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RESEARCH ARTICLE

Reinvasion of restored California vernal pools reveals the importance of long-term restoration planning

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Ecological restoration often focuses on short-term intervention efforts with the goal of creating restored ecosystems that do not require continuous human maintenance. Here, we ask: Do short-term restoration efforts result in self-sustaining native assemblages, or do these restored ecosystems require long-term management to prevent reinvasion of exotic species? We address this question using restored vernal pool wetlands in coastal California. Restoration efforts in vernal pool ecosystems are often hindered because many restored vernal pools exist within a grassland matrix that is highly invaded by exotic annual grasses and forbs. To test whether restored pools experienced reinvasion, we assessed plant species abundance and diversity at varying times after intensive weeding had ceased. The central bottom of pools, where inundation duration is the longest, showed stable or even increasing native cover and no trends in exotic abundance over time. However, exotic cover and richness increased in the upland edges of the pools, where drier conditions allow exotic grasses from the surrounding unrestored grassland to grow. Our findings indicate that edges of restored ecosystems are susceptible to invasion over time, but that this depends on abiotic and biotic conditions within the ecosystem, such as pool shape and landscape matrix, that can potentially be manipulated through initial planning (e.g., constructing circular pools) and long-term management (e.g., annual weeding). Our findings highlight the importance of ongoing monitoring and adaptive management and support a paradigm shift away from short-term interventions and toward viewing restoration as a longstanding relationship with the land that may require continuous human management.

Key words: adaptive management, California grassland, ecological restoration, invasion, long-term management, monitoring

Implications for Practice

- Reinvasion by unwanted exotic plant species, and subsequent decline in native plant abundance and diversity, is likely to occur after the active management of restoration projects ceases.
- To combat the reinvasion of exotic species and to successfully restore resilient native plant assemblages, restoration projects need to invest in a long-term relationship with the sites.
- Restoration and long-term stewardship include long-term monitoring, adaptive management, and community engagement.
- Restored vernal pools can be maintained through the strategic construction of circular pools in small parcels, and the edges of the pools need to be actively managed and weeded to prevent reinvasion.

Introduction

Modern ecological restoration projects generally focus on short-term interventions due to limited funding, finite resources, and short policy or grant cycles. We define short-term intervention efforts as the "implementation phase" recognized by the Society for Ecological Restoration, which includes the initial 1–5 years of restoration (Gann et al. 2019). This implementation phase involves substantial money, labor, equipment, and other resources to alter the abiotic environment, remove exotic species, and introduce native species. The implementation phase initiates ecosystem recovery by targeting and manipulating key determinants of successional pathways (e.g., altering abiotic environmental site conditions and the abundance of species; Pickett

et al. 2009). After short-term restoration efforts cease, the restored ecosystems become subject to ambient drivers of succession, such as the natural recruitment of plants via existing populations (including exotic species) and uncontrolled environmental conditions that favor some species over others (Aoyama et al. 2022). For desired native populations to persist past the initial implementation phase, natural recruitment and environmental conditions must favor these native species.

Landscape context has long been recognized as an important factor influencing the trajectory of a restoration site (Naveh 1994; Holl & Aide 2011; Crouzeilles et al. 2016). Landscape heterogeneity, such as grasslands scattered with trees, can contain species-rich microhabitats that increase overall species diversity (Janišová et al. 2014). Land use history also affects species diversity, as undisturbed landscapes can harbor species-rich seed banks. Seed availability and dispersal also affect species diversity in restoration sites, and there is a tendency for restoration sites to become dominated by weedy species that are already present at the site (Tscharntke et al. 2011). For natural recruitment into a restored site to be dominated by desirable species, the most abundant populations in the matrix surrounding the restoration site should be native species (White et al. 2004). Initial restoration plantings often establish small populations of desirable species that frequently exist as patches within a fragmented landscape otherwise dominated by undesirable exotic species and isolated from other native populations (Scott et al. 2001). In such settings, after the implementation phase ends, isolated restored sites may become reinvaded quickly by undesirable species from the surrounding landscape. Even if there are native individuals present, environmental conditions (e.g., climate change, competition) may prevent population growth and even result in local extirpation (Aoyama et al. 2022). For example, restored wetlands that established an average of 28 native species within the implementation phase subsequently experienced a decline in richness to 12 native species 6 years later (Gutrich et al. 2009).

Reinvasion of restored ecosystems by exotic species is a common challenge faced by restoration practitioners, and it is well known that exotic species are particularly adept at colonizing open niche spaces following disturbances and under shifting climatic conditions (Mack & D'Antonio 1998; Walther et al. 2009). One-time exotic species removal efforts can also lead to a secondary invasion, wherein another (sometimes more problematic) invasive species establishes after the removal of the original invasive species (D'Antonio et al. 2017). Pearson et al. (2016) found that secondary invasion of exotic species occurred in all 60 of the weed management projects they surveyed in a global meta-analysis. They found a strong inverse relationship between secondary invader abundance and original invader abundance, suggesting that secondary invaders took advantage of reduced competition and more resources after the original invaders were eradicated.

