coronopifolia	My-O	I	P
M	U - M	Butter & Eggs	Triphysaria	eriantha	F-A	N	A
U	U	California Poppy	Eschscholzia	californica	F-S	N	A
M	U - M	Common Groundsel	Senecio	vulgaris	J-D	I	A
L	L	Coyote-thistle	Eryngium	aristulatum	J-S	N	P
U	U	Cut-leaf Filaree	Erodium	cicutarium	F-J	I	A
M	U - M	Dwarf Sack Clover	Trifolium	depauperatum	F-My	N	A
U	U	Fiddleneck	Amsinckia	mensiesii	M-My	N	A

Table 2.2 cont.

Zone	*Zone Range*	*Common Name*	*Genera*	*Species*	*Calflora (Beginning - End)*	*N/I*	*P/A*
U	U - L	Filaree	Erodium	botrys	F-My	I	A
L	L	Fringed Downingia	Downingia	concolor	M-Jy	N	A
U	U	Frying Pan Poppy	Eschscholiza	lobbii	M-J	N	A
L	L	Hogwallow Starfish	Hesperevax	caulescens	A-J	N	A
U	U	Italian Ryegrass	Festuca	perennis	My-S	I	P
M	U - M	Little Quacking Grass	Briza	minor	A-Jy	I	A
L	L	Little Spikerush	Eleocharis	macrostachya	My-J	N	P
U	U	Meadow Barley	Hordeum	brachyantherum	J-Jy	N	P
L	L	Meadow Foxtail	Alopecurus	saccatus	A-Jy	N	A
L	M - L	Meadowfoam	Limnanthes	douglasii	M-Jy	N	A
U	U	Muilla	Muilla	maritima	M-J	N	P
U	U - M	Purple Sanicle	Sanicula	bipinnatifida	M-My	N	P
U	U	Red Maids	Calandrinia	ciliata	F-My	N	A

Table 2.2 cont.

Zone	*Zone Range*	*Common Name*	*Genera*	*Species*	*Calflora (Beginning - End)*	*N/I*	*P/A*
L	L	Round Wooly Marbles	Psilocarphus	chilensis	M-Jy	N	A
U	U	Rusty Haired Popcornflower	Plagiobothrys	nothofulvus	F-A	N	A
L	L	Sacromento Beardstyle	Pogogyne	zizyphoroides	M-J	N	A
U	U	Shepherd's Purse	Capsella	bursa-pastoris	J-D	I	A
U	U - M	Shinning Peppergrass	Lepidium	nitidum	F-My	N	A
U	U	Six Week Fescue	Vulpia	bromoides	-	I	A
L	M - L	Small Popcorn Flower	Plagiobothrys	humistratus	F-M	N	A
U	U	Smallhead Clover	Trifolium	microcephalum	A-J	N	A
U	U - M	Smooth Cat's Ear	Hypochaeris	glabra	M-My	I	A
U	U - M	Soft Chess Brome	Bromus	hordeaceus	A-M	I	A
L	L	Tricolor Monkeyflower	Mimulus	tricolor	J-Jy	N	P
M	U - M	Valley Tassels	Castilleja	attenuata	M-My	N	A

Table 2.2 cont.

Zone	*Zone Range*	*Common Name*	*Genera*	*Species*	*Calflora (Beginning - End)*	*N/I*	*P/A*
L	M - L	Vernal Pool Goldfields	Lastenia	fremontii	A-My	N	A
M	M - L	Vernal Pool Hairgrass	Deschampsia	danthonioides	M-J	N	A
M	M	White Dwarf Sack	Trifolium	depauperatum	M-My	N	A
U	U	White Hyacinth	Triteleia	hyacinthina	A-My	N	P
L	U - L	White Tipped Clover	Trifolium	variegatum	M-Jy	N	A
U	U	White-stem Filaree	Erodium	moschatum	F-My	I	A
U	U	Wild Oats	Avena	fatua	A-My	I	A

Table 2.3 Mean Sorenson's index of similarity (SIS) of each zone. A mean value of 1 indicates complete species similarity of two communities, whereas a mean value of 0 indicates that there are no common species among the two communities being compared. Zone comparisons were within zone (ex. Bottom to Bottom) or between zones (ex. Bottom to Edge). The p-value from Dunnett's means tests is reported.

Zone Group	*Zone Comparisons*	*Mean SIS*	*Comparison of Means LSD Threshold p-value*
Bottom	Bottom to Bottom	0.85	
	Bottom to Edge	0.47	< 0.0001
	Bottom to Upland	0.09	< 0.0001
Edge	Edge to Edge	0.83	
	Edge to Bottom	0.47	< 0.0001
	Edge to Upland	0.55	< 0.0001
Upland	Upland to Upland	0.77	
	Upland to Edge	0.55	< 0.0001
	Upland to Bottom	0.09	< 0.0001

Table 2.4 Multiple regressions of the total native species richness of each zone by non-native species richness, average winter temperature, and winter precipitation. Observations refer to the number of replications of each zone across 3 pools and 3 years (3 X 3 = 9). There are three models shown with identical predictor variables; non-native species richness, average winter temperature, and winter precipitation. There is one model for the bottom, one model for the edge and one model for the upland. For each model, the fitted estimate and the p-value of the predictor is indicated. Significant variables (p<0.05) are bolded. Overall model statistics are shown at the bottom: the sample size (Observations, typically n=9 due to 3 years of observations across 3 pools) and the overall R^2 and adjusted R^2 for the model.

	Bottom Native Species Richness		**Edge Native Species Richness**		**Upland Native Species Richness**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
(Intercept)	-4.34	0.889	3.87	0.705	6.33	0.763
Non-native species richness	-0.62	0.526	0.40	0.235	-1.17	**0.007**
Average Winter Temp	1.26	0.686	0.07	0.943	0.53	0.806
Winter Precipitation	0.00	0.958	0.00	0.849	0.02	0.524
Observations	9		9		9	
R^2 / R^2 adjusted	0.188 / -0.300		0.267 / -0.173		0.850 / 0.760	

Table 2.5 Multiple regressions of the total native species richness of each zone by proportion of non-native species, average winter temperature, and winter precipitation. Observations refer to the number of replications of each zone across 3 pools and 3 years (3 X 3 = 9). There are three models shown with identical predictor variables; proportion of non-native species, average winter temperature, and winter precipitation. There is one model for the bottom, one model for the edge and one model for the upland. For each model, the fitted estimate and the p-value of the predictor is indicated. Significant variables ($p<0.05$) are bolded. Overall model statistics are shown at the bottom: the sample size (Observations, typically n=9 due to 3 years of observations across 3 pools) and the overall R^2 and adjusted R^2 for the model.

	Bottom Native Species Richness		**Edge Native Species Richness**		**Upland Native Species Richness**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
(Intercept)	-8.22	0.767	4.15	0.710	4.55	0.537
Proportion Non-native Species	-6.84	0.257	2.28	0.433	-14.11	**<0.001**
Average Winter Temperature	1.68	0.546	0.05	0.963	0.78	0.316
Winter Precipitation	0.01	0.849	0.00	0.876	0.02	0.151
Observations	9		9		9	
R^2 / R^2 adjusted	0.332 / -0.070		0.127 / -0.397		0.981 / 0.970	

Table 2.6 Multiple regressions of the observed start date by proportion of non-native species, average winter temperature, and winter precipitation by zone. Observations refers to the total number first flowering dates observed from all species found within a zone between 2019-2021There are three models shown with identical predictor variables; proportion of non-native species, average winter temperature, and winter precipitation. There is one model for the bottom, one model for the edge and one model for the upland. For each model, the fitted estimate and the p-value of the predictor is indicated. Significant variables ($p<0.05$) are bolded. Overall model statistics are shown at the bottom: the sample size (Observations, typically n=9 due to 3 years of observations across 3 pools) and the overall R^2 and adjusted R^2 for the model.

