

The Effects of Hydroregime on Vernal Pool Plant Communities in Northeastern California

KYLE E MERRIAM

USDA Forest Service, Plumas National Forest
159 Lawrence Street, Quincy, CA, 95971
kmerriam@fs.fed.us

MEREDITH C. GOSEJOHAN

Department of Conservation and Natural Resources, Division of State Lands,
901 S. Stewart Street, Suite 5003, Carson City, NV 89701-5246

PETER J. WEISBERG

Department of Natural Resources and Environmental Science
University of Nevada, 1664 N. Virginia Street, Reno, NV, 89557

ABSTRACT. Although vernal pool plant communities have been classified in other regions of California, little is known about the plant communities or the hydroregimes of vernal pools in northeastern California. We quantified inundation length, maximum water depth, and species composition at two vernal pool study sites in northeastern California. Our goal was to quantify the role of hydrology in structuring vernal pool plant communities in this region, and to evaluate the response of a rare species, *Orcuttia tenuis*, to hydrologic variables. We found that the distribution of plant species was strongly correlated with both inundation length and maximum water depth, and we classified three community groups according to thresholds of inundation length. Our study extends existing vernal pool plant classification schemes to northeastern California. We observed large differences between our two study sites. The vernal pool where livestock have been excluded since 1991 had more litter accumulation, shorter inundation periods, lower numbers of *O. tenuis*, and higher topographical variability than our study site that is grazed annually. Our results highlight the importance of hydroregime in structuring vernal pool plant communities in northeastern California, as well as the potential role grazing management may play to influence these variables.

CITATION. Merriam, K.E., M.C. Gosejohan, and P.J. Weisberg. 2019. The effects of hydroregime on vernal pool plant communities in northeastern California. Pages 45-59 in R.A. Schlising, E.E. Gottschalk Fisher, G.M. Williams, and B. Castro (Editors), Vernal Pool Landscapes: Past Present and Future. Studies from the Herbarium Number 20, California State University, Chico, CA.

INTRODUCTION

Vernal pools represent stressful and rapidly changing environments, characterized by complete inundation during the winter and spring, followed by hot, arid conditions during the summer (Hanes and Stromberg, 1998, Keeley and Zedler, 1998; Solomeshch et al., 2007). Plant species that occur in vernal pools are often highly specialized to tolerate these rapid en-

vironmental shifts, with many having both aquatic and terrestrial phases in their life cycle (Keeley and Zedler, 1998). One such species endemic to vernal pools is *Orcuttia tenuis* (slender Orcutt grass), an annual grass found in the northern Central Valley and the Modoc Plateau in northeastern California (USDI, 2005). The *O. tenuis* life cycle, including underwater germination, the development of both aquatic and terrestrial leaves, and seed dor-

mancy, is highly adapted to the timing and duration of vernal pool inundation, and this species is generally found in deeper pools with longer inundation periods (Griggs, 1980; Griggs and Jain, 1983; USDA and USDI, 1989; Keeley, 1998). Due to its limited distribution and significant threats to its habitat, *O. tenuis* is federally listed as threatened and state listed in California as endangered (USDI, 1997; CDFW, 2014).

Like *O. tenuis*, most vernal pool plants inhabit specific locations within vernal pool basins according to their tolerance to the vernal pool hydroregime, including the depth, timing, duration, and frequency of water inundation (Holland and Jain, 1984; Zedler, 1984; Bliss and Zedler, 1998; Bauder, 2000; Emery et al., 2009). Variation in species distributions along these environmental gradients creates zones of vegetation which can be divided into floristic community groups (Barbour et al., 2005; Deil, 2005; Solomeshch et al., 2007). Although hydroregime is generally understood as the primary determinant of wetland plant establishment and survival (Deil, 2005), past research has primarily focused on frequency of species within groups to classify plant communities and few studies have directly related hydrologic variables to spatial patterning of vernal pool plant communities. In the most comprehensive classification system for vernal pool plants to date, Solomeshch et al., (2007) assigned all California vernal pool vegetation to the class Downingio-Lasthenietea, named after two diagnostic species *Downingia bicornuta* and *Lasthenia fremontii*. Within this class, three orders were delineated: 1) long-inundated communities, 2) short-inundated communities, and 3) communities occurring in saline or alkaline pools. The distribution of these communities is primarily restricted to the Central Valley of California (CNPS, 2018), and one of the two major diagnostic species for the long-inundated community (order Lasthenietalia glaberrimae Solomeshch et Holland ord. Nov. hoc loco),

Lasthenia glaberrima, does not occur in northeastern California. Many vernal pool species, such as *O. tenuis*, do occur in both northeastern California and in other vernal pool regions, suggesting similarity in species composition across regions, however, a classification of plant communities in northeastern California has not been completed. Vernal pools in northeastern California differ from those in other portions of the state in a number of ways. They occur at higher elevations, experience longer inundation periods, endure colder winter climates, are filled primarily by snowfall, are generally larger (10^2 - 10^3 ha), are located within the Great Basin floristic province (Baldwin et al., 2012), and are surrounded by shrub and tree-dominated vegetation types.

Study Objectives

In this paper we summarize our work (Gosejohan et al., 2017) and present additional information describing vernal pool hydroregimes and classification of vernal pool plant communities in northeastern California. We choose two vernal pool study sites which both support populations of *O. tenuis*, but that differ in grazing management. Our aim was to answer the following questions: 1) How does hydroregime affect vernal pool plants in northeastern California?; 2) Can we classify vernal pool plant communities in this region?; 3) How does hydroregime affect *O. tenuis* specifically?; and 4) Are there differences between our two study sites that differ in grazing history?

METHODS

Study Area

Our two vernal pool study sites are located in northeastern California, approximately 57 km apart (Figure 1). The climate in this region is classified as Mediterranean Montane (Bailey, 1995), with annual average precipitation of approximately 47 cm occurring primarily be-

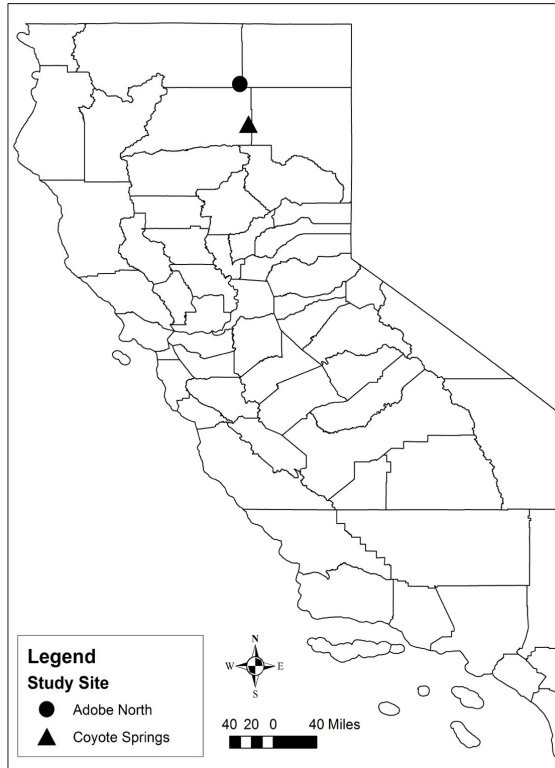


FIGURE 2. Map of vernal pool study sites.

tween the months of October and May (WRCC, 2018). The region can experience isolated summer storms, although these monsoons are rare. Adobe North vernal pool ($41^{\circ}13'42''\text{N}$, $121^{\circ}28'52''\text{W}$), occupies 5.4 ha and occurs at 1097 m elevation. Coyote Springs vernal pool ($40^{\circ}43'0''\text{N}$, $121^{\circ}22'5''\text{W}$) is 3.5 ha in size and is found at 1521 m elevation. Our study sites differ in grazing management; Adobe North vernal pool has been fenced to exclude livestock since 1991, while Coyote Springs is annually grazed by cattle from June through September (USDA and USDI, 2012). Soils at both study sites are from the Skalan-Bobbitt families association (USDA, NRCS, 2018) derived from eroded lava flows, from Pliocene and Pleistocene era volcanoes (Keeler-Wolf et al., 1998). Both of our study sites support populations of *O. tenuis*, and the vegetation surrounding both pools is composed of *Pseudotsuga menziesii*, *Calocedrus decurrens*, *Pinus jeffreyi*, *Pinus ponderosa*, *Purshia tridentata*, and *Artemisia tridentata*.