Vernal pool assemblages in California, U.S.A., are especially susceptible to reinvasion by exotic plants after initial restoration, particularly by annual grasses from Europe (Stromberg et al. 2007; Cox & Allen 2011). In California's Mediterranean climate, vernal pools form atop an impermeable subsurface soil layer during the cool, wet winters and then dry out during the warm, dry summers (Barbour et al. 2007). Endemic plant species flourish in this unique environment with adaptations that allow them to survive prolonged flooding, while also growing and reproducing quickly before pools completely desiccate during the summer (Zedler 1987). Specialist species that have adapted to withstand this hydrologic regime can take advantage of the lower amount of competition in these harsh environments (Emery et al. 2009). Some native plant species, such as *Lasthenia fremontii* (vernal pool goldfields), are only found in the deepest, most inundated zone of the pool and cannot withstand drier conditions, whereas other species, such as *Limnanthes alba* (white meadowfoam), are adapted to slightly drier conditions along the shallow edge zones of the pool and cannot withstand extreme flooding events (Emery et al. 2009). The pool landscape can be heterogeneous within the space of a few meters, which has direct implications (and complications) for native species growth and persistence and thus restoration and management. In addition, pools typically exist within a landscape matrix that is dominated by invasive exotic plant species, resulting in edge effects wherein the pool margins are exposed to the invasion front of surrounding exotic species (Keeley & Zedler 1998).

Vernal pool restoration projects have had varying levels of success, particularly in southern California (Black & Zedler 1998). This may be due to variable site characteristics and competitive pressures from exotic plant species in some zones of the pool or some parts of the pool complex (Gerhardt & Collinge 2007). Restoration actions often consist of topographic excavation of deeper pool basins, resulting in prolonged flooding of the central zone of the pool, followed by the addition of native plants. Creating wet abiotic conditions allows any added native seed to grow and reproduce without competition from invasive exotic species that cannot withstand inundation. Yet, as elevation increases up to the pool's edge, conditions become drier, and the community is more susceptible to invasion by generalist European grasses that can opportunistically invade drier open niche space (Zedler 1987; Bliss & Zedler 1997). Gerhardt and Collinge (2007) showed that, even when native species were abundant, a longer inundation period was needed to preclude subsequent exotic invasion. They manipulated the inundation period in a greenhouse experiment and found that, although the growth and reproduction of some exotic species were reduced when grown with native species, longer inundation significantly decreased the survival of exotic species. A field study by Faist and Beals (2018) similarly found that pools with higher invasive species cover also had shorter inundation periods. Drier years can cause an increase in exotic forbs in pool basins, likely due to the lack of abiotic resistance normally afforded by flooding (Bauder 2000).

In addition to the abiotic conditions that need to be established in the pool center to reduce its invasibility, biotic manipulation of the pool edges may need to be a continual effort to prevent exotic reinvasion (Davis et al. 2000). Marty (2015) reported that an increase in exotic species cover coincided with the discontinuation of a vernal pool site's weed management program, which had included grazing. Marty found that reintroducing grazing allowed pool plant communities to recover

significantly higher native cover than ungrazed pools, with the greatest increase in native plant cover found around the pool edges. These edge effects, or conditions at the edges of sites that alter abiotic conditions, species composition, and ecological processes, can often have detrimental ecological consequences (Porensky & Young 2013). For example, hotter, drier, and more variable conditions along exposed forest edges can result in higher tree mortality rates, and exotic propagule pressure and anthropogenic disturbance can correlate with higher exotic plant species and lower native plant species on the edges of preserved grasslands (Laurance et al. 2002; Gieselman et al. 2013). In vernal pools, pools with more edge area exposed to surrounding unrestored grassland (e.g., higher pool perimeter-to-area ratio) may also be more susceptible to similar edge effects, including invasion. Habitat fragmentation studies have shown that fragments with higher perimeter-to-area ratios exhibit higher exotic cover (Gorchov et al. 2014). Restoration efforts in these drier zones often include weeding out invading exotics, which is generally not needed in the central zone where inundation excludes invasive species (Emery et al. 2009). This biotic manipulation can allow native species to reestablish, but the duration of weeding is often limited to the implementation phase due to financial constraints (Holl et al. 2022).