	Bottom Observed Start Bloom		**Edge Observed Start Bloom**		**Upland Observed Start Bloom**	
Predictors	*Estimate*	*p*	*Estimate*	*p*	*Estimate*	*p*
(Intercept)	-166.89	0.180	-70.89	0.586	-10.43	0.911
Proportion of Non-native Species	-37.29	0.127	22.86	0.486	-12.13	0.326
Average Winter Temp	22.13	0.072	12.18	0.335	10.47	0.264
Winter Precipitation	0.38	**0.016**	0.26	0.128	0.09	0.492
Observations	73		49		90	
R^2 / R^2 adjusted	0.147 / 0.110		0.076 / 0.014		0.030 / -0.004	

FIGURES

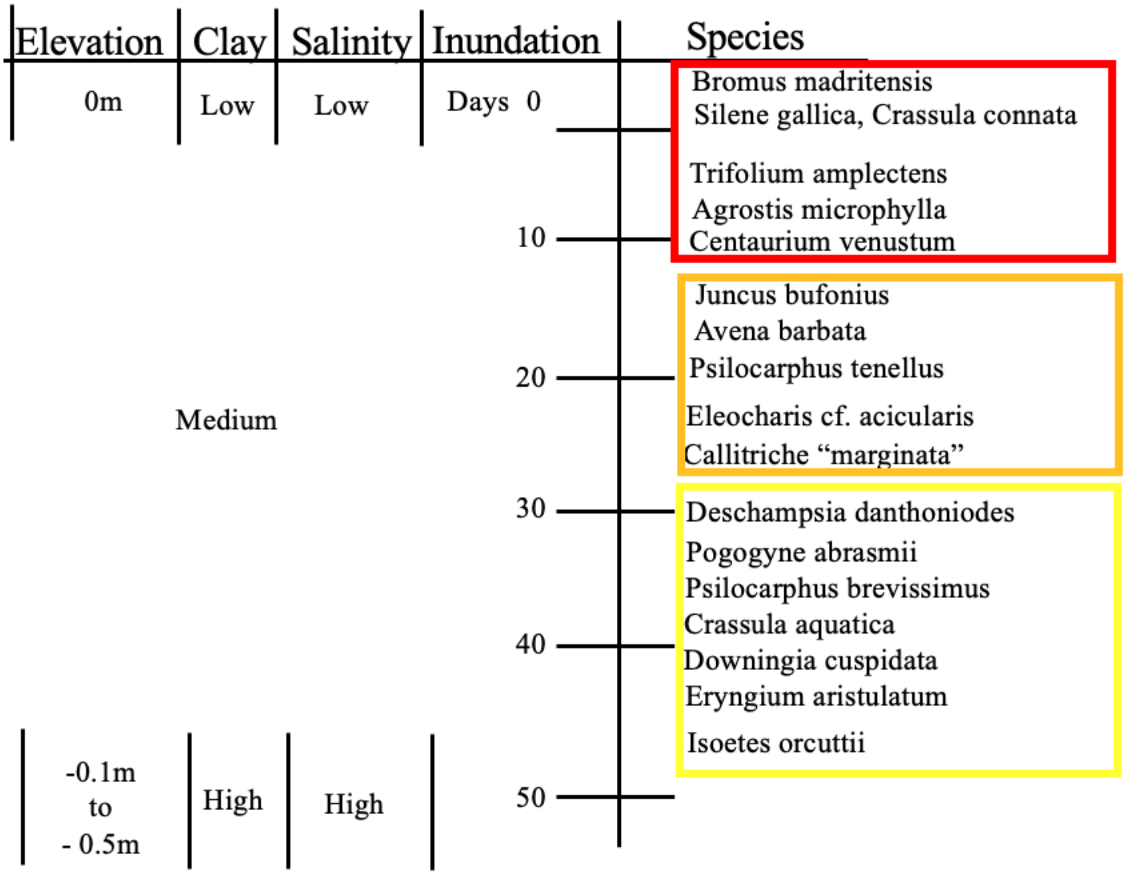


Figure 2.1 Vernal pool species that emerge along the inundation gradient of a vernal pool, which parallels a gradient of elevation, clay and salinity. The species are described in Keeley and Zedler 1998, and inspiration of the plant communities comes from Gosejohan et al. 2017. Plant communities are subdivided by low inundation (red), medium inundation (orange) and long inundation periods (yellow). The elevation starts at 0m, which corresponds to the upland. The pool depth can range from -0.1 meters from the upland to -0.5 meters from the upland. Clay concentration of soil is low in the upland region and increases deeper into the pool. As water evaporates the salinity rises, and thus deeper sections of the pool have higher salinity.

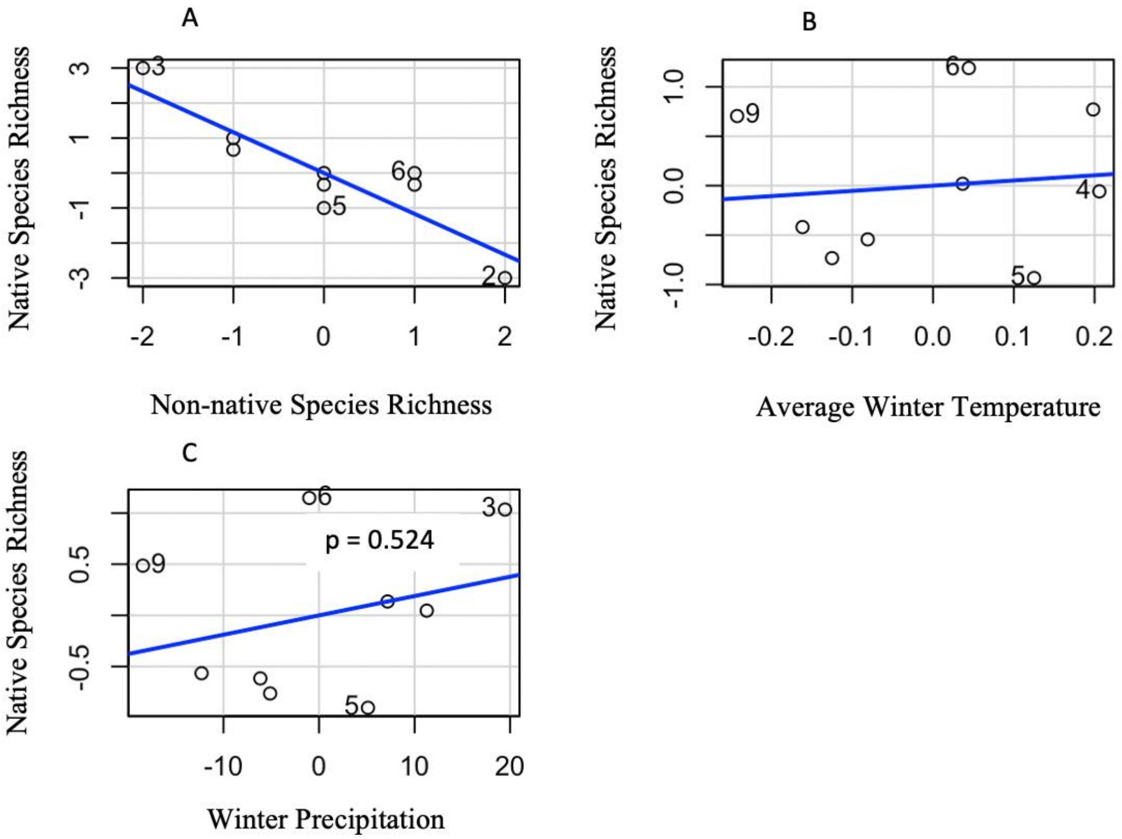


Figure 2.2 Partial regression plots depicting the residuals of native species found in the upland by three predictor variables used in a multiple regression: (A) invasive species richness (slope = -1.17, p = 0.007), (B) average winter temperature (slope = 0.53, p = 0.81), and (C) winter precipitation (slope = 0.02, p = 0.52).