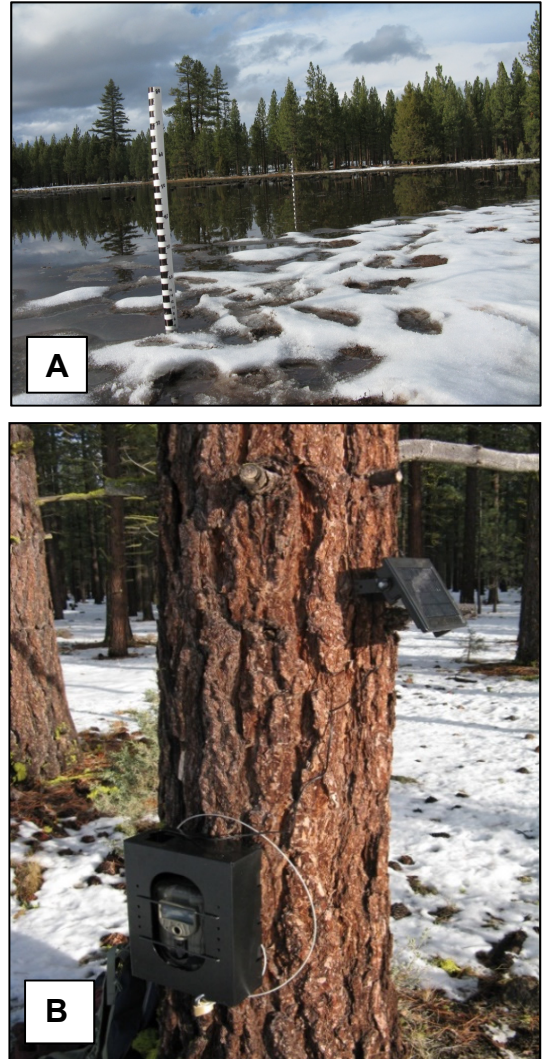


FIGURE 1. Stage gauges (A) and remote cameras (B) used to measure hydroregime.

Hydroregime Monitoring

As described in Gosejohan (2017), the hydroregime of our two vernal pool study sites was reconstructed from December 2010 – June 2011 using remote photography of water depth stage gauges in combination with a detailed topographic survey (Figure 2). The topographic survey recorded precise elevations at intersections of a systematic grid in each vernal pool, totaling 197 locations at Adobe North and 144 locations at Coyote Springs. Mounted game cameras captured daily photographs of two stage gauges to record water depth to the near-

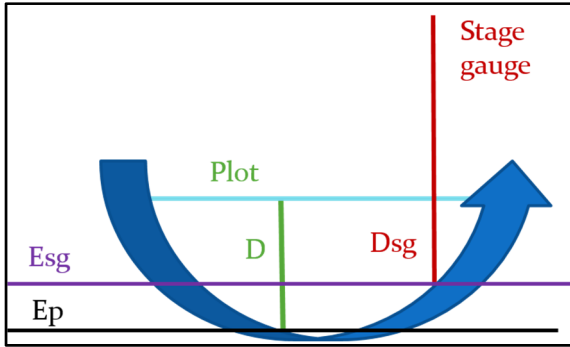


FIGURE 4. Depth for each sampling plot was calculated using the equation: $D = (E_{sg} - E_p) + D_{sg}$ where D is water depth at the plot location; E_{sg} is elevation at the stage gauge; E_p is elevation at plot; and D_{sg} is water depth at stage gauge (Gosejohan et al., 2017).

est cm. Water depth measurements at each gauge were then extrapolated to every location throughout both pools using elevation data (Figure 3). Maximum depth was calculated as the highest water level observed during the winter season and inundation period as the total number of days for which water depth was greater than zero.

Vegetation Sampling

Vegetation data were collected in 1m^2 plots at the same locations where hydroregime data was quantified (Figure 4). In each 1m^2 plot, all plant species were identified and species cover was estimated using modified Daubenmire cover classes (Daubenmire, 1959). The number of *O. tenuis* plants, if present, were measured within a 0.2-m^2 frequency frame located in the northeast corner of the 1m^2 plot. Litter depth was also measured at the northeast corner of each 1m^2 plot.

Data Analysis

Community data. We utilized non-metric multidimensional scaling (NMS) to examine how plant community composition varied along hydrologic gradients using the statistical software package PC Ord ver. 6 (McCune and Mefford,

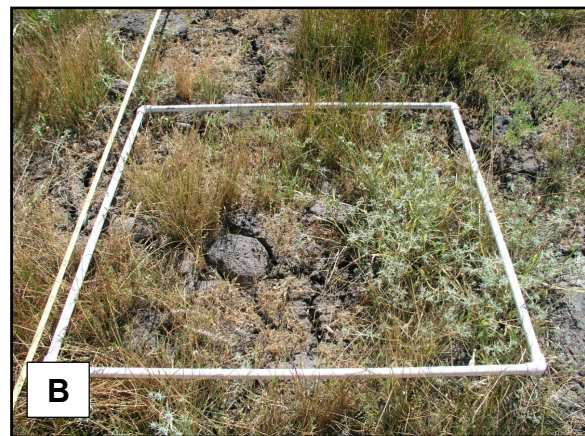
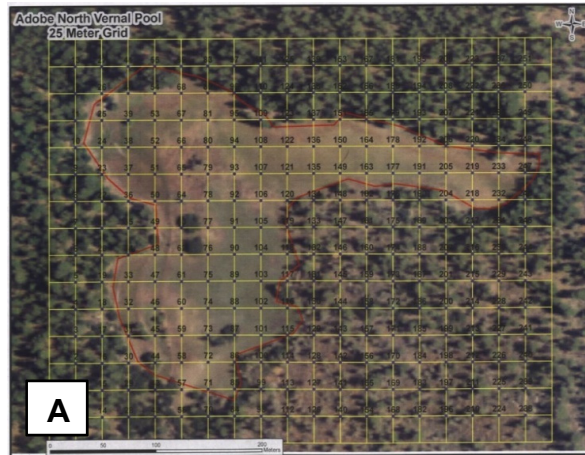


FIGURE 3. Vegetation sampling was conducted along a systematic grid (a) in 344 1m^2 plots (b).

2011). Rare species and outlier plots were removed from the dataset to reduce the influence of infrequent species on the results (McCune and Grace, 2002), leaving 40 species and 334 plots for analysis. Community composition data was ordinated as relativized estimates of species cover using NMS autopilot ‘slow and thorough’ mode with the Sørensen (Bray-Curtis) distance measure. The proportion of variance represented by each ordination axis was calculated post-hoc as the R^2 between distance in the ordination space and distance in the original matrix (McCune et al., 2002).