Overall, the management challenges faced by restored vernal pool assemblages are tenacious and long-lasting, while most restoration projects are restricted to the short timescale of the implementation phase. To date, most research on vernal pool restoration has been focused on short-term measures of restoration success, but it is unclear how successful short-term interventions are in the long run. We explored the long-term success of restored vernal pools through two approaches. First, we conducted a 3-year study on a complex of pools that were transitioning from the implementation phase to the post-restoration phase during the study period. By evaluating changes in vegetation composition in these pools during this pivotal transition period, we asked: (1) How did exotic plant abundance and richness change in these restored pools over time? (2) How did native plant abundance and richness change in these restored pools over time? As restored pools receive less weeding and native planting over time, we might expect the reinvasion of exotic grasses from the surrounding grassland matrix.

Our second approach involved a broad survey of 69 vernal pools from nine different restoration projects carried out over 33 years, which allowed us to explore how climatic and landscape conditions correlate with the abundance and diversity of plant species within restored vernal pools after the implementation phase. If exotic plant species reinvade vernal pools over time, we might expect various site landscape factors to influence the plant assemblages. For example, pools that experience more precipitation and/or have deeper basins may sustain longer inundation periods that favor more native species, while pools that have more edge area exposed to the exotic-dominated surrounding grassland may be more susceptible to invasion (Platenkamp 1998; Bauder 2000; Gorchov et al. 2014). We asked: (3) What abiotic factors correlate with higher exotic plant abundance and richness in restored pools over time? (4) What abiotic factors correlate with lower native plant abundance and richness in restored pools over time?

Methods

Study Area

We studied restored vernal pools on land managed by the University of California, Santa Barbara (UCSB), the Isla Vista Recreation and Parks District, and the City of Goleta, in Santa Barbara County, California, U.S.A. (Fig. 1). This land is part of unceded ancestral territory of the Chumash people. The study areas lie within 1 mile of the Pacific Ocean and experience a Mediterranean climate with cool (13.3°C average) and wet conditions from November to April and warm (15.6°C average) and dry conditions during the remainder of the year (PRISM 2019). Rainfall averages approximately 43.18 cm per year with high variation associated with extreme rainfall events and droughts. The proximity of the area to the Pacific Ocean moderates winter lows, and frost is rare. Summer fog moderates summer highs, although offshore "sundowner" winds may bring hot (over 32°C) dry conditions to the area, especially in the late summer and fall (Blier 1998). Soil formation is dominated by weathering of uplifted shales, and soils have a high clay content. Soils are Mollisols, with the dominant soil series being Concepción fine sandy loam and Diablo clay (Soil Survey Staff 2022).

Approach 1: Multiyear Monitoring Study

We monitored 7 restored vernal pools within UCSB's North Parcel, which consists of vernal pools built amidst university faculty housing. The pools were created between 2011 and 2014 by grading to form pool basins ranging from 67 to 425 m^2 in area and 14–18 cm deep (see Supplement S1 for a full description of restoration actions). Approximately 70 species of locally-sourced native plants were introduced to pool basins, including species endemic to vernal pools and generalist wetland and upland species. Most species were introduced by planting seedlings in patches to mimic landscape patterns generally observed in nature, according to soil types, hydrology, and other site factors. Installed plantings were watered using movable drip irrigation and hand-watering until establishment was achieved. Some annual species were direct-seeded. Exotic species were mainly controlled by hand-weeding, although solarization, herbicide, and green flaming treatments were also employed to a lesser degree. All these restoration actions took place within a 5-year implementation phase.

Within each restored vernal pool, we established a series of permanent monitoring quadrats. We delineated each pool into central (experiencing longest inundation period), transition (inundated or hydric soil during longest inundation period), and upland (inundated during extreme storms but otherwise non-hydric soils) zones (Fig. 2A). Within each of these zones, we haphazardly placed three 1 m^2 quadrats, for a total of 9 quadrats per pool. We monitored the vernal pools monthly from November 2016 to December 2019. Because the pools were different ages at the start of the experiment, sampling over 3 years allowed us to evaluate the vegetation community in pools ages 2–9 years old. Within each quadrat, we determined the identity and percent cover of all species present. We also recorded the percent cover of bare ground, water, and thatch (dead plant

Figure 1. Map showing 69 surveyed pools (highlighted in yellow) throughout nine sites (highlighted in orange): Del Sol Vernal Pool Preserve (11 pools), Camino Corto Open Space (7 pools), Manzanita Village (5 pools), North Campus Open Space (8 pools), North Parcel (9 pools), Sierra Madre (1 pool), South Parcel (10 pools), Storke Ranch (5 pools), West Campus Bluffs (12 pools).

matter). In addition, we estimated the number and percent cover of germinating seedlings for native species. Because low-growing graminoids and forbs were often overlaid by taller species, the total percent cover could exceed 100% in each quadrat. To measure the pool area, we used a Trimble GPS to map out the perimeters of each pool. We used a laser level to measure the depth of each pool. We obtained climate data from the National Oceanic and Atmospheric Administration Daily Summaries dataset for the Santa Barbara Municipal Airport weather station to calculate the average annual rainfall each pool experienced after it was restored (National Oceanic and Atmospheric Administration, National Centers for Environmental Information 2018).