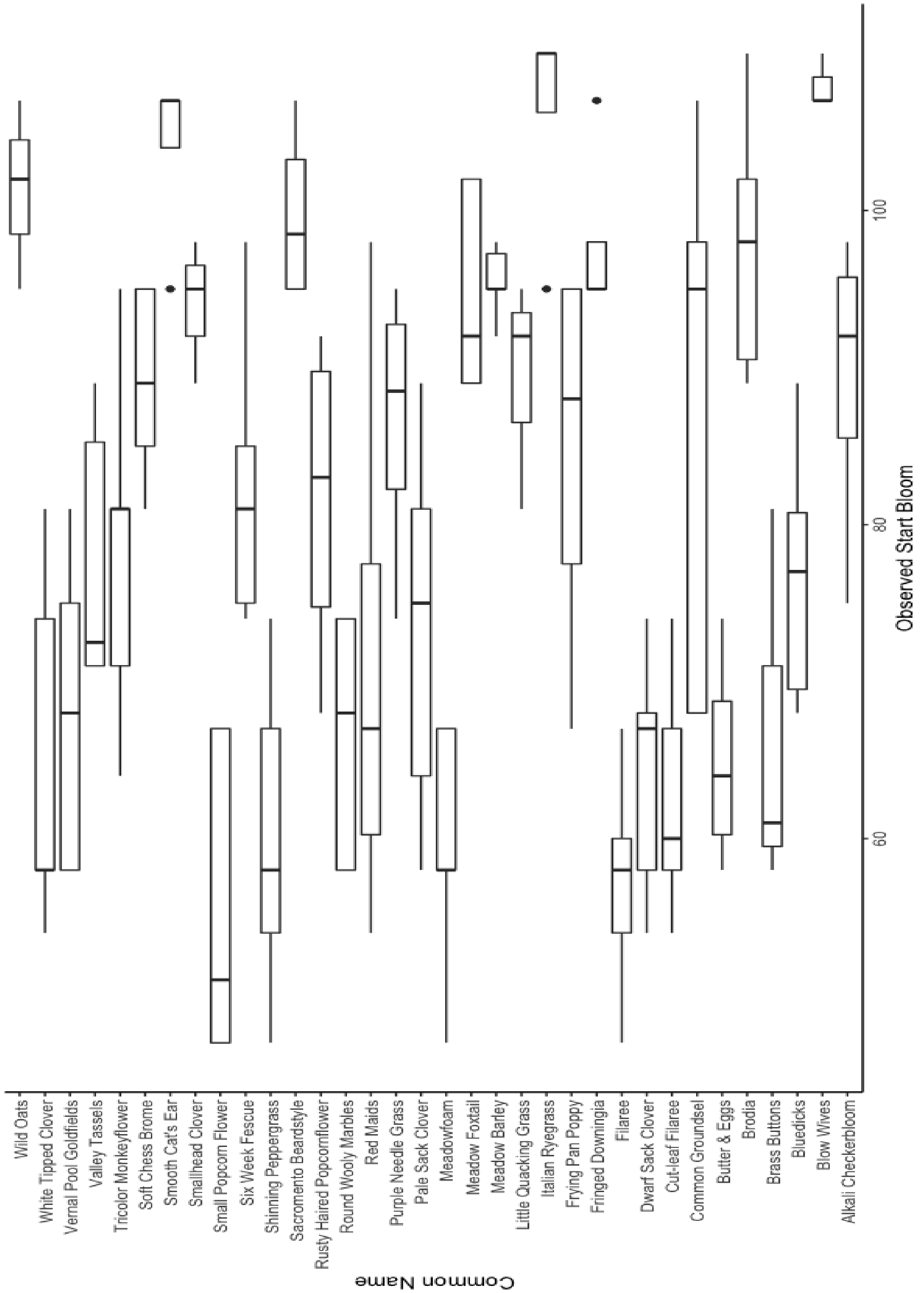


Figure 2.3 Horizontal boxplots of each species' first flowering dates from three pool across three years. Each species was not recorded flowering in all years or pools, and thus the number of observations varies by species. The observed start date is measured from 1 to 365, starting on January 1st. The bars represent the interquartile range of first flowering dates of each species.

LITERATURE CITED

Abu-Asab, M., Peterson, P.M., Shetler, S.G., & Orli, S. S (2001) Earlier plant flowering in spring as a response to global warming in the Washington, DC, area. Biodiversity and conservation, 10(4), 597-612.

Babbitt, B. (1998) Statement by Secretary of the Interior on invasive alien species. Proceedings, National Weed Symposium, BLM Weed Page. April 8 -10.

Barbour, M.G., Solomeshsch, A. I., & Buck, J. J. (2007) Classification, ecological characterization, and presence of listed plant taxa of vernal pool associations in California. Final Report, US Fish Wildlife Service

Barry, S. (1995) Vernal Pools on California's Annual Grasslands.Rangelands, 17(5), 173-175.

Barry, S. (1998) Managing the Sacramento Valley vernal pool landscape to sustain the native flora. .In, C.W. Witham, E.T. Bauder, D. Belk, W.R. Ferren Jr., and R. Ornduff (Eds.). Ecology, Conservation, and Management of Vernal Pool Ecosystems – Proceedings from a 1996 Conference. California Native Plant Society, Sacramento, California. 1998.

Bauder, ET. (2000) Inundation effects on small-scale distributions in San Diego, California vernal pools. Aquatic Ecology, 34,43-61.

Berghujis, W.R., Woods, R.A., & Hrachowitz, M. (2014) A precipitation shift from snow towards rain leads to a decrease in streamflow. National Climate Change, 4(7), 583-586.
Bertness, M.D., & Coverdale, T.C. (2013) An invasive species facilitates the recovery of salt marsh ecosystems on Cape Cod. Ecology, 94: 1937-1943.

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., & Richardson, D. M. (2011) A proposed unified framework for biological invasions. Trends in Ecology & Evolution, 26, 333–339.

Bliss, S.A., & Zedler, P. (1997) The germination process in vernal pools: sensitivity to environmental condition and effects on community structure. Oecologia, 113: 67-73.

Bradshaw, W. E., & Holzapfel, C. M. (2006) Evolutionary response to rapid climate change. Science, 312(5779),1477-1478.

California, State of. CIMIS, https://cimis.water.ca.gov

Cardinale, B. J., Gonzalez, J. E., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace,

J. B., Larigauderie, A., Srivastava, D. S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. Nature, 486, 59-67.

Cayan, D.R., Kammerdiener, S., Dettinger, M.D., Caprio ,J.M., & Peterson, D.H. (2001) Changes in the onset of spring in the western United States. Bull Am Meteorology Society, 82(3), 399–415.

Cayan, D., Tyree, M., Dettinger, M., Hidalgo, H., Das, T., Maurer, E., Bromirski, P., Graham, N., & Flick, R. (2009) Climate Change Scenarios and Sea Level Rise Estimates. California Climate Change Center.

Clausnitzer, D., Huddleston, J. H., Horn, E., & Keller, M. (2003) Hydric soils in a southeastern Oregon vernal pool. Soil science society of America journal, 67(3).

Cleland, E.E., Chiariello, N.R., Loarie, S.R., Mooney, H.A., & Field, C.B. (2006). Diverse responses of phenology to global changes in grassland ecosystems. PNAS, 103(37), 13740-13744.

Collinge, S.K., & Ray (2009) Transient patterns in the assembly of vernal pool plant communities. Ecology, 90,3313–3323.

Cords, H. P. (1960) Factors affecting the competitive ability of foxtail barley (Hordeum jubatum). Weeds, 8, 636–644.

Crowe, E. A., Busacca, A. J., Reganold, J. P., & Zamora, B. A. (1994) Vegetation zones and soil characteristics in vernal pools in the Channeled Scabland of eastern Washington. Great Basin Naturalist, 54(3).

Davies, K.W. (2008) Medusa head dispersal and establishment in sagebrush steppe plant communities. Rangeland Ecology Management, 61, 110-115.

Davies, K., & Nafus, A. (2013) Exotic annual grass alters fuel amounts, continuity and moisture to promote a grass-fire cycle. International Journal of Wildland Fire, 22, 353–358.

Davies, K.W. (2008) Medusa head dispersal and establishment in sagebrush steppe plant communities. Rangeland Ecology Management, 61, 110-115.

Deil, U. (2005) A review on habitats, plant traits and vegetation of ephemeral wetlands a global perspective. Phytocoenologia, 35, 533–705.

Delgado-Baquerizo, M., Maestre, F. T., Reich, P. B., Jeffries, T. C., Gaitan, J. J., Encinar, D., Berdugo, M., Campbell, C. D., & Singh, B. K. (2015) Microbial diversity drives multifunctionality in terrestrial ecosystems. Nature Communications, 7(10541).

Dettinger, M.D., & Cayan, D.R. (1995) Large-scale atmospheric forcing of recent trends toward early snowmelt in California. Journal of Climatology, 8, 606-623.

di Castri, F. (1989) History of biological invasions with special emphasis on the Old World. In: J.A. Drake et al., eds. Biological Invasions: A Global Perspective. John Wiley and Sons, 1-30.

Dole, J. (1988) Results of a Field Survey for the Butte County Meadowfoam in the Vicinity of the City of Chico, California. City of Chico, Chico, CA.

Emery, N.C., Stanton, M. L., & Rice, K.J. (2009) Factors driving distribution limits in an annual plant community. The New Phytologist, 181, 734-747.

Evans, R.A., & Young, J. A. (1970) Plant litter and establishment of alien annual weed species in rangeland communities. Weed Science, 18, 697-703.

“Explore.” Calflora, https://www.calflora.org/.

Facelli, J. M., & Pickett, S.T. (1991) Plant litter: its dynamics and effects on plant community structure. The Botanical Review ,57, 1–32.

Faist, A. M., Ferrenberg, S., & Collinge, S.K. (2013) Banking on the past: seed banks as a reservoir for rare and native species in restored vernal pools. AoB Plants, 5.

Faist, A., & Collinge, S. (2015) Seed bank composition varies along invasion and inundation gradients in vernal pool wetlands. Plant Ecology, 216(4), 553-564.

Ferren, W. R., Hubbard, D. M., Wiseman, S., Parikh, A. K., & Gale, N. (1998) Review of ten years of vernal pool restoration and creation in Santa Barbara, California. Ecology, conservation, and management of vernal pool ecosystems – Proceedings from a 1996 conference (ed. by C.W. Witham, E.T. Bauder, D. Belk, W.R. Ferren Jr and R. Ornduff), pp. 206–216. California Native Plant Society, Sacramento, CA.,

Fitter, A. H., & Fitter, R.S.R. (2002) Rapid Changes in Flowering Time in British Plants. Science, 296(5573), 1689-1691.

Fox, J., & Weisberg, S. (2019) car: Companion to Applied Regression. R package, version 3.0-13.

Gerhardt, F., & Collinge, S.K. (2003) Plant invasions of vernal pools in the Central Valley of California, USA. Journal of Biogeography, 30, 1043–1052.