Classification of community groups. Clustering and indicator species analyses were used to identify distinct community groups along hydrologic gradients in PC-Ord ver. 6 (McCune

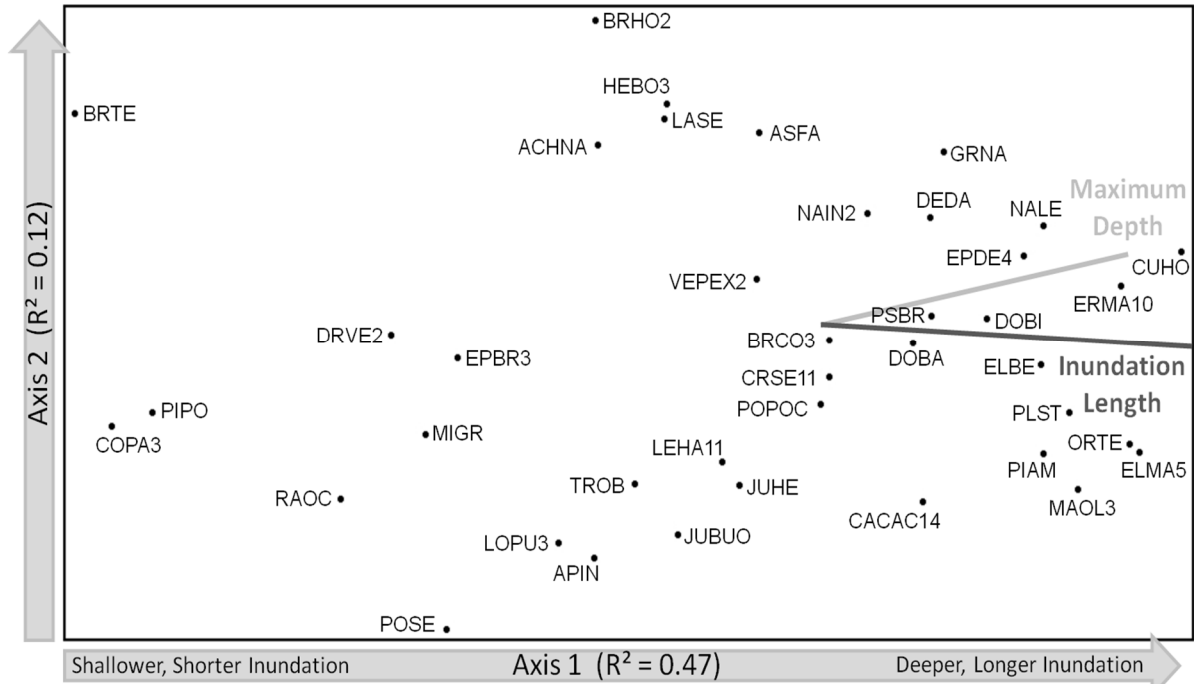


FIGURE 5. Non-metric multidimensional scaling ordination of species data. The amount of variance explained by each axis is shown as R^2 . Joint plot overlays indicate the relationship between species and the two hydrologic variables, maximum depth (light gray) and inundation period (dark gray). Symbols for individual species from USDA Plants Database (2015), from Gosejohan et al. (2017).

and Mefford, 2011). Hierarchical agglomerative cluster analysis (Legendre and Legendre 1998) was used to merge plots into clusters by maximizing the similarity of species composition according to the Sørensen distance measure and flexible beta group linkage method (flexible $\beta = -0.25$). We used indicator species analysis to identify species with both high specificity and fidelity for each plant community group (Dufrière and Legendre, 1997). Species with indicator values >25 were reported as diagnostic species for the group. A Multi-Response Permutation Procedure using a rank-transformed Sørensen distance measure was run in PC-Ord ver. 6 (Mielke and Berry, 2001; McCune and Mefford, 2011) to test whether plant community groups had significantly different species composition and to obtain the chance-corrected within-group agreement.

Species responses. The spatial distribution of inundation length and species cover was visu-

alized using Arc GIS ver. 10 (ESRI 2011). The relationship between *O. tenuis* responses, hydrologic variables, and litter depth were modeled in the statistical software package JMP ver. 11, using standard least squares regression (SAS Institute Inc., 2013). The sampling unit for all analyses was the 1m² plot.

RESULTS

We identified a total of 116 plant species in our 341 sampling plots. The most common were *Eryngium mathiasiae*, *Navarretia leucocephala*, *Eleocharis macrostachya*, and *Orcuttia tenuis*. The NMS ordination demonstrated that the vernal pool plant community was strongly related to both inundation period and maximum depth (Figure 5), with the most parsimonious 2-dimensional solution explaining 59% of the variance in the data (i.e., $R^2 = 0.59$). Axis 1 was correlated with both inundation ($R^2 = 0.77$) and maximum depth ($R^2 = 0.67$), and Axis 2 was

Vernal Pool Landscapes: Past, Present and Future

TABLE 1. Vernal pool community groups identified by clustering and indicator species, including inundation period and indicator species for each group. Non-native species are shown in bold, (n) refers to the number of plots for each group.

Community group (n)	Inundation Period (days)	Indicator Species
Short (120)	< 71	<i>Acmispon americanus</i> var. <i>americanus</i> <i>Bromus hordeaceus</i> <i>Epilobium brachycarpum</i> <i>Lactuca serriola</i> <i>Microsteris gracilis</i> <i>Trichostema oblongum</i>
Medium (153)	71 - 209	<i>Cuscuta howelliana</i> <i>Deschampsia danthonioides</i> <i>Epilobium densiflorum</i> <i>Grindelia nana</i>
Long (61)	> 209	<i>Castilleja campestris</i> ssp. <i>campestris</i> <i>Eleocharis bella</i> <i>Marsilea oligospora</i> <i>Pilularia americana</i> <i>Plagiobothrys stipitatus</i> <i>Psilocarphus brevissimus</i>

also correlated with maximum depth ($R^2 = 0.30$).

We identified three distinct vernal pool plant communities characterized by specific thresholds of inundation length and defined by diagnostic indicator species (Table 1). These communities were associated with short (< 71 days), medium (71-210 days), and long (> 210 days) periods of inundation. The overall misclassification rate of the model was 16% (classification accuracy = 0.84; $\kappa = 0.8$). Multi-Response Permutation Procedure analysis showed that species composition within the three community groups was more similar than expected due to chance, and a rank-transformed distance matrix showed significant chance-corrected within-group agreement (agreement = 0.35, $T = -146.44$, $p < 0.0001$). Most indicator species were associated with specific inundation periods, although some tolerated a wider range than others (Table 2). Abundant or widespread species that were not diagnostic indicators of community groups tended to occur on sites with

longer inundation periods. Plots supporting *O. tenuis* averaged 192.7 days of inundation, ranging from 136 days to 221 days.

Our two study sites supported different hydro-regimes. Adobe North was deeper but had shorter inundation periods than Coyote Springs (Figure 6). Adobe North supported a much wider range of inundation depths than Coyote Springs, and was filled to an average maximum water depth of 45 cm, with individual sampling points varying from 0 to 89 cm in depth. At Coyote Springs, maximum water depth averaged 19 cm, with individual sample points ranging from 0 to 49 cm. Adobe North was inundated for an average of 97 days (ranging from 0 – 204 days at individual points), while the mean inundation period at Coyote Springs was 139 days (ranging from 0 – 221 at individual points). Inundation patterns varied spatially across both sites (Figure 7).

We combined species-specific inundation requirements (Table 1) and the spatial distribu-

Merriam et al.: Effects of Hydroregime on Vernal Pool Plants in NE California

TABLE 2. Mean and standard deviation of inundation length (days) for community group indicator species, arranged in order of increasing mean inundation period. Other species that were not community group indicators, but that commonly occurred in our study plots, are shown in bold.