Approach 2: Chronosequence Survey

The 69 pools surveyed in this study were restored between 1986 and 2017. The pools all shared similar attributes in terms of past and restored abiotic and biotic conditions, so we constructed a chronosequence that used a space-for-time substitution to examine the effect of time since restoration on native and exotic cover and richness. Past restoration actions included grading and berm enhancement to attain basin topography with an area ranging from 66 to 1,367 m^2 and a maximum depth ranging from 53.5 to 80 cm, planting of locally-sourced native plant species via seeding and transplanting, and hand-weeding and herbicide treatments of exotic species during a 2- to 5-year implementation phase (see Supplement S2 for details on pool characteristics).

In the spring of 2019, we conducted vegetation surveys in each pool when the majority of the native species were at peak biomass. For each pool, we laid out 2 transects bisecting the pool along its elliptical major and minor axes (Fig. 2B). Every other meter along each transect, we laid down a 1 m^2 quadrat with 1% subdivisions. We identified every plant species present and estimated its percent cover in each quadrat. We also estimated the percent cover of bare ground and thatch. Because low-growing graminoids and forbs were overlaid with taller species, the total percent cover could exceed 100% in each quadrat. We also categorized each quadrat as being in the central, transition, or upland zone of the pool. To measure relative elevation, we
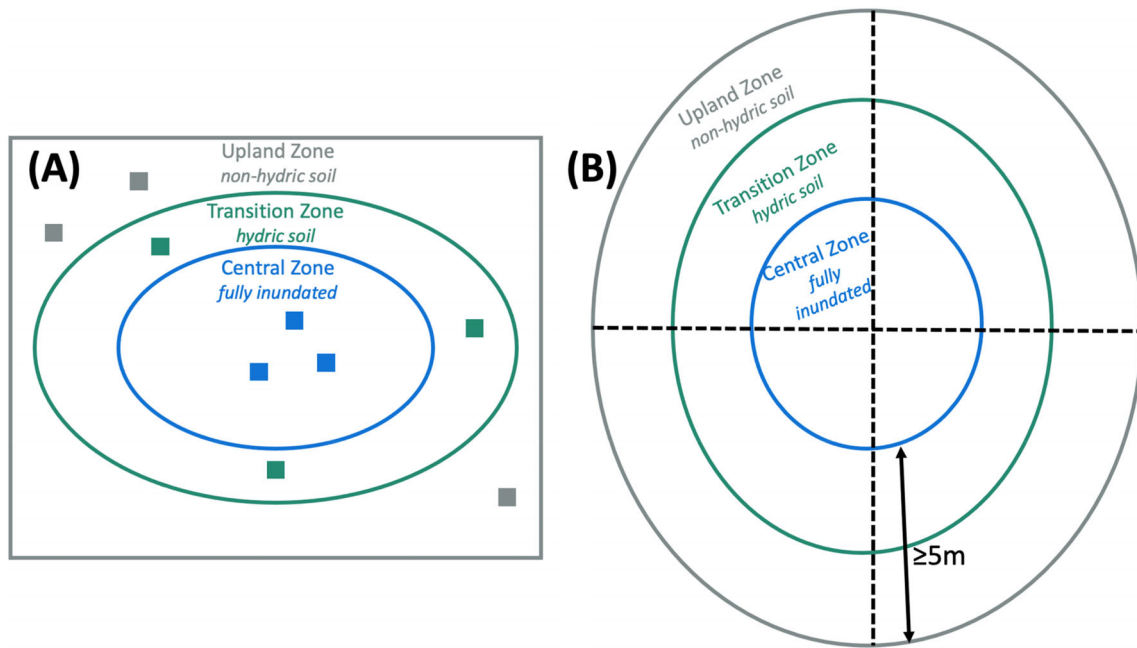
Figure 2. (A) Schematic of the sampling design for the multiyear monitoring study. Each pool was divided into central (blue), transition (green), and upland (gray) zones. Squares represent the haphazard approach taken to determine the location of permanent quadrats used for long-term monitoring; the exact location of the quadrats varied for each pool. (B) Schematic of the sampling design used for the 2019 chronosequence survey. Each pool was divided into central (blue), transition (green), and upland (gray) zones. 2 sampling transects bisected each pool, along which quadrats were placed every other meter; the exact location of the transects varied for each pool.

used a laser level to calculate the elevation of each quadrat above the deepest point of the pool. To determine pool hydroperiod, we installed 0.8 m rulers in the deepest part of each pool in January 2019 and recorded the depth of the water in each pool every week beginning 11 January until all the pools dried up by 5 July. To measure the site and pool area, we used a Trimble GPS to map out the perimeters of the sites and the pools. We also used these data to calculate each pool's perimeter-to-area ratio and the distance of each pool from the edge of the restoration site. We obtained climate data from the National Oceanic and Atmospheric Administration Daily Summaries dataset for the Santa Barbara Municipal Airport weather station to calculate the precipitation each pool experienced the year before restoration began, the precipitation each pool experienced the year that restoration began, the precipitation each pool experienced the year after restoration began, and the average annual precipitation each pool experienced after restoration began (National Oceanic and Atmospheric Administration, National Centers for Environmental Information 2018).