Gerhardt, F., & Collinge, S. (2007) Abiotic constraints eclipse biotic resistance in determining invasibility along experimental vernal pool gradients. Ecological Applications, 17(3), 922-933.

Gosejohan, M. C., Weisberg, P. J., & Merriam, K. E. (2017) Hydrologic Influences on Plant Community Structure in Vernal Pools of Northeastern California. Wetlands, 37(2), 257-268.

Harden, J. W.(1987) Soils developed in granitic alluvium near Merced, California.U.S. Geological Survey Bulletin 1590-A.

Harrison, S., Rice, K., & Maron, J. (2001) Habitat patchiness promotes invasion by alien grasses on serpentine soil. Biological Conservation, 100, 45–53.

Hettinger, N. (2001) Exotic Species, Naturalization, and Biological Nativism. Environmental Values, 10, 193-224Holland, R.F., & Jain, S.K. (1988) Vernal pools. in M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. Special Publication Number 9. California Native Plant Society, Sacramento, California, USA.,515– 533.

Holland, R.F., & Dains, V.I. (1990) The edaphic factor in vernal pool vegetation. Pages.in D. H. Ikeda and R. A. Schlising, editors. Vernal pool plants: their habitat and biology. Studies from the Herbarium. Number 8. California State University, Chico, California, USA.,31–48

Holland, R.F, & Jain, S.K. (1981) Insular biogeography of vernal pools in the Central Valley of California. American Naturalist, 117, 24-37.

Howard, R. D. (1979) Estimating reproductive success in natural populations. American Naturalist, 114, 221-231.

Keeley, J.E., & Zedler, P.H. (1998) Characterization and global distribution of vernal pools. .In: Witham, C.W., Bauder, E.T., Belk, D., Ferren Jr., W.R., Ornduff, R. (Eds.), Ecology, Conservation, and Management of Vernal Pool ecosystems – Proceed- ings from a 1996 conference. California, California Native Plant Society, Sacramento, pp. 1–14.

Kota, N. L. (2005) Comparative seed dispersal, seedling establishment and growth of exotic, invasive Ailanthus altissima (Mill.) Swingle and native Liriodendron tulipifera (L.). Thesis at West Virginia University.

Lesica, P., & Kittelson, P.M. (2010) Precipitation and temperature are associated with advanced flowering phenology in a semi-arid grassland. Journal of Arid Environments, 74(9), 1013-1017.

Linhart, (1976) Evolutionary studies of plant populations in vernal pools. in S. K. Jain, editor. Vernal pools: their ecology and conservation. Institute of Ecology, University of California, Davis, California, USA, 40–46.

Marchand, D. E. & Allwardt, A. (1981) Late Cenozoic stratigraphic units, northeastern San Joaquin Valley, California. .US Geological Survey Bulletin,1470. 70 pgs. + 2 maps.

Marty, J. T. (2005) Effect of cattle grazing on diversity in ephemeral wetlands. Conservation Biology, 19, 1626-1632.

Maurer, E.P. (2007) Uncertainty in hydrologic impacts of climate change in the Sierra Nevada, California, under two emissions scenarios. Climate Change, 82, 309–325.

Merced Vernal Pools & Grassland Reserve, https://vernalpools.ucmerced.edu/.

Miller-Rushing, A.J., Katsuki, T., Primack, R.B., Ishii, Y., Lee, S.D., & Higuchi, H. (2007) Impact of global warming on a group of related species and their hybrids: cherry tree (Rosaceae) flowering at Mt. Takao, Japan. American Journal of Botany, 94, 1470–1478.

Miller-Rushing, A.J., & Primack, R.B. (2008) Global warming and flowering times in Thoreau's Concord: A community perspective. Ecology 89, 332-341.

Montrone, A., Saito, L., Weisberg, P. J., Gosejohan, M., Merriam, K., & Mejia, J. F. (2019) Climate change impacts on vernal pool hydrology and vegetation in northern California. Journal of Hydrology, 574, 1003-1013.

Pollak, O., & Kan, T. (1998) The use of prescribed fire to control invasive exotic weeds at Jepson Prairie Preserve. Ecology, conservation, and management of vernal pool ecosystems -proceedings from a 1996 conference (ed. by C.W. Witham, E.T. Bauder, D. Belk, W.R. Ferren Jr and R. Ornduff), pp. 241–249. California Native Plant Society, Sacramento, CA.

Primack, D., Imbres, C., Primack, R.B., Miller-Rushing, A.J., & Del Tredici, P. (2004) Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. American Journal of Botany, 91, 1260–1264.

Richardson J.E., Fay, M.F., Cronk, Q.C.B., Bowman, D., Chase, M.W. (2000) A phylogenetic analysis of Rhamnaceae using rbcL and trnL-F plastid DNA sequences. American Journal of Botany,87, 1309–1324.

Richer-de-Forges, A., Arrouays, D., Chen, S., Dobarco, M. R., Libohova, Z., Roudier, P., Minasny, B., & Bourennane, H. (2022) Hand-feel soil texture and particle-size distribution in central France. Relationships and Implications. Catena, 213.

Salley, S.W., Herrick, J.E., Holmes, C.V., Karl, J.W., Levi, M.R., McCord, S.E., van de Waal, C., & Van Zee, J.W., (2018) A Comparison of Soil Texture-by-Feel Estimates:

Implications for the Citizen Soil Scientist. Soil Science Society American Journal,82, 1526–1537.

Schlaepfer, M.A., Sax, D.F., & Olden, J.D. (2011) The potential conservation value of non-native species. Conservation Biology, 25, 428–437.

Smith D.W., & Verrill, W.L. (1998) Vernal pool-soil-landform relationships in the Central Valley, California. In: Witham CW, Bauder ET, Belk D, Ferren Jr WR, OrnduffR (eds) Ecology, conservation, and management ofv ernal pool ecosystems. proceedings from a 1996 conference. California Native Plant Society, Sacramento, pp. 15–23.

Solomeshch, A.I., Barbour, M.G., & Holland, R.F. (2007) Vernal pools. In: Barbour MG, Keeler-Wolf T, Schoenherr AA (eds) Terrestrial vegetation of California. University of California Press, Berkeley, pp. 394–424.

Sparks, T.H., & Carey, P.D. (1995) The responses of species to climate over two centuries: an analysis of the Marsham phenological record, 1736-1947. Journal of Ecology, 83, 321–329.

Sperry, J. H., O'Hearn, D., Drake, D.R., Hruska, A. M., Case, S. B., Vizentin-Bugoni, J., Arnett, C., Chambers, T., & Tarwater, C.E. (2021) Fruit and seed traits of native and invasive plant species in Hawaiʻi: implications for seed dispersal by non-native birds. Biological Invasions, 23, 1819-1835.

Stamp, N.E. (1989) Seed dispersal of four sympatric grassland annual species pf erodium. Journal of Ecology, 77, 1005-1020.

Stewart, I.T., Cayan, D.R., & Dettinger, M.D. (2004) Changes in snowmelt runoff timing in western North America under a “business as usual” climate change scenario. Climate Change, 62(1-3), 217-232.

Thien (1979) A flow diagram for teaching texture-by-feel analysis. Journal of Agronomic Education, 8, 54-55.

Thompson, K., & Grime, J.P. (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology, 67, 893–921.

Thórhallsdóttir, T.E. (1998) Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. Oecologia, 114, 43–49.

Westoff, V., & Van der Maarel, E. (1978) The Braun-Blanquet Approach. in Classification of plant communities ,287 – 399.

Williamson, M., & Fitter, A. (1996) The Varying Success of Invaders. Ecology, 77, 1661-1666.

Zedler, P.H. (2003) Vernal pools and the concept of ‘isolated wetlands’. Wetlands, 23, 597–607.

Chapter 3: A Case Study of Low-cost Recruitment and Retention Techniques

Abstract:

Community science is becoming a common research tool for collecting vast amounts of data by engaging local-residents and experts to independently contribute their findings. The techniques that attract potential volunteers and retain current volunteers vary in their cost, practicality, and success, and identifying the best strategy is a learning process for researchers. In addition, the shibboleth of community science is that anybody can be a scientist, though the number of community science opportunities in low income, rural regions is scarce despite environmental impacts of climate change being concentrated in such regions. In this study, I review the various techniques that can recruit and retain volunteers, and I attempt to implement those techniques to improve an ecological project in the Central Valley of California. Over three years, volunteers were recruited using two methods, email announcements and in-person presentations, while I used a flexible schedule and newsletter to retain recruits. Additionally, I recruited from two different classes of undergraduate students that varied in their composition of majors and educational levels. Recruitment was higher when using in-person presentations compared to email flyers, and a larger diversity of students was obtained when using in-person presentations. The use of newsletters and flexible scheduling resulted in a higher retention rate than without newsletters and a preset schedule. The lesson from this study is that community science is a great tool for collecting data and engaging the public, and that the design of the recruitment and retention techniques should also be considered alongside the design of the scientific study or experiment volunteers are assisting with.