Species	Mean Inundation Length (days)	Standard Deviation (days)
<i>Epilobium brachycarpum</i>	31.6	43.3
<i>Microsteris gracilis</i>	38.7	57.1
<i>Bromus hordeaceus</i>	42.6	41.4
<i>Lactuca serriola</i>	43.7	36
<i>Trichostema oblongum</i>	68.1	66.5
<i>Acmispon americanus</i> var. <i>americanus</i>	70.3	71.7
<i>Grindelia nana</i>	101.5	55.3
<i>Deschampsia danthonioides</i>	109.6	58.9
<i>Epilobium densiflorum</i>	133.1	61.8
<i>Psilocarphus brevissimus</i>	140.8	69.6
<i>Eryngium mathiasiae</i>	148.6	63.5
<i>Navarretia leucocephala</i>	156.3	62.1
<i>Cuscuta howelliana</i>	159.9	55.1
<i>Plagiobothrys stipitatus</i>	167.4	59.3
<i>Castilleja campestris</i> ssp. <i>campestris</i>	172.8	68.2
<i>Eleocharis macrostachya</i>	174.7	49.5
<i>Pilularia americana</i>	182.5	49
<i>Eleocharis bella</i>	187.4	42.3
<i>Orcuttia tenuis</i>	192.7	27.7
<i>Marsilea oligospora</i>	205.5	33.3

tion of inundation lengths (Figure 7), to map the predicted distribution of species in our study vernal pools (Figure 8). We also compared the predicted distribution of *O. tenuis* based on the minimum observed inundation length of 136 days with the measured density of *O. tenuis* at each sample point (Figure 9). At Coyote Springs, *O. tenuis* occurred in 55% of plots that were inundated for 136 days or longer, while at Adobe North, *O. tenuis* was found in only 26% of the plots with this minimum inundation length or greater.

The density of *O. tenuis* varied with both inundation length and maximum depth (Figure 10). This relationship was linear for inundation length ($O. tenuis$ density = $-24.53 + 0.18 * \text{inundation length}$; $F_{1, 70} = 12.9$, $R^2 = 0.16$, $p <$

0.001). On the other hand, the relationship between *O. tenuis* density and maximum water depth was best represented by curvilinear relationship ($O. tenuis$ density = $7.44 + 0.26 * \text{depth} - 0.015196 * [\text{depth} - 40.281]^2$; $F_{1, 70} = 5.6$, $R^2 = 0.14$, $p < 0.01$). *Orcuttia tenuis* density reached a maximum between 30 and 60 cm of depth, beyond which *O. tenuis* density declined. Maximum inundation depths of greater than 50 cm only occurred at Adobe North.

Litter depth was significantly associated with reduced inundation lengths; for every additional 1 cm of litter depth, inundation periods were 18.5 days shorter (Figure 11). *Orcuttia tenuis* did not occur in plots where litter depth was greater than 8 mm, and plots where *O. tenuis* was present had significantly lower litter

Vernal Pool Landscapes: Past, Present and Future

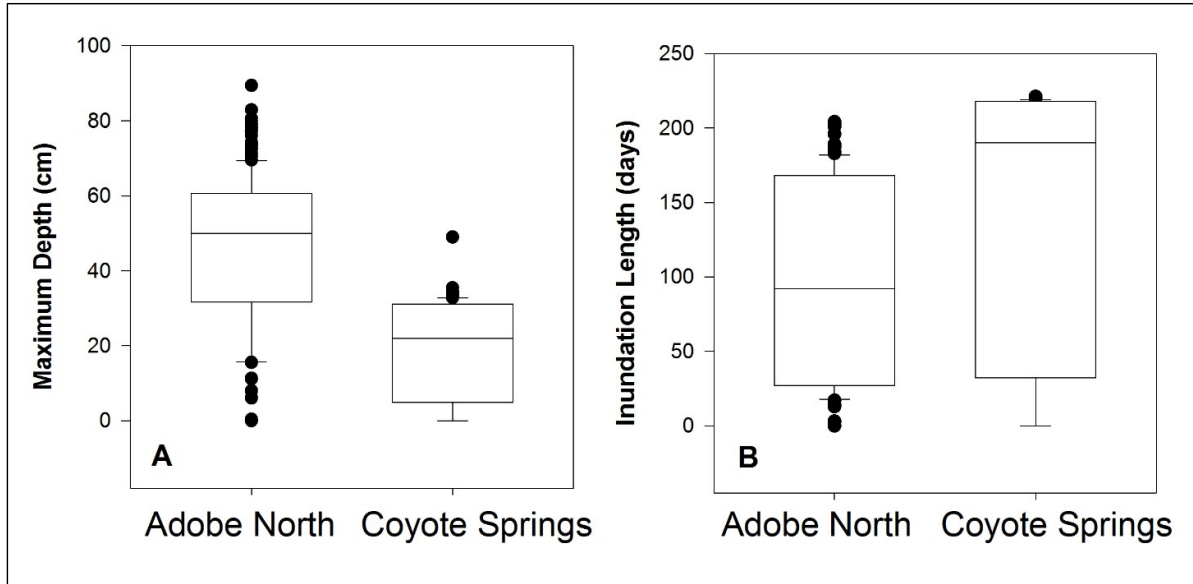


FIGURE 6. Boxplots of inundation depth (a) and length (b) at our two vernal pool study sites. Horizontal lines in boxes show median values; box boundaries show interquartile ranges, whiskers extend to 1.5 times the interquartile range, and outlier plots are shown as filled circles.