Data Analysis

General Features. Data analysis was performed in RStudio version 1.4.1106 (R Core Team 2021). Because most datasets were not normally distributed or independent, which precluded analyses of variance (ANOVA) on raw untransformed data, we generated several types of linear models and performed statistical tests on model outputs. We generated linear mixed effects models using the "lme4" package (Bates

et al. 2015). We generated generalized linear mixed effects models using the "glmmTMB" package (Brooks et al. 2017). We generated zero-inflated binomial generalized linear mixed effects models with Bayesian priors for fixed effects using the "MCMCglmm" package (Hadfield 2010). We simulated model predictions using the "ggeffects" package (Lüdecke 2018). Model predictions were compared using ANOVA and post hoc Tukey's Honest Significant Difference tests to determine differences in cover and richness in each zone over time. We used the *aov* and *anova* functions from the "stats" package to perform analyses of variance. We performed post hoc Tukey's least squares means comparisons using the "emmeans" package (Lenth et al. 2021). An alpha of $p < 0.05$ was used to determine significant differences. We generated all graphs using the "ggplot2" package (Wickham 2016).

Model Construction for Approach 1: Multiyear Monitoring Study. For each quadrat in each sampling year, we calculated the maximum monthly exotic plant species percent cover, total exotic plant species richness, maximum monthly native plant species percent cover, and total native plant species richness. The exotic species cover distribution was skewed right as determined by histogram and Q–Q plot analyses, so we used raw data to construct a generalized linear mixed effects model with a gamma distribution, using a logarithmic link function. The exotic species richness and native species richness distributions were not normally distributed as determined by histogram and Q–Q plot analyses, so we

used raw data to construct a generalized linear mixed effects model with a Poisson distribution. The native species cover distribution was normally distributed according to histogram and Q–Q plot analyses, so we used raw data to construct a linear mixed effects model. All four models were predicted by the age of the pool during each sampling year and the zone (central, transition, upland), and the interaction thereof, as fixed effects, with sampling year, quadrat name (nested in zone and pool name to account for pseudoreplication), pool depth (cm), pool area (m^2), and average annual precipitation (cm) included as random effects.

Model Construction for Approach 2: Chronosequence Survey.

For each quadrat, we calculated the total exotic plant species percent cover, total native plant species percent cover, exotic plant species richness, and native plant species richness. Raw untransformed data for exotic species cover and native species cover were zero-inflated and did not follow a normal distribution as determined by histogram and Q–Q plot analyses, so we used raw data to construct zero-inflated generalized linear mixed effects hurdle models with a gamma distribution, using a logarithmic link function (Tables S5, S6, S8, & S9). We

Figure 3. Close-up map of vernal pools (highlighted in yellow) in the South Parcel restoration site, with examples of pools with high pool edge ratio (top) and low pool edge ratio (middle, bottom).

treated time since restoration (years), the pool edge ratio (ratio of pool perimeter, in m, to the pool area, m^2; see, e.g., Fig. 3), pool distance from the edge of the restoration site (i.e. distance pool embedded in the grassland matrix, in m), pool inundation period (days), relative elevation (height above the deepest point of the pool, in cm), historical annual precipitation (average annual precipitation the pool experienced after restoration, in cm), precipitation the year before restoration began (cm), precipitation the year that restoration began (cm), and precipitation the next year after restoration began (cm) as fixed effects, each interacted with pool zone. We also designated zone nested in the pool name and in the restoration site name as random effects to account for pseudoreplication. We used the same random and fixed effects for exotic species richness and native species richness but used Poisson distributions to account for discrete response variables.

We performed similar analyses using Shannon's Index of Diversity and Simpson's Dominance Index for native and exotic plant species and performed nonmetric multidimensional scaling on community matrices, but the results did not reveal any additional patterns that were not also described by cover and richness, so we focus our results and discussion on cover and richness.