INTRODUCTION:

Community science is the collaboration between professional scientists and public volunteers to answer specific questions (Dickinson et al 2010). Crowdsourcing for research projects can reduce costs, improve data collection speed, and vastly expand the diversity or geographic breadth of data included in a study (Conrad & Hilchey 2011; Worthington et al. 2012). Data-collection efforts that have most intensively engaged public volunteers in the ecological sciences have included bird surveys (Sullivan et al. 2009; Butcher & Niven 2007), invasive species surveys (Delaney et al 2008; Crall et al 2010; Gallo & Waitt 2011), vegetation mapping (Brandon et al. 2003; Galloway et al. 2006; Jacobson et al 2006; Oscarson & Calhoun 2007), and phenological surveys (Mayer 2010). Initially intended to increase the diversity of people engaging with scientific endeavors, the majority of community science participants remain educated, median income adults (Cooper et al. 2021). The democratization of science requires that projects are designed to engage underserved communities (Bonney et al. 2016), however, groups that remain overlooked are young, relatively uneducated, and lower income individuals from regions with less university outreach (Ockenden 2008. The field of community science has grown tremendously in the past 20 years, though there are still great gaps in knowledge about how to successfully recruit volunteers, increase the diversity of participants, and maintain their active participation (West & Pateman 2016; Cooper et al. 2021). The gap in knowledge is significant given the strong correlation between a project's success and the level of volunteer participation (Morais et al 2013).

Additionally, expanding the backgrounds of participants included in environmental volunteering can bolster social cohesion, as well as impart health and economic benefits (Morris 2003). In this project, I explore various recruitment and retention methods that increase the diversity of majors and educational expertise amongst undergraduate college participants, while also increasing recruitment rate and retention of volunteers.

Projects that aim to engage underrepresented groups must understand the different barriers that initially limit diversity, which can range from socioeconomic factors to logistical assumptions during the recruitment process. Much research takes place at large and well-funded universities based in cities with municipal support for conservation, thus individuals living in rural regions that historically lack science outreach are not equally exposed to research opportunities. Consequently, people from rural regions are traditionally underrepresented in environmental volunteering (Ockenden 2008). In the Central Valley of California in particular, there remains a shortage of scientific opportunities for local members partially because research does not consider the communities' perspectives (Flores-Landeros et al. 2021). Logistically, recruiters focus their efforts on attracting highly educated adults with preexisting expertise in a field (Connors et al. 2012; Burgess et al. 2017), functionally filtering out younger volunteers from diverse backgrounds that may be able to access local knowledge research scientists could not (Corburn 2003). This recruiter bias remains prevalent despite evidence that volunteers will quickly learn how to collect data better over time (Kosmala et al. 2016) and eventually provide comparable data to well-trained researchers (Thornton and Scheer 2012). Taken together, young volunteers without prior experience in environmental surveys from low-income communities in rural regions of the Central Valley are overlooked in the recruitment process.

Beyond the initial barriers that reduce inclusivity, the techniques that are commonly used to attract participants are likely to influence the diversity of volunteers. The efficacy of recruitment techniques like word-of-mouth referrals or outreach presentations for garnering a diversity of volunteers with various educational backgrounds has not been assessed, sociological theories suggesting these techniques may make a big difference in recruitment. For instance, the theory of homophily suggests that social interactions occur most often between people who share similar interests and characteristics (Mcpherson 2001), therefore, word-of-mouth referrals may not reach a wider diversity of people than those already engaged in the project. Alternatively, assumptions made about the extrinsic or intrinsic motivational factors of potential volunteers will often direct researchers to recruit from organizations or groups with parallel interests (Finkelstein 2009; Edwards 2014). While targeting groups with environmental affiliations could ensure a high recruitment rate for environmental surveys, the range of people with diverse educational backgrounds that receive an email flyer or in-person presentation is subsequently limited. The use of common techniques for recruiting individuals must be vetted for their effect on diversity so that community science can better engage the people it intends to serve.

The goal of this study is to review and compare several low-cost and transferable strategies that improve the diversity of participants, increase the rate of recruitment, and increase retention of volunteers in a community science project based out of the Central Valley of California.

Community Science Structure:

Community science projects (CSPs) can be categorized into different organizational models by the extent to which volunteers participate in the scientific process: “co-created,” “collaborative,” and “contributory” (Bonney et al 2009). Projects using the “co-created” model are characterized by public participation throughout all stages of an experiment (i.e., developing questions, designing methods, sampling data, analyzing data, and disseminating findings), whereas the contributory model places principal responsibility onto a professional scientist who is then aided by public volunteers to carry out sample collection. The collaborative model is intermediate, where the public is involved at all steps of the experiment other than defining questions, developing hypotheses, and gathering foundational information. The contributory model has been the standard for CSPs (West & Pateman 2016), so much so that “community science” has become synonymous with ‘contributory projects’ (Bonney 1996; Bonney 2007). Most experiments investigating the tactics that improve data quality and participation have been performed on contributory CSPs, and consequently, most recruitment and organizational techniques have been developed for contributory CSPs.

Recruitment Techniques:

Although there is no shortage of existing volunteers, reaching interested parties for new programs is a challenge. There are several efficient and inexpensive strategies that can reach a wide audience for the purpose of directing volunteers to an appropriate opportunity: in-person presentations, emails, print flyers, and word-of-mouth referrals. Each method has costs and unique benefits, and both should be considered in the context of the research goals and resource limitations. For example, compared to an in-person presentation, email solicitations are less expensive and less-time consuming. However, many emails from mass broadcasting methods are often automatically sent to a spam folder and ignored by recipients, which severely restricts the number of new recruits. The costs of in-person presentations include travel, scheduling, and preparation. The cost and burden of scheduling an in-person presentation can be significantly reduced by using a gatekeeper, which is any member of an external academic, public, or private institution that brokers volunteering opportunities between a project leader and interested parties (Unell & Castle 2012). Word of mouth referrals are highly effective (Ockenden 2008), however, it requires pre-existing volunteers which is not possible for new community science projects.

In addition to the goals and resources of researchers, these recruitment techniques should be designed with respect to the extrinsic and intrinsic motivational factors of volunteers (Finkelstein 2009; Edwards 2014). Extrinsic motivational factors are social or financial obligations whereas intrinsic motivational factors reflect an individual’s personal interests. Both motivational factors can drive a person’s behavior, either synchronously or independently. Although volunteers do not receive financial benefits, fostering a supportive and edifying atmosphere for a project that appeals to an individual’s personal interests can leverage both motivational factors and improve recruitment.

Retention:

Any project that uses community scientists must also consider practices for retaining existing volunteers since recruitment and training can be expensive, recurring costs. Common barriers to participation among volunteers who express an interest, yet decide not to participate, include a lack of time (Unell & Castle 2012) as well as anxiety concerning their responsibilities and necessary time commitment. The discrepancy between the number of registrants and actual volunteers is commonly quite large. For example, the Evolution MegaLab, which is a Europe-based ecological survey of snail species, only had 38% participation among the initially large, 6000-person group of registrants (Worthington et al. 2012). The explanation offered by the authors was that the time commitment needed for the required training the researchers implemented dissuaded volunteers. Many people from low-income regions are limited in their capacity to devote time to unpaid research, and therefore without considering the financial and time obligations of volunteers, recruits will not commit to a project. Since time constraints are a legitimate concern for both volunteers and the investigators, it is likely that scheduling flexibility will influence the final decision of recruits to participate.

In contrast to initial, short-term retention, long-term participation spanning weeks, months or even years can greatly improve the quality of data by retaining highly skilled volunteers and by aiding with recruitment using word-of-mouth referrals. There are several personal, organizational, and dispositional factors that may affect long-term engagement and consistency of volunteers. For example, volunteers frequently report feelings of being undervalued and overwhelmed as key reasons for prematurely leaving a project (Ryan et al. 2001; Locke et al. 2003). Jacobson et al. (2012) found that volunteers favored well-organized projects with good leadership, clear expectations, and meaningful tasks. In the same vein, the “matching hypothesis” (Clary and Snyder 1999) predicts that retention is linked to a participant’s expectations being reflected in the tasks performed (Ryan et al. 2001). In this vein, Ryan et al. (2001) suggests that clearly outlining and repeating the needed tasks on a regular basis can make volunteers feel productive (Bruyere & Rappe 2007) and part of a community (Bell et al. 2008). Nevertheless, the number of times a person participates does not necessarily ensure high skill or high-quality data collection because a volunteer may forget practices between trips. Rather, it is the frequency a person participates that is correlated with training speed and impact. Research on the psychology of habit formation has shown that consistency is the most important variable to forming new habits (Lally et al. 2009; Gardner & Lally 2018). Lally et al. (2009) found that individuals differed substantially in the speed at which a skill was acquired, though consistency was strongly associated with habit formation in all individuals. Weekly reminders can reignite interest each week, provide organizational information for volunteers to easily follow, and serve as a display of strong leadership and organization (Bell et al. 2008; Garner & Garner 2011; Unell & Castle 2012; Morais et al. 2013).