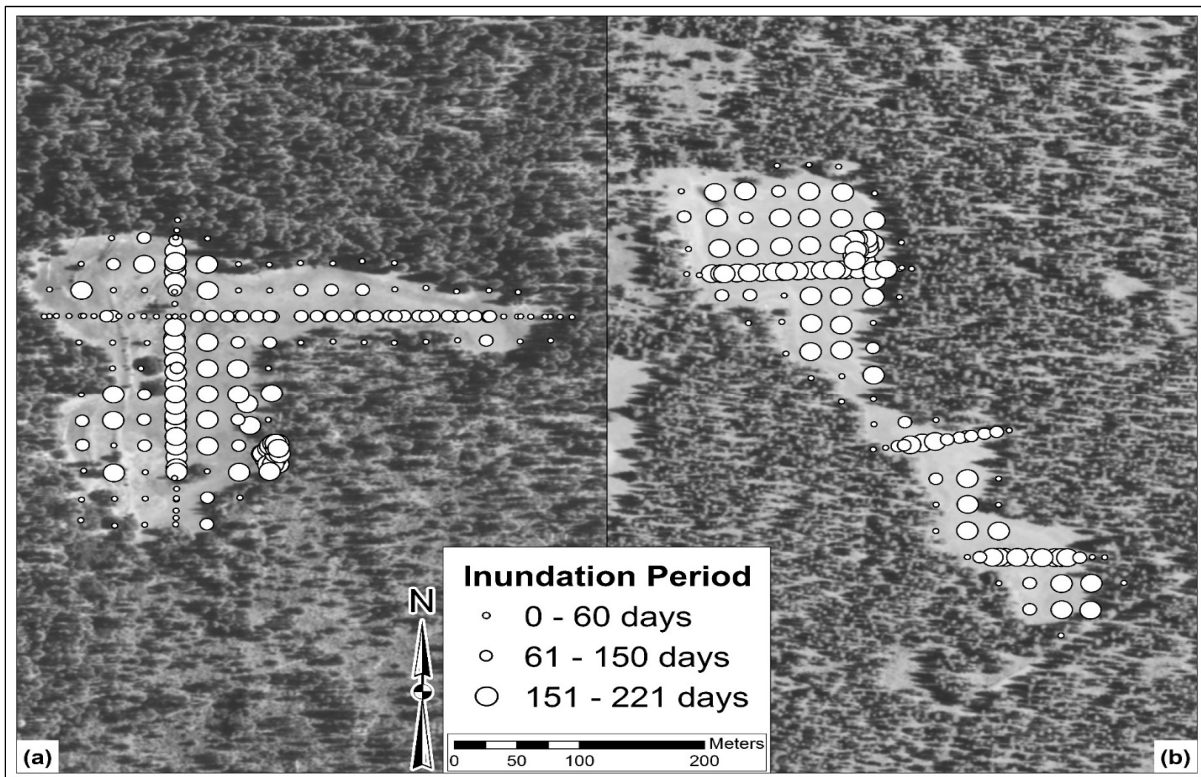


FIGURE 7. Both Adobe North (a) and Coyote Springs (b) exhibited spatial variation in maximum inundation lengths, from Gosejohan et al. (2017).

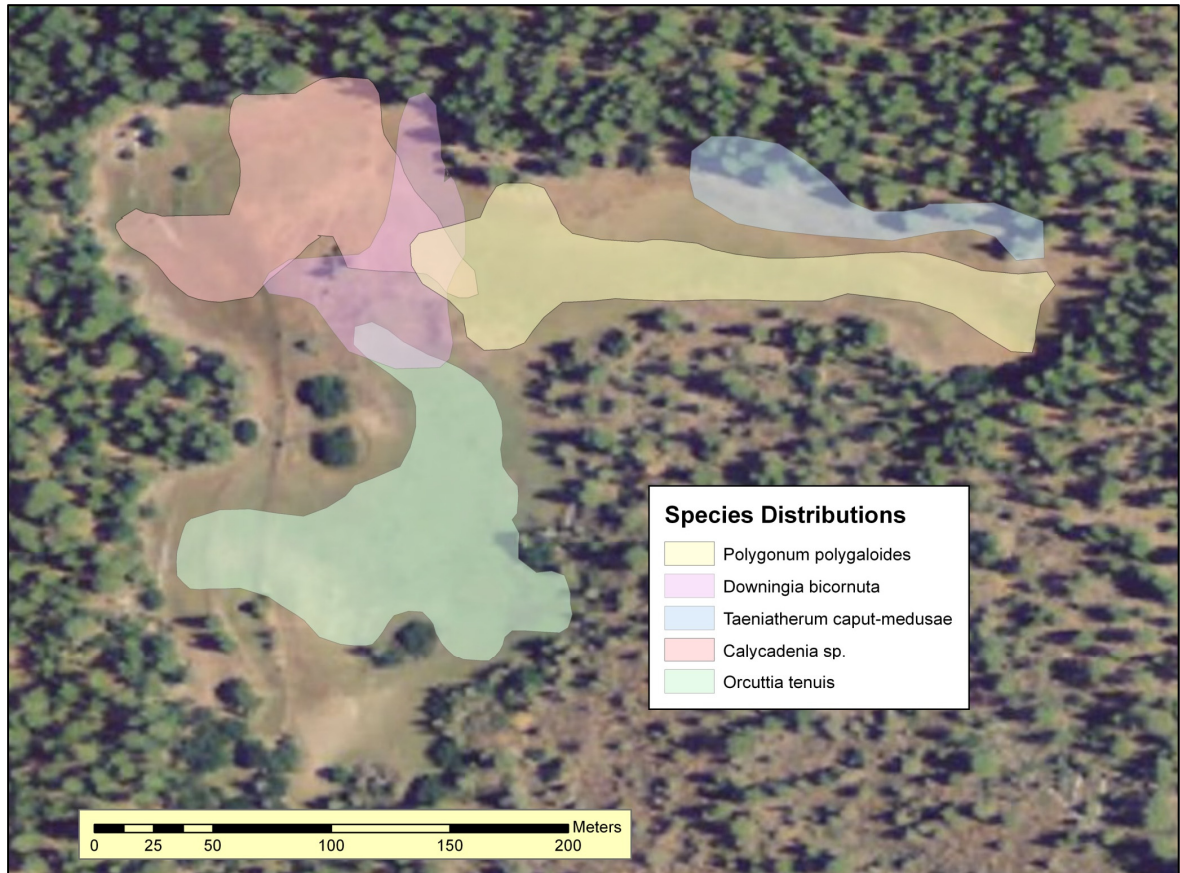


FIGURE 8. Predicted species distributions based on inundation requirements at Adobe North vernal pool.

depths than plots where *O. tenuis* was absent ($F_{1, 340} = 6.76, p < 0.001$), and (Figure 12).

DISCUSSION

Community Classification

Consistent with patterns described for vernal pools in other regions, plant community structure in northeastern California vernal pools is driven by hydrology. Our study sites exhibited zonation of plant community types according to the tolerance of individual species to the local inundation regime (Holland and Jain, 1984; Bliss and Zedler, 1998; Bauder, 2000; Deil, 2005; Emery et al., 2009; Gosejohan et al., 2017). Our study extends existing vernal pool plant classification schemes to northeastern California, and the long-inundated community

we identified (Table 1) represents a newly described community for California vernal pools (Gosejohan et al., 2017). This community group occurs in areas holding water longer than 209 consecutive days, a much longer inundation period than has been described for vernal pools in other areas of California, which generally stay inundated for less than 60 days (Solomeshch et al., 2007). However, most vernal pool species have strong germination cues, such as temperature, to prevent them from emerging under unfavorable conditions (Griggs, 1980; Keeley, 1988; Bliss and Zedler, 1998; Faist and Collinge, 2015), and many species at our study sites may not germinate until temperatures reach a specific minimum threshold. It is likely that the duration of the life cycles of vernal pool plant species observed in our study is consistent across their ranges, de-

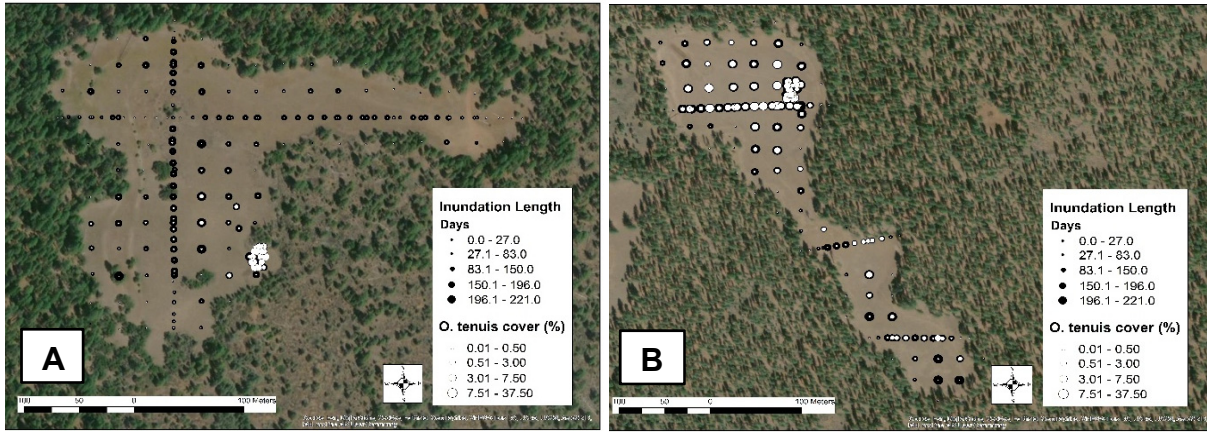


FIGURE 9. Percent cover of *O. tenuis* (filled circles) superimposed on length of inundation (days, open circles) at Adobe North (A) and Coyote Springs (B) vernal pools.