Results

Approach 1: Multiyear Monitoring Study

Q1: How does exotic plant abundance and richness change in restored vernal pools over time?. In the multiyear monitoring study, total exotic plant species cover significantly increased over time, but only in the transition ($p = 0.001$) and upland zones ($p < 0.001$; Table S1; Fig. 4). Exotic plant species richness did not significantly change over time, but ranged from 1 to 11 species between pools (Table S2; Fig. S1). Dominant
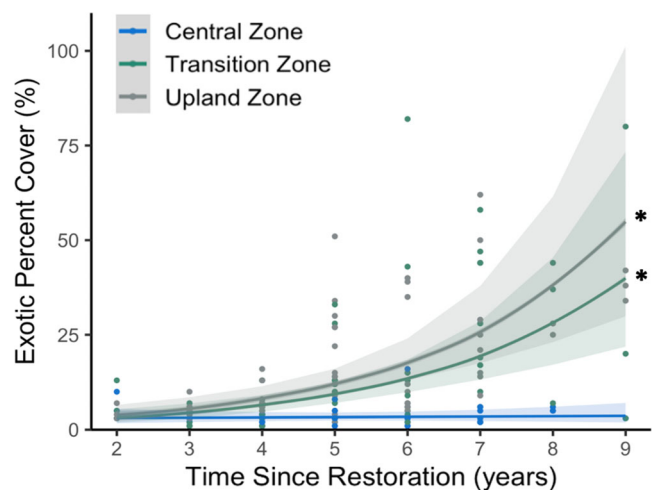

Figure 4. Total exotic species percent cover in restored vernal pool zones over time for multiyear monitoring study plotted with GLMER predictions and 95% CI as linear models. Asterisks indicate a significant interaction between zone and time since restoration for exotic percent cover ($p < 0.05$).
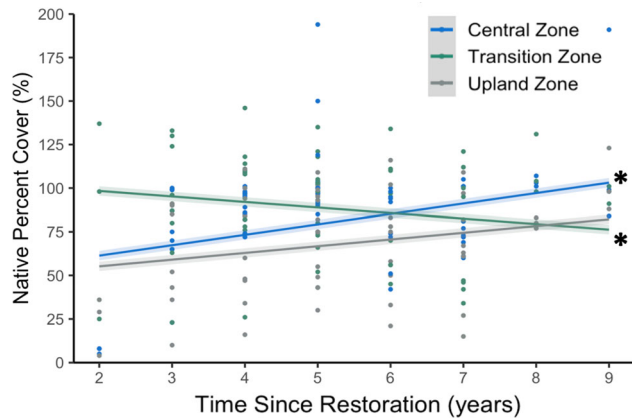
Figure 5. Total native species percent cover in restored vernal pool zones over time for multiyear monitoring study plotted with LMER predictions and ± SE as linear models. Asterisks indicate a significant interaction between zone and time since restoration for native percent cover ($p < 0.05$).

Figure 6. Average total exotic species percent cover per pool zone over time in 2019 chronosequence, shown with GLMER estimates and ± SE as linear models. Asterisks indicate a significant interaction between zone and time since restoration for exotic percent cover ($p < 0.05$).

Figure 7. Average total native species percent cover per pool zone over time in 2019 chronosequence, shown with GLMER estimates and ± SE as linear models. Asterisks indicate a significant interaction between zone and time since restoration for native percent cover ($p < 0.05$).

exotic plant species covering an average of greater than 10% included *Polypogon monspeliensis* (rabbitsfoot grass), *Bromus hordeaceus* (soft brome), *Bromus diandrus* (ripgut brome), *Poa annua* (annual bluegrass), *Festuca myuros* (rattail sixweeks grass), *Festuca perennis* (Italian ryegrass), and *Hordeum murinum* (foxtail barley).

Q2: How does native plant abundance and richness change in restored vernal pools over time?. Total native plant species cover significantly increased in the central zone over time ($p = 0.030$) but significantly decreased in the transition zone over time ($p = 0.004$; Table S3; Fig. 5). Native plant species richness similarly significantly increased in the central zone over time ($p = 0.012$) but significantly decreased in the transition zone over time ($p = 0.030$; Table S4; Fig. S2). Dominant native species (>10% average cover) in the central zone included *Eleocharis macrostachya* (common spikerush), *Juncus mexicanus* (Mexican rush), *Juncus phaeocephalus* (brown-headed rush), *Schoenoplectus pungens* (common threesquare), *Stipa pulchra* (purple needlegrass), and *Plagiobothrys undulatus* (coast allocarya). Dominant native species in the transition zone included *Elymus triticoides* (creeping wild rye), *S. pulchra*, *J. mexicanus*, *Carex praegracilis* (clustered field sedge), *Distichlis spicata* (saltgrass), *E. macrostachya*, *Eryngium vaseyi* (coyote thistle), *Cyperus eragrostis* (tall flatsedge), *Juncus bufonius* (toad rush), *S. pungens*, and *Alopecurus saccatus* (Pacific foxtail). Dominant native species in the upland zone included *S. pulchra*, *Epilobium canum* (California fuchsia), *Hordeum brachyantherum* (meadow barley), *Lepidium nitidum* (peppergrass), and *J. bufonius*.