Case Study:

Nearly 90% of vernal pool habitats in California have been destroyed by human activities, making the remaining habitats valuable cultural assets for regions such as Merced, CA, which is home to one of the largest vernal pool complexes in the state (Fig. 3.1). Raising awareness about vernal pools amongst locals is a key strategy for preserving the landscape, and in addition, engaging locals in research has shown to empower volunteers to advocate for their community resources (Corburn 2003; Strasser et al. 2019). Synergizing the conservation goals of research institutions and the interests of local communities can benefit both parties and can be used to preserve natural landscapes that are quickly disappearing.

The research project, titled Vernal Pool Phenology Survey, tracks long-term plant phenological patterns in rare and endangered California vernal pool ecosystems (Fig. 3.2). I recruited volunteers to work on the project in several ways (emails and presentations) and attempted to retain volunteers using multiple methods (schedule flexibility and newsletters). The results of this case study are preliminary, and serve as a stepping-stone towards larger, more robust studies of recruitment and retention. Here, I ask: 1. Does the use of emails and in-person presentations considerably influence the diversity of recruits and rate of recruitment? 2. Is the attrition rate of initial recruits significantly affected by schedule flexibility? and, 3) do newsletters promote higher retention of volunteers?

Methods:

Background of Vernal Pool Project:

The collaborative community science project was initially established in 2015 by several senior undergraduate student interns participating in the Yosemite Leadership Program at UC Merced under the supervision of a faculty mentor. The scientific aim of the project was to create a long-term record of the flowering dates of all spring wildflower species within three representative vernal pools, as well as to record a more detailed account of the phenological progression of two common vernal pool wildflower species, *Limnanthes douglassi* var. *rosea* (rosy meadowfoam) and *Trifolium variegatum* (whitetip clover). Student volunteers were trained in the field by a supervisor on how to record and identify various phenological stages: vegetative, flower, seed, senescence. After the project's initial establishment, undergraduate volunteers were recruited to continue seasonal data collection and the recruitment data for three spring seasons between 2018 to 2020 are examined in this study. The sampling season of spring 2020 was cut short due to COVID restrictions on the campus. Although the initial recruitment rate should be unaffected by the COVID response, the long-term retention of volunteers certainly was.

Recruitment Techniques:

Two different techniques were used to recruit volunteers, including in-person presentations and email solicitations, and the efficacy of each technique was compared. Both techniques allow for an exact count of the recipient audience, whereas an exact count of the number of people passing by a flyer or watching a commercial cannot be taken. The count of people receiving the email was recorded automatically by the email server. The number of people receiving an in-person presentation was done by counting the people in the room listening to the presentation. In-person presentations were made in front of two biology-focused college classes (Introductory Biology and Introduction to Marine Science) on two separate years. Presentations were given by college instructors (Unell & Castle 2012), who also provided me with the proportion of the class that was upper division and biology majors. The instructors read from only three slides that contained the project description, volunteer duties, and contact information. Similarly, the email solicitation contained a simple flyer describing the project, the tasks, and relevant contact information. The in-person solicitations were designed to match email solicitations in terms of brevity and content to allow for more accurate comparisons between methods. For each method, the number of initial responses were measured and divided by the total number of students who received the solicitation to determine the recruitment rate of each recruitment campaign.

Retention Techniques:

In order to assess techniques that reduce initial recruitment attrition, I compared two scheduling techniques: an inflexible and predetermined schedule vs a flexible, volunteer-driven schedule. A Doodle poll was implemented as a flexible scheduling strategy that allowed recruits to submit times when they could potentially volunteer. The working time block (3 hours) that polled the highest was chosen and this time block was maintained for the season. In contrast, the predetermined schedule was concretely set on Thursdays from 11am – 2pm. The Doodle poll link or the preplanned schedule were sent to recruits a week after the presentations or email recruitment campaign to control for loss of interest over time (Penner 2002; West & Pateman 2016). Initial participation rate was measured as the proportion of interested recruits (i.e., students who sent a response email) that participated at least once throughout the project (Worthington et al. 2012).

Two retention factors/treatments were compared for their effects on volunteer retention rate: newsletter reminders and whether participation is mandatory or not. For years one and two, weekly reminders in the form of a newsletter were sent to volunteers containing information about the daily tasks, material required for the day (e.g. boots and a jacket if raining), and the time/place to meet. Alternatively, in year three, no weekly newsletter was released. Additionally, in year two an expectation of a commitment to participate was made explicitly at the first meeting and reinforced in a follow up email. In years one and three, there was no expectation that volunteers participate each week. Unfortunately, I did not conduct a fourth year of the study due to COVID restrictions, thus I was not able to examine the effect that no mandatory expectation with no newsletter had on retention. Consequently, the independent effect of a newsletter and a mandatory commitment to participate cannot be teased apart. Thus, I treat each year on a scale of flexibility (i.e., participation mandatory or not) and a ‘scale of inclusivity’ (i.e., newsletter or not). In this scale, Year 1 is the most flexible and inclusive, Year 3 is flexible though not inclusive, whereas Year 2 is inflexible though inclusive. I did not include a year that was both inflexible and non-inclusive because I wanted to have enough volunteers for the survey project, however, the lack of this treatment is a caveat of the study.

Retention was estimated in two ways: 1) the average number of participation days by a single volunteer; and 2) the proportion of volunteers present at the end of each season (1= present for one or both of the last two trips, 0 = not present for both of the last two trips).

Attempted Controls:

A variety of other factors that could potentially influence recruitment, retention and consistency remained the same across the life of the project, such as the distance walked for the survey, the project leader's identity, the collection methodology, the length of time between recruitment and volunteering, and the number and intensity of training sessions. To my knowledge, this is the first exploratory study that consistently controlled for factors beyond the recruitment and retention techniques implemented, therefore making the findings of this project novel and more accurate than conclusions drawn from metanalyses of various community science projects with potentially different logistical and methodological conditions.

RESULTS:

Recruitment

In Year 1, an in-person presentation was given to the 'Introduction to Marine Biology' class, and in Year 3 an in-person presentation was given to the 'Introductory Biology' class. Presentations were repeated at two meeting sessions of the same class. The first, 'Introduction to Marine Biology', was composed of 92 students: 62% biology majors and 38% non-biology majors spanning freshman to senior level. The second class, Introductory Biology, had 185 students and was primarily composed of biology majors (94%) and lower division students (92%). The alternative recruitment method was an electronic flyer sent to all undergraduates in STEM majors.

The number of students in the 'Introduction to Marine Biology' class (n=92) who responded to the solicitation was 12 (13% of the audience) (Table 3.1). The proportion of recruits that were biology majors was 75%, and 33.33% were upper division students. The third year, when a presentation was made to the class, 'Introduction to Biology' (n=185 students), 24 students (13%) responded by email to express their interest. The proportion of recruits that were biology students were 87.5% and 29% were upper division.

The recruitment method used the second year was a solicitation email disseminated by the STEM departments at UC Merced, which include the School of Natural Sciences (2,085 students) and School of Engineering (2,262 students). The number of initial responses was 6. This equates to a recruitment rate of 0.13% (6 Recruits /4,347 STEM Students). Although the emails were sent from two different schools covering all STEM fields, all responses were from biology majors (100%) in their junior (33%) and senior years (66%).

Initial Participation

The initial recruitment rate varied by year and because of schedule flexibility (Table 3.2). The number of people who emailed me, and the number who eventually volunteered was 12 and 8 the first year, respectively, a turnout of 66% (Table 3.2). This was when students decided the date and time of the survey. The same method used the second year resulted in 5 participants out of 6 recruits, a turnout of 83% (Table 3.2). The average turnout using a flexible schedule is 74.5%. When the schedule was predetermined and immovable (Friday at 11am-2pm), 12 out of the 24 people who expressed an interest volunteered at least once, an initial retention rate of 50%.

Retention and Participation Consistency

The long-term retention of volunteers throughout a sampling season varied among years in which a newsletter was used and not used (Table 3.2). During the first year when a newsletter was used without a mandatory expectation, the average volunteer participated 3.75 times out of 7, or 53.6% of trips. In addition, the number of volunteers present at the end of the first-year survey was 6 out of 8, or 75%. The second year, when a mandatory expectation and a newsletter were utilized, the average number of trips per volunteer was 6.2 out of 8 survey periods, or 77.5%. The total number of volunteers at the start of year 2 was 6, and 5 volunteers were present by the end of the survey season, a retention rate of 84% (Table 3.2). In contrast to the first two years, the third year did not use either a newsletter or a mandatory expectation to promote retention. Volunteers attended 2.8 trips, on average, out of 6 trips. This translates into an average participation rate of 46.8%. By the end of the third-year survey, 6 out of 12 students remained, i.e., 50% of the initial volunteers.