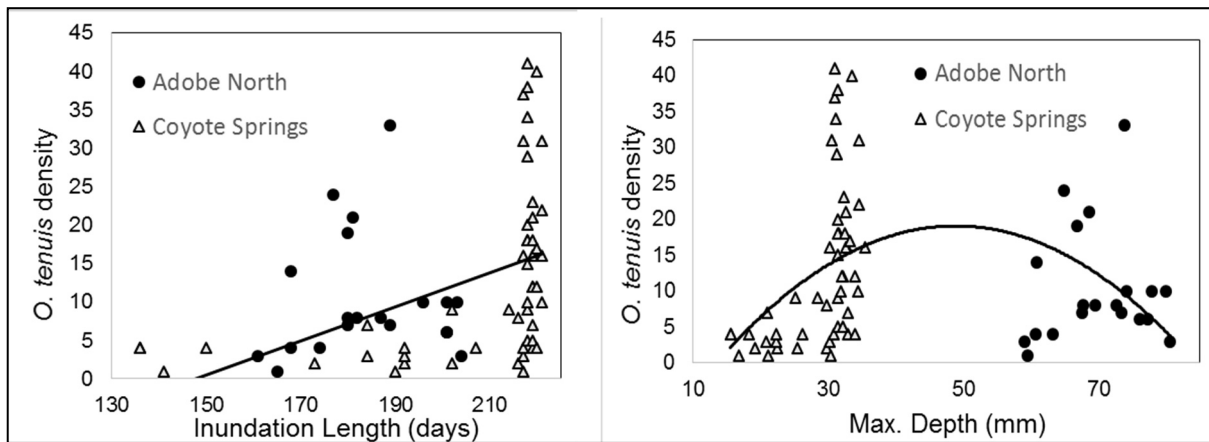


FIGURE 10. Density of *O. tenuis* as a function of inundation length (a) and depth (b). The relationship was linear for length ($O. tenuis$ density = $-24.53 + 0.1 * \text{inundation length}$; $F_{1,70} = 12.9$, $R^2 = 0.16$, $p < 0.001$), and quadratic for depth ($O. tenuis$ density = $7.44 + 0.26 * \text{depth} - 0.015196 * [\text{depth} - 40.281]^2$; $F_{1,70} = 5.6$, $R^2 = 0.14$, $p < 0.01$).

spite differences in the total length of pool inundation observed across regions.

We identified two non-native species, *Bromus hordeaceus* and *Lactuca serriola*, as indicators of the short-inundated community group, demonstrating that these species are able to tolerate some amount of inundation (Table 1), and that even in northeastern California non-native species may invade vernal pools. These species are likely to persist near pool edges, accumulate seeds in the soil seed bank, and encroach into vernal pool basins during drought years

(Gerhardt and Collinge, 2007; Collinge et al., 2011).

Orcuttia tenuis

Our results confirm the observations of other authors that *O. tenuis* benefits from longer inundation periods (Griggs, 1981; Griggs and Jain, 1983; Keeley, 1998). However, the relationship between *O. tenuis* and water depth may be complex. *Orcuttia tenuis* density was associated with increasing water depth until a maximum of approximately 30 - 60 cm, after

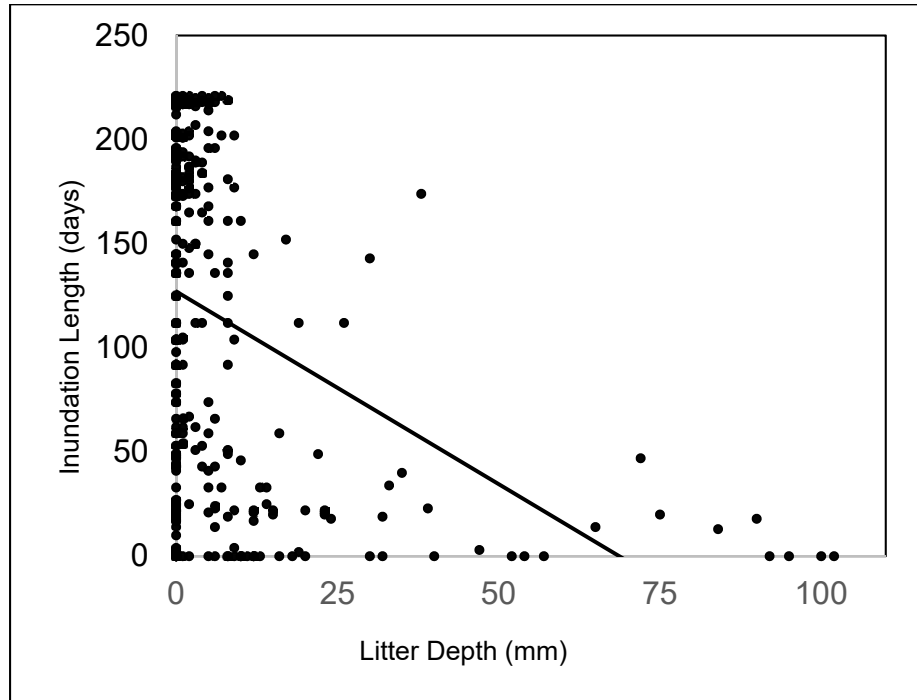


FIGURE 11. Litter depth significantly reduced inundation lengths ($F_{1,340} = 52$, $p < 0.001$)

which *O. tenuis* density decreased. Clark et al. (2008) found that *O. tenuis* was limited to portions of vernal pools that were less than 40 cm deep. *Orcuttia tenuis* may be limited by water depth because its aquatic leaves utilize the C4 photosynthetic pathway, which requires high light, temperature, and oxygen concentrations (Keeley, 1998). As suggested by Clark et al. (2008), the decline in *O. tenuis* we observed at higher water depths may be related to a reduction in oxygen or light availability that interfered with C4 photosynthesis. There may also be limits to how long juvenile *O. tenuis* leaves, which float on the surface of the water, can grow.

Livestock Grazing

The hydroregimes of our two study sites differed dramatically, particularly in the relationship between inundation length and depth (Figure 6). On average, Coyote Springs was inundated for approximately 40 days longer than Adobe North, while mean water depth was al-

most 26 cm less. The range of depths observed at Adobe North was almost twice that observed Coyote Springs, indicating more topographical heterogeneity. Vernal pool hydroregime is determined by a number of factors, including geology, soil type, depth to hardpan layer, patterns of subsurface and overland flow, and factors related to climate and vegetation such as precipitation and evapotranspiration (Holland and Dains, 1990; Hanes and Stromberg, 1998; Keeley and Zedler, 1998; Brooks and Hayashi, 2002). However, our study sites were similar in terms of climate, vegetation, and soils, suggesting that other, more localized variables might explain the differences in hydroregime we observed. One such variable is livestock management. Adobe North vernal pool has been fenced to exclude livestock since 1991, while Coyote Springs has been continuously grazed (USDA and USDI, 2012). The longer inundation periods we observed at Coyote Springs are consistent with the findings of other studies that grazed vernal pools have longer inundation periods than pools where livestock are excluded

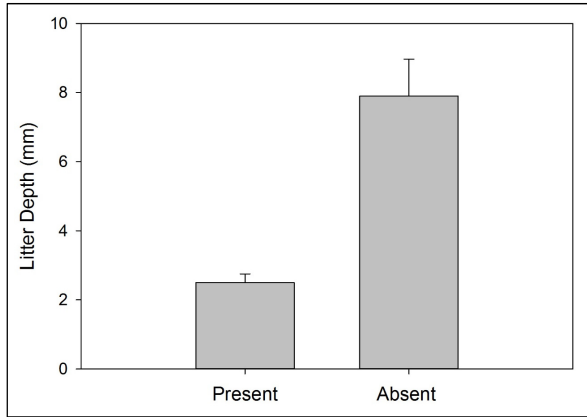


FIGURE 12. Litter depth was significantly lower in plots where *Orcuttia tenuis* was present compared with plots where no *O. tenuis* was recorded ($F_{1,340} = 6.75$, $p < 0.01$, error bars = standard error).