Approach 2: Chronosequence Survey

Q3: What abiotic factors correlate with higher exotic plant abundance and richness in restored pools over time?. Exotic cover did not significantly correlate with time since restoration (Table S6; Fig. 6). Yet, the central zone had significantly lower average cover (mean $= 11.49 \pm 0.81\%$) than the transition
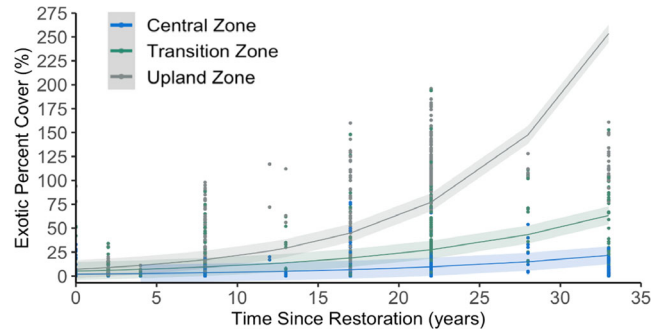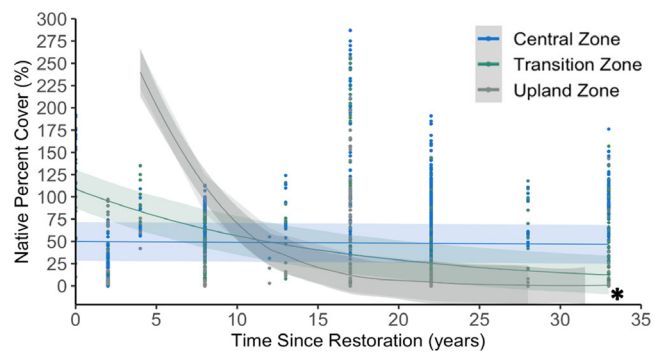
zone (mean $= 39.93 \pm 1.65\%$; $p < 0.001$) and upland zone (mean $= 68.50 \pm 2.36\%$; $p < 0.001$). Exotic plant species richness also did not significantly correlate with time since restoration (Table S7; Fig. S3). Yet, the central zone had significantly lower average richness (mean $= 2.03 \pm 0.05$ species) than the transition zone (mean $= 3.78 \pm 0.09$ species; $p < 0.001$) and upland zone (mean $= 5.03 \pm 0.12$ species; $p < 0.001$).

The most abundant exotic invasive species was *F. perennis* (average of 9.99% in the central zone, 23.89% in the transition zone, and 37.67% in the upland zone). Other exotic grasses and forbs listed by the California Invasive Plant Council as invasive species capable of displacing native species and forming monocultures that were present in the pools include *F. myuros*, *P. monspeliensis*, *B. diandrus*, *B. hordeaceus*, *Avena fatua* (wild oats), *Hordeum marinum* (seaside barley), *Plantago lanceolata* (English plantain), and *Lythrum hyssopifolia* (hyssop loosestrife; California Invasive Plant Council 2022; https://www.cal-ipc.org/plants/inventory/).

Q4: What abiotic factors correlate with lower native plant abundance and richness in restored pools over time?. Changes in native plant species cover over time were dependent

Table 1. Significant fixed effects from GLMERs for exotic cover, exotic richness, native cover, and native richness ($p < 0.05$). Sign indicates the direction of significant relationships. C = central zone, T = transition, U = upland; "time since restoration" is years since restoration began; "pool edge ratio" is perimeter-to-area ratio of each pool; "distance embedded in grassland" is distance of each pool from the edge of the restoration site; "inundation period" is the number of days each pool was inundated; "elevation" is relative elevation of each quadrat above the deepest point of each pool; "historical precipitation" is the average annual precipitation that each pool experienced after it was restored; "precipitation before restoration" is the total precipitation that each pool experienced the year before restoration began; "precipitation during restoration" is the total precipitation that each pool experienced the year that restoration began; "precipitation after restoration" is the total precipitation that each pool experienced the year after restoration began.

	Exotic Cover		Exotic Richness		Native Cover		Native Richness			Management Suggestion
Time since restoration						−U			−U	Manage long term
Pool edge ratio	+C				−C	−U				Construct circular pools
Distance embedded in grassland						−U				Construct pools in smaller grassland sites
Inundation period										
Elevation	+C	−U	+C	−U	−T	−U	+C	−T	−U	Plant in higher areas
Historical precipitation						+U				More water benefits natives
Precipitation before restoration					+C	−U				Do not plant after a wet year; actively manage upland zone
Precipitation during restoration				−U						Plant in wet years
Precipitation after restoration										

upon the pool zone. The native cover was significantly lower in older pools, but only in the upland zone ($p < 0.001$; Table S9; Fig. 7). In addition, the upland zone had significantly lower native cover (mean = $34.90 \pm 1.85\%$) compared to the central zone (mean = $74.52 \pm 1.75\%$; $p < 0.001$). In the upland zone, the native cover was also lower in quadrats at higher relative elevations ($p < 0.001$), pools that had more pool edge ratio (i.e. more pools exposed to the invasion front; $p = 0.019$), pools that were farther away from the restoration site edge (e.g., more deeply embedded in invaded grassland matrix; $p < 0.035$), pools that experienced lower historical annual precipitation ($p = 0.004$), and pools that experienced higher precipitation the year before restoration ($p < 0.001$; Table 1).