DISCUSSION:

Community science projects succeed when the community is actively engaged, which can be improved through cost efficient methods that simultaneously increase the diversity of volunteers such as in person presentations, flexible scheduling, and newsletters. I found that designing projects around the needs, wishes, and limitations of local volunteers is necessary for ensuring high recruitment and retention. Also, because volunteers are not homogenous, reaching a larger diversity of participants will require further research into how different motivations, dispositional factors, and interests influence the success of certain recruitment strategies. While not a rigorous experiment with full controls and replications, the findings of this serve as an informative exploration into the methods that worked to increase diversity, recruitment, and retention in an ecological study. In the following paragraphs, I provide a review of my results and give suggestions for other researchers wishing to perform community science.

Email solicitations are attractive because of the low cost, low time commitment, and broad reach they offer. However, I find that mass broadcasting methods like emails are potentially less effective recruitment tools. The recruitment rate of email flyers in this study was 0.13%, which is commensurate to the recruitment rate of the Evolution Mega lab's mass broadcasting technique (Worthington et al. 2012). On the other hand, in-person presentations were more successful than email flyers at acquiring more volunteers as well as a higher diversity of volunteers, as measured by varying college levels (freshman, sophomore, etc.) and majors. The results of this project suggest that in-person presentations will result a greater magnitude of recruitment than email flyers and impersonal broadcasting. In all years, biology majors were significantly overrepresented in the final cohort, with 100% of volunteers being biology majors when using email flyers. An in-person presentation to an audience of 94% biology majors yielded 91% biology students, whereas an in-person presentation to an audience of 62% biology majors yielded 75%. This finding emphasizes the importance of appealing to the intrinsic motivations of potential recruits (Finkelstein 2009) and provides further support for the matching hypothesis (Clary and Snyder 1999). However, when the in-person presentation was given to a class composed of multiple college majors, a greater diversity of students was recruited. In addition, the recruitment rate was unchanged when presenting to a biology-focused audience verses to a biology-interested-audience, suggesting that diversity can be attained without sacrificing recruitment rate. This suggests that the professional or educational track is not an indicator of who will be interested in an environmental survey. The literature supports the claim that environmental surveys appeal to a larger audience than professional environmentalists or current environmental advocates. More research is required to confirm these hypotheses.

Long-term volunteers can act as recruiters themselves, spreading the community science project's information to friends, family, and class members, which in turn can further reduce recruitment costs. The 62.5% and 70% frequency of lower division students in sample years 1 and 3, respectively, highlight the fact that freshman and sophomore students are not innately uninterested in volunteering or getting involved with scientific research, rather the opposite. Lower division students are extremely interested in volunteer work and as Penner (2002) suggests, "they [only] need to know the opportunity is appropriate for them". The benefits of freshman and sophomore students is that they are available for three or more years to assist on a project. In addition, research opportunities for lower division students can build their resume early, improve their critical thinking skills, and aid in their long-term goals of research or higher education.

Volunteers, like scientific professionals, are limited by the number of hours they can commit to unpaid service. This study found that a volunteer-driven schedule can result in a 49% increase of recruits who successfully participate. This finding may only pertain to surveys requiring a group to assemble for a designated interval of time, though it underscores the importance of tailoring the schedule of a community science endeavor to the time constraints of interested recruits. Providing schedules for participation that conform to the time constraints of volunteers can be an effective way to retain recruits who show interest in a program yet are busy themselves. If volunteers have an opportunity to have their voices heard early in the project's timeline, the project will benefit from reduced recruitment costs and more skilled participants. For some studies, recruits may be asked to complete a survey, take a training course (Worthington et al. 2017), or register on a website before participating, all of which cause some level of attrition of initial recruits. The reasons that lead to volunteers leaving a community science project are varied and unique to each person, though the two most common explanations are that they eventually lose interest in the project and their time is limited. Although motivations were not explored in this paper, organizing around volunteer's schedules and time constraints seemed to increase the number of recruits that volunteered in the project, which points to the fact that timing is a major factor causing initial recruitment attrition. Therefore, I advise, if possible, that volunteers choose when to collect data. Also, given that people naturally lose interest in a project as more time passes, I advise that the time between a recruitment campaign and data collection be minimized as much as possible. I suggest that training sessions be performed simultaneously with data collection, whenever possible, as such a practice truncates the time between recruitment and participation while providing hands on, and individually tailored, experience with a well-trained guide.

To improve the long-term retention of volunteers, a weekly newsletter is an inexpensive method that increases group cohesion throughout a community science project. However, volunteers may participate infrequently, and thus we suggest creating an expectation of mandatory participation. This finding agrees with prior evidence that volunteer participation tends to be low intensity and infrequent (Wilkinson et al. 2010) though will be motivated to participate when they see progress being made using weekly updates (Unell & Castle 2012). In addition, prior research shows that imposing stringent training (Worthington et al. 2012) and timing requirements on volunteers degrades interest as it often overwhelms volunteers (Locke et al. 2003). I find that placing a mandatory commitment to participate did not consistently lower retention or initial participation rates. As such, a mandatory commitment to volunteering may be an effective extrinsic motivational factor that doesn't overburden volunteers, who by virtue of participating are exhibiting that they want to volunteer. Additionally, because proper organization is a factor strongly influencing retention amongst volunteers (Jacobson et al. 2012), mandatory expectations could be perceived as good organizational practices that in turn improves retention.

The findings of this study are preliminary, and as such, the fidelity of these findings have not been tested rigorously. However, using the principles set out by other community science researchers did have the desired outcomes for my multiyear environmental survey. The application of in-person presentations and newsletters did improve recruitment and retention, respectively, and could likely work for other projects. The goals of this project were to identify techniques that could increase diversity, recruitment, and retention, and by implementing the advice given by community science literature I significantly improved data collection and fostered a holistic work environment where hopefully all educational backgrounds felt included and productive. The advice I can give to other researchers thinking of engaging the public is to try multiple methods of recruitment, then improve upon those methods until you reach the desired outcomes.

TABLES

Table 3.1 Summary of the recruitment method used alongside the corresponding audience size and the resulting recruitment rate. In addition, the percentage of biology majors and upper division students of each recruited cohort are reported**.**

Technique		*Recipients*	*Recruits*	*Recruitment Rate*	*% Biology Majors*	*% Upper Division*
Email		4347	6	0.14%	100%	100%
In-Person Presentation						
	Class 1	92	12	13.04%	75%	33.33%
	Class 2	185	24	12.97%	87.50%	29%

Table 3.2 Summary of retention techniques used for initial retention of recruits and long-term retention of volunteers throughout a sampling season. The long-term retention techniques were a combination of flexibility (ie. no mandatory expectation to participate) and inclusivity (ie. newsletter). The rate for initial retention is calculated by dividing the number of people that volunteered at least once by the number of people recruited.

Retention	*Technique*	*Rate*
Initial Retention		
	Student Schedule	74.50%
	Preset Schedule	46.80%
Long-term Retention		
	Flexible/Inclusive	54%
	Inflexible/Inclusive	78%
	Flexible/Not Inclusive	47%

FIGURES

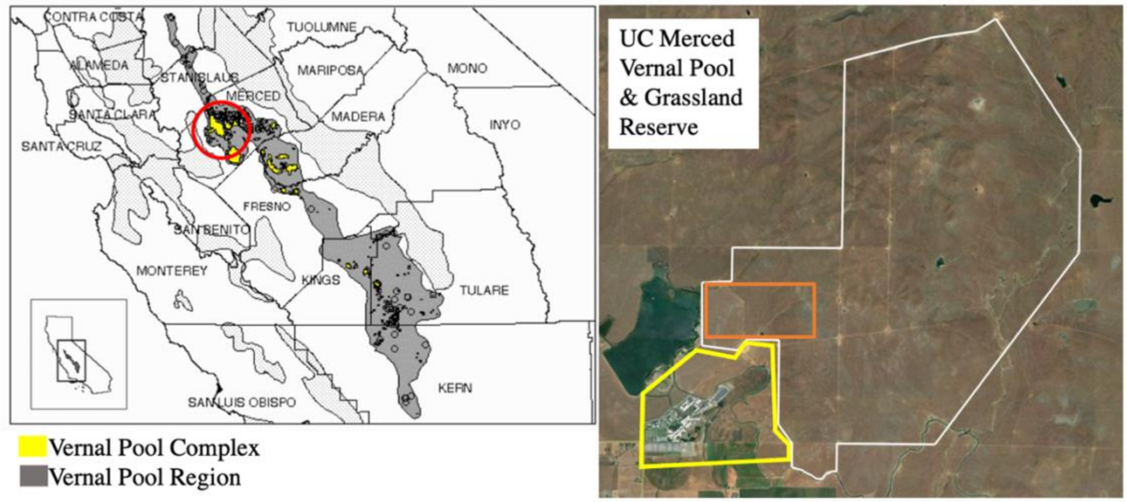


Figure 3.1 Vernal pool region os San Joaquin Valley in Merced County alongside the UC Merced Vernal Pools and Grassland Reserve. (right) Modified figure from Keeley & Zedler 1998, depicting the San Joaquin Valley Vernal Pool region (grey) and the vernal pool complexes within Merced, Fresno, and Madera County (yellow). The red circle encompasses the UC Merced Vernal Pools & Grassland Reserve (MVPGR) within Merced County. (left) The MVPGR (white perimeter) is located next to the University of California, Merced campus (yellow). A subsection of MVPGR was used for ecological surveying (orange).