(Marty, 2005; Pyke and Marty, 2005; Marty, 2015; Faist and Beals, 2018). Marty (2015) found that continuously grazed pools averaged 41 days of inundation, while ungrazed pools were inundated for only 15 days. Livestock utilization has also been shown to reduce microtopographical variation as a result of trampling (Nash et al., 2003, 2004), which may explain the lower variation in water depth observed at Coyote Springs.

We found that litter depth was significantly associated with reduced inundation lengths (Figure 11), and there was significantly more litter accumulation at our ungrazed study site (Figure 13), contributing to a growing body of evidence that litter accumulation associated with livestock exclusion may decrease inundation lengths in vernal pools (Marty, 2005; Pyke and Marty, 2005; Marty, 2015; Faist and Beals, 2018). In the Central Valley, where cover of non-native grasses can exceed 80%, it is not surprising that litter would accumulate without grazing. However, results presented here and other work conducted in the vernal pools of northeastern California demonstrate that litter accumulation can be significant in the absence of grazing in this region as well (Merriam et al., 2016). Our data show that *O. tenuis* was associated with lower litter depths, and was never

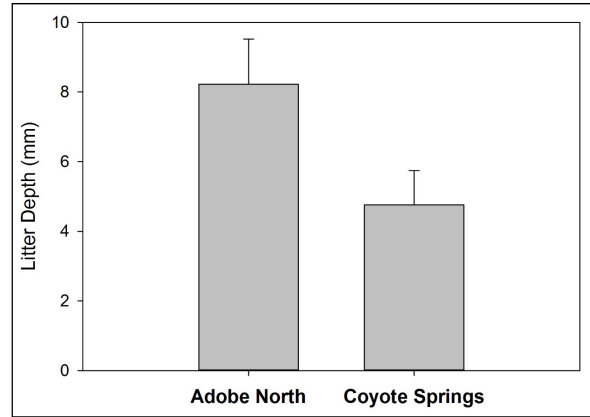


FIGURE 13. Litter depth was significantly lower at Coyote Springs vernal pool ($F_{1,340} = 4.0$, $p < 0.01$, error bars = standard error).

present in plots with more than 8 mm of litter (Figure 12). Merriam et al. (2016) found that as litter cover increased, *O. tenuis* presence, density and cover decreased, and hypothesized that negative associations between *O. tenuis* and litter cover were related to effects on germination and seedling growth. However, our results suggest this pattern may have also been a function of changes to the vernal pool hydroregime caused by litter accumulations; *O. tenuis* may have been excluded from plots with high amounts of litter because this reduced the vernal pool inundation period below the minimum 136 days required by this species.

Management Recommendations

Vernal pools in northeastern California have been degraded by a number of activities that have modified vernal pool hydrology, including the construction of dams, ditches and roads. Holland (2006) found that over 30% of the 660 pools mapped on the Modoc National Forest exhibited hydrologic degradation. Restoration of vernal pool hydrology has been identified as a primary management goal for vernal pool species, including *O. tenuis* (USDA and USDI, 1989; USDI, 2005; USDA and USDI, 2012). In addition to hydrologic restoration, our results are consistent with those of a number of other studies suggesting that active management of

Merriam et al.: Effects of Hydroregime on Vernal Pool Plants in NE California

vernal pool landscapes may be necessary to limit litter accumulation and maintain vernal pool hydroregimes, for example through livestock grazing. However, livestock grazing can negatively affect vernal pool specialist perennials, and excessive soil damage from cattle hoofprints can negatively affect vernal pool annuals (Merriam et al., 2016; Bovee et al., 2018). Therefore, livestock utilization must be carefully monitored and managed to prevent negative effects, and other methods of controlling litter accumulation, such as mowing or prescribed burning, may be warranted in some areas.

ACKNOWLEDGEMENTS

Funding for this research was provided by the United States Forest Service, the USDA National Institute of Food and Agriculture Hatch project NEV052XG, California Department of Fish and Game, the Bureau of Land Management, California Native Plant Society, Northern California Botanists, and the University of Nevada Reno College of Agriculture, Biotechnology, and Natural Resources. We would like to thank Laurel Saito for insight on the use of stage gauges in the field method design. We would also like to thank Ian Grinter, Brian Hindman, Tim Kellison, Don Lepley, Ashton Montrone, Cassandra Rivas and Derek Young for their assistance with field data collection.

LITERATURE CITED

- BAILEY, R.G. 1995. Descriptions of the ecoregions of the United States, 2nd edition. Miscellaneous Publication 1391. USDA Forest Service, Washington, D.C.
- BALDWIN, B.G., D.H. GOLDMAN, D.J. KEIL, R. PATTERSON, T.J. ROSATTI, and D.H. WILKEN. 2012. The Jepson Manual: Vascular plants of California, 2nd edition. University of California Press, Berkeley, CA.
- BARBOUR, M.G., A.I. SOLOMESHCH, R.F. HOLLAND, C.W. WITHAM, R.L. MACDONALD, S.S. CILLIERS, J.A. MOLINA, J.J. BUCK, and J.M. HILLMAN. 2005. Vernal pool vegetation of California: communities of long-inundated deep habitats. *Phytocoenologia* 35:177-200.
- BAUDER, E.T. 2000. Inundation effects on small-scale distributions in San Diego, California vernal pools. *Aquatic Ecology* 34:43-61.
- BLISS, S.A., and P.H. ZEDLER. 1998. The germination process in vernal pools: sensitivity to environmental conditions and effects on community structure. *Oecologia* 113:67-73.
- BOVEE, K.M., K.E. MERRIAM, and M.C. GOSEJOHAN. 2018. Livestock grazing affects vernal pool specialists more than habitat generalists in montane vernal pools. *Applied Vegetation Science* 21:12-20.
- BROOKS, R.T., and M. HAYASHI. 2002. Depth-area-volume and hydroperiod relationships of ephemeral (vernal) forest pools in southern New England. *Wetlands* 22: 247-255.
- CALIFORNIA NATIVE PLANT SOCIETY (CNPS). 2018. A Manual of California Vegetation, Online Edition. <http://www.cnps.org/cnps/vegetation/> accessed April 3, 2018. California Native Plant Society, Sacramento, CA.
- CALIFORNIA DEPARTMENT OF FISH AND WILDLIFE (CDFW). 2018. Nongame Wildlife Program, Special Plant and Animal Lists. Sacramento, CA.
- CLARK, M., R. LIS, D. FAIRBANKS, and K. SCHIERENBECK. 2008. A spatial and temporal investigation of *Eleocharis macrostachya* and *Orcuttia tenuis*. *Madrõno* 55:257-268.
- COLLINGE, S.K., C. RAY, and F. GERHARDT. 2011. Long-term dynamics of biotic and abiotic resistance to exotic species invasion in restored vernal pool plant communities. *Ecological Applications* 21: 2105-2118.

Vernal Pool Landscapes: Past, Present and Future

- DAUBENMIRE, R. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33:43-64.
- DEIL, U. 2005. A review on habitats, plant traits and vegetation of ephemeral wet-lands—a global perspective. *Phytocoenologia* 35:533-706.
- DUFRENE, M., and P. LEGENDRE. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345-366.
- EMERY, N.C., M.L. STANTON, and K.J. RICE. 2009. Factors driving distribution limits in an annual plant community. *New Phytologist* 181:734-747.
- ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE (ESRI). 2011. ArcGIS desktop, version 10. Redlands, CA.
- FAIST, A.M., and S.C. BEALS. 2018. Invasive plant feedbacks promote alternative states in California vernal pools. *Restoration Ecology* 26: 255-263.
- FAIST, A.M., and S.K. COLLINGE. 2015. Seed bank composition varies along invasion and inundation gradients in vernal pool wetlands. *Plant Ecology* 216:553-564.
- GERHARDT, F., and S.K. COLLINGE. 2007. Abiotic constraints eclipse biotic resistance in determining invisibility along experimental vernal pool gradients. *Ecological Applications* 17:922-933.
- GOSEJOHAN, M.C., P.J. WEISBERG, and K.E. MERRIAM. 2017. Hydrologic influences on plant community structure in vernal pools of northeastern California. *Wetlands* 37:257-268.
- GRIGGS, F.T. 1980. Population studies in the genus *Orcuttia* (Poaceae). PhD Thesis, University of California, Davis, CA.
- GRIGGS, F.T. 1981. Life histories of vernal pool annual grasses. *Fremontia* 9:14-17.
- GRIGGS, F.T., and S.K. JAIN. 1983. Conservation of vernal pool plants in California, II. Population biology of a rare and unique grass genus *Orcuttia*. *Biological Conservation* 27:171-193.
- HANES, T., and L. STROMBERG. 1998. Hydrology of vernal pools on non-volcanic soils in the Sacramento Valley. Pages 38-49 in C.W. Witham, E.T. Bauder, D. Belk, W.R. Ferren, Jr., and R. Ornduff (Editors). *Ecology, conservation, and management of vernal pool ecosystems – proceedings from a 1996 conference*. California Native Plant Society, Sacramento, CA.
- HOLLAND, R.F., and V.I. DAINS. 1990. The edaphic factor in vernal pool vegetation. Pages 31-48 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, CA.
- HOLLAND, R.F., and S.K. JAIN. 1984. Spatial and temporal variation in plant species diversity of vernal pools. Pages 198-209 in S. Jain and P. Moyle (Editors). *Vernal pools and intermittent streams*. Institute of Ecology, University of California, Davis, CA.
- KEELER-WOLF, T., D.R. ELAM, K. LEWIS, and S.A. FLINT. 1998. California Vernal Pool Assessment Preliminary Report. California Department of Fish and Game, Sacramento, CA.
- 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. 1998. C4 photosynthetic modifications in the evolutionary transition from land to water in aquatic grasses. *Oecologia* 116:85-97.
- KEELEY, J.E., and P.H. ZEDLER. 1998. Characterization and global distribution of vernal pools. Pages 1-14 in C.W. Witham, E.T. Bauder, D. Belk, W.R. Ferren, Jr., and R. Ornduff (Editors). *Ecology, conservation, and management of vernal pool ecosystems – proceedings from a 1996 conference*. California Native Plant Society, Sacramento, CA.

Merriam et al.: Effects of Hydroregime on Vernal Pool Plants in NE California

- LEGENDRE, P., and L. LEGENDRE. 1998. Numerical ecology. 2nd edition. Elsevier Science, Amsterdam, Netherlands.
- MARTY, J.T. 2005. Effects of cattle grazing on diversity in ephemeral wetlands. *Conservation Biology* 19:1626-1632.
- MARTY, J.T. 2015. Loss of biodiversity and hydrologic function in seasonal wetlands persists over 10 years of livestock grazing removal. *Restoration Ecology* 23:548-554.
- MCCUNE, B., and J.B. GRACE. 2002. Analysis of ecological communities. MjM software design. Glenden Beach, OR.
- MCCUNE, B., and M.J. MEFFORD. 2011. PC-ORD. Multivariate Analysis of Ecological Data, version 6.0. MjM software design. Glenden Beach, OR.
- MERRIAM, K., M. GOSEJOHAN, P. WEISBERG, and K. BOVEE. 2016. Livestock use has mixed effects on slender orcutt grass in Northeastern California Vernal Pools. *Rangeland Ecology & Management* 69: 185-194.
- MIELKE, P.W., and K.J. BERRY. 2001. Permutation methods: A distance function approach. Springer-Verlag, New York, NY.
- NASH, M.S., E. JACKSON, and W.G. WHITFORD. 2003. Soil microtopography on grazing gradients in Chihuahuan desert grasslands. *Journal of Arid Environments* 55:181-192.
- NASH, M.S., E. JACKSON, and W.G. WHITFORD. 2004. Effects of intense, short-duration grazing on microtopography in a Chihuahuan Desert grassland. *Journal of Arid Environments* 56:383-393.
- PYKE, C.R., and J.T. MARTY. 2005. Cattle grazing mediates climate change impacts on ephemeral wetlands. *Conservation Biology* 19:1619-1625.
- STATISTICAL ANALYSIS SOLUTIONS (SAS). 2013. JMP Statistical Software version 11. Cary, NC.
- SOLOMESHCH, A.I., M.G. BARBOUR, and R.F. HOLLAND. 2007. Vernal pools. Pages 394-424 in M.G. Barbour, T. Keeler-Wolf, and A.A. Schoenherr (Editors), *Terrestrial Vegetation of California*. University of California Press, Berkeley, CA.
- U.S. DEPARTMENT OF AGRICULTURE (USDA) and U.S. DEPARTMENT OF INTERIOR (USDI). 2012. Conservation strategy for slender Orcutt grass on federal lands of the Southern Cascades and Modoc Plateau. USDA Forest Service, Lassen and Modoc National Forests, USDI Bureau of Land Management, Alturas Field Office, Alturas, CA.
- U.S. DEPARTMENT OF AGRICULTURE (USDA) and U.S. DEPARTMENT OF INTERIOR (USDI). 1989. *Orcuttia tenuis* species management guide in B. Corbin and G. Schoolcraft (Editors), Lassen National Forest, Pacific Southwest Region 5, and the Susanville District of the Bureau of Land Management, Susanville, CA.
- U.S. DEPARTMENT OF INTERIOR (USDI). 1997. Endangered and threatened wildlife and plants; determination of endangered status for three plants and threatened status for five plants from vernal pools in the Central Valley of California. *Federal Register* 62:14338-14352.
- U.S. DEPARTMENT OF INTERIOR (USDI). 2005. Recovery Plan for Vernal Pool Ecosystems of California and Southern Oregon. U.S. Fish and Wildlife Service, Portland, OR.
- U.S. DEPARTMENT OF AGRICULTURE (USDA), NATURAL RESOURCE CONSERVATION SERVICE (NRCS). 2018. Web Soil Survey. Accessed at <https://www.nrcs.usda.gov/wps/portal/nrcs/main/soils/survey/>
- ZEDLER, P.H. 1984. Micro-distribution of vernal pool plants of Kearny Mesa, San Diego County. Pages 185-197 in S. Jain and S. Moyle (Editors), *Vernal Pools and Intermittent Streams*. Institute of Ecology, University of California, Davis, CA.

Vernal Pool Landscapes: Past, Present and Future