Figure 3.2 Volunteers recording the presence of meadowfoam (white flowers in left photo) and whitetip clover along north-south and east-west transects spanning the length of a vernal pool.

LITERATURE CITED

Bell, S., Marzano, M., Cent, J., Kobierska, H., Podjed, D., Vandzinskaite, D., Reinert, H., Armaitiene, A., Grodzińska-Jurczak, M., & Muršič, R. (2008) What counts? Volunteers and their organizations in the recording and monitoring of biodiversity. Biodiversity and Conservation, 17(14), 3443–3454.

Bonney, R. (1996) Citizen science: A lab tradition. Living Bird, 15(4), 7-15.

Bonney, R., Ballard, H., Jordan, R., McCallie, E., Phillips, T., Shirk, J., & Wilderman, C.C., (2009). Public participation in scientific research: Defining the field and assessing Its potential for informal science education. A CAISE Inquiry Group Report. Washington, DC: Center for Advancement of Informal Science Education (CAISE).

Bonney, R. (2007) Citizen science at the Cornell Lab of Ornithology. pg. 213-229. In R.E. Yager & J.H. Falk eds. Exemplary Science in Informal Education Settings: Standards-Based Success Stories. Washington, D.C., NSTA Press.

Bonney, R., Phillips, T.B., Ballard, H.L., & Enck, J.W. (2016). Can citizen science enhance public understanding of science? Public Understanding Science, 25(1), 2-16.

Brandon, A., Spyreas, G., Molano-Flores, B., Carroll, C., & Ellis, J. (2003) Can volunteers provide reliable data for forest vegetation surveys? Natural Areas Journal, 23, 254–261.

Bruyere, B., & Rappe, S. (2007) Identifying the motivations of environmental volunteers. Journal of Environmental Planning and Management, 50(4), 503–516.

Burgess, H.K., DeBay, L.B., Froehlich, H.E., & Schmidt, N. (2017) The science of citizen science: Exploring barriers to use as a primary research tool. Biological Conservation, 208(11).

Butcher, G.S., & Niven, D.K. (2007) Combining Data from the Christmas Bird Count and the Breeding Bird Survey to Determine the Continental Status and Trends of North America Birds. National Audubon Society, Ivyland, PA.

Clary, E.G., & Snyder, M. (1999) The Motivations to Volunteer: Theoretical and Practical Considerations. Current Directions in Psychological Science, 8(5), 156-159.

Connors, J.P.C., Lei, S., & Kelly, M. (2012) Citizen science in the age of neogeography: utilizing volunteered geographic information for environmental monitoring. Annals of the American Association of Geographers, 102(6), 1267-1289.

Conrad, C.C. & Hilchey, K.G. (2011) A review of citizen science and community-based environmental monitoring: issues and opportunities. Environmental Monitoring and Assessment, 176, 273–291.

Cooper, C., Hawn, C.L., Larson, L.R., & Parrish, J.K. (2021) Inclusion in citizen science: The condrum of rebranding. Science, 372(6549), 1386-1388.

Coburn, C.E. (2003) Rethinking Scale: Moving beyond numbers to deep and lasting change. Educational Researcher, 32(6), 3-12.

Crall, A.W., Gregory, G.J., Jarnevich, C.S., Stohlgren, T.J., Waller, D.M., & Graham, J. (2010) Improving and integrating data on invasive species collected by citizen scientists. Biological Invasions, 12, 3419–3428.

Delaney, D.G., Sperling, C.D., Adams, C.S., & Leung, B. (2008) Marine invasive species: validation of citizen science and implications for national monitoring networks. Biological Invasions, 10, 117–128.

Dickinson, J.L., Zuckerberg, B.m & Bonter, D.N. (2010) Citizen science as an ecological research tool: challenges and benefits. Annual Review of Ecology, Evolution, and Systematics, 41, 149–172.

Edwards, R. (2014) Citizen science and lifelong learning. Studies in the Education of Adults, 46(2), 132–144.

Finkelstein, M.A. (2009) Intrinsic vs. extrinsic motivational orientations and the volunteer process. Personality and Individual Differences, 46(5–6), 653–658.

Flores-Landeros, H., Pells, C., Martinnez, M.S.C., & Fernandez-Bou, A.S. (2021). Community Perspectives and Environmental Justice in California’s San Joaquin Valley. Environmental Justice

Gallo, T., & Waitt, D. (2011) Creating a successful citizen science model to detect and report invasive species. BioScience, 61, 459–465.

Galloway, A.W.E., Tudor, M.T., & Vander Haegen, W.M. (2006) The reliability of citizen science: a case study of Oregon white oak stand surveys. Wildlife Society Bulletin, 34, 1425–1429.

Gardner, B., & Lally, P. (2018) Modelling Habit Formation and Its Determinants: Theory, Mechanisms, Change, and Contexts. pg. 207-229. In The Psychology of Habit.

Garner, J.T., & Garner, L.T. (2011) Volunteering and Opinion: Organizational Voice and Volunteer Retention in Nonprofit Organizations. Nonprofit and Voluntary Sector Quarterly.

Jacobson, S.K., Morris, J.K., Sanders, J.S., Wiley, E.N., Brooks, M., Bennetts, R.E., Percival, H.F., & Marynowski, S. (2006) Understanding barriers to implementation of an adaptive land management program. Conservation Biology, 20, 1516–1527.

Jacobson, S.K., Carlton, J.S., & Monroe, M.C. (2012) Motivation and satisfaction of volunteers at a Florida natural resource agency. Journal of Park and Recreation Administration, 30(1), 51–67.

Kosmala, M., Wiggins, A., Swanson, A., & Simmons, B. (2016) Assessing data quality in citizen science. Frontiers in Ecology and the Environment, 14(10), 551-560.

Lally, P., van Jaarsveld, C.H.M., Potts, H.W.W., & Wardle, J. (2009) How are habits formed: Modelling habit formation in the real world. European Journal of Social Psychology 40(6), 998-1009.

Mcpherson, M., Smith-Lovin, L., & Cook, J.M. (2001) Birds of a Feather: Homophily in Social Networks. Annual Review of Sociology, 27(1), 415-444.

Locke, M., Ellis, A., & Smith, D.J. 2003. Hold on to what you've got: The volunteer retention literature. Voluntary Action, 5(3), 81-99.

Mayer, A. (2010). Phenology and citizen science. *BioScience*, 60(3), 172–175.

Morais, A.M.M., Raddick, J., & dos Santos, R.D.C. (2013) Visualization and characterization of users in a citizen science project. In: Proc SPIE 8758, Defense, Security and Sensing, Next Generation Analyst, Baltimore MD on 29 April 2013.

Morris, N. (2003) Health, Well-Being and Open Space. Open Space.

Ockenden, N. (2008) Environmental volunteering in North East of England. London, UK: Institute of Volunteering Research.

Oscarson, D.B., & Calhoun, A.J.K. (2007) Developing vernal pool conservation plans at the local level using citizen-scientists. Wetlands, 27, 80–95.

Penner, L.A. (2002) Dispositional and organizational influences on sustained volunteerism: An interactionist perspective. Journal of Social Issues, 58(3), 447–67.

Ryan, R., Kaplan, R., & Grese, R.E. (2001) Predicting volunteer commitment in environmental stewardship programs. Journal of Environmental Planning and Management, 44(40, 629-648.

Strasser, B.J., Baudry, J., Mahr, D., Sanchez, G.A., & Tancoigne, E. (2019). “Citizen Science”? Rethinking science and public participation. Science and Technology Studies, 32(2).

Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D., & Kelling, S. (2009) eBird: A citizen-based bird observation network in the biological sciences. Biological Conservation, 142(10), 2282-2292.

Thornton, T.F., & Scheer, A.M. (2012) Collaborative engagement of local and traditional knowledge and science in marine environments: a review. Ecology and Society**, 17**(3), 8.

Unell, J., & Castle, R. (2012) Developing sustainable volunteering within the Natural Connections Demonstration Project: A review of evidence. Natural England Commissioned Report NECR096.

West, S., & Pateman, R. (2016) Recruiting and Retaining Participants in Citizen Science: What Can be Learned from the Volunteering Literature? Citizen Science: Theory and Practice, 1(2), 1-10.

Wilkinson, A., Gollan, P.J., Marchington, M., & Lewin, D. (2010) Conceptualizing Employee Participation in Organizations. pg. 3-25. In A. Wilkinson, P. J. Gollan, M. Marchington & D. Lewin (Eds.), The Oxford Handbook of Participation in Organizations, Oxford: Oxford University Press.

Worthington, J.P., Silvertown, J., Cook, L., Cameron, R., Dodd, M., Greenwood, R.M., McConway, K., & Skelton, P. (2012) Evolution MegaLab: A case study in citizen science methods. Methods in Ecology and Evolution, 3: 303–309.