Native plant species richness was similarly significantly lower in older pools only in the upland zone ($p < 0.001$; Table S10; Fig. S4). In addition, the upland zone had significantly lower native richness (mean = 2.82 ± 0.07 species) compared to the central zone (mean = 3.78 ± 0.07 species; $p < 0.001$). In the upland zone, native richness was also lower in quadrats at higher elevations ($p < 0.001$; Table 1). Dominant native species (>10% average cover) in the central and transition zones included *E. macrostachya*, *E. vaseyi*, and *Eleocharis acicularis* (needle spikerush). Dominant native species in the upland zone included *E. macrostachya* and *S. pulchra*.

Discussion

The short-term implementation phase of vernal pool restoration did establish native plant assemblages, but these native assemblages only persisted in the wettest parts of the vernal pools. The central zones of these restored pools were planted with and remained dominated by wetland graminoids, such as *Eleocharis macrostachya*, *Eleocharis acicularis*, *Juncus mexicanus*, and *Juncus phaeocephalus*, even in sites after over 30 years post-implementation. Previous research has also found that strong abiotic filters associated with vernal pools, such as prolonged annual inundation in the deeper zones, precludes generalist exotic plant species from invading the pool centers (Bliss & Zedler 1997; Javornik & Collinge 2016). Other studies have found that growth and reproduction decreased in common invasive species (*Brassica rapa* [common mustard], *Centaura solstitialis* [yellow star thistle], *Vicia villosa* [hairy vetch], *Hordeum marinum*, and *Festuca perennis*) when those species were exposed to prolonged inundation (Gerhardt & Collinge 2007). This suggests that restoration efforts focused on prolonging inundation period, such as excavation of larger, deeper pool basins, may inhibit exotic species and promote larger and more persistent populations of native species in the central zone. However, the high native cover in the central zones contrasts with higher exotic cover in the transition and upland zones where inundation is predictably shorter or absent.

Reinvasion of Restored Vernal Pools Over Time

The increase in exotic cover and richness in our multiyear monitoring study suggests that short-term restoration efforts do not guarantee long-term success in the transition and upland zones of restored pools. The pools in this study were created and planted with native species within a grassland landscape. Intensive exotic species weeding continued for about 2–5 years after each pool was created, but then the pools entered the maintenance phase and were only periodically hand-weeded or cleared with a weed-whacker. Although the initial intensive weeding kept exotic cover low, exotic cover increased in the transition and upland zones over time. This suggests that the initial weeding successfully reduced exotic species, which is why exotic

cover remained low for several years after the implementation phase. However, without continual removal, recruitment from exotic populations adjacent to the restored pools allowed for eventual recolonization of the site. Previous studies have shown that restored native populations can subsequently decline and even go extinct due to low growth rates that are negatively affected by interannual environmental variability and competition by invasive species (Aoyama et al. 2022). Indeed, other long-term monitoring studies in other ecosystems, such as grasslands and forests, have also shown that restored plant communities never reach the species diversity of natural reference ecosystems (McClain et al. 2011; Lesage et al. 2018). Our study adds to a growing body of evidence that short-term restoration projects do not guarantee the long-term persistence of diverse native assemblages.

Our results indicated that exotic plants invaded pool transition and upland zones, but not central zones, suggesting that invasion into the pool edges comes from the surrounding invaded grassland matrix. Invasive exotic species are often unsuccessful in the central zones because of their inability to tolerate prolonged inundation (Gerhardt & Collinge 2007). However, increased drought due to climate change may result in drier conditions even in the deepest parts of pools, perhaps making the zone less hospitable for vernal pool specialists and more susceptible to natural recruitment by invasive species (Sall et al. 2021). Other studies have reported higher invasive species in drier parts of the pools and during drier years (Bauder 2000; Gerhardt & Collinge 2003). Although restoration efforts may plant and establish native populations within a vernal pool, the surrounding landscape often consists of unrestored grassland invaded by exotic grasses, which may contribute many propagules to pool edges. In addition, once propagules establish in the pool, positive feedbacks such as litter build-up can cause exotic populations to invade and persist (Faist & Beals 2018). These edge effects are common throughout restored ecosystems (Laurance et al. 2002). Small-scale restoration projects, which typically occur amidst fragmented habitat in the form of patches, can be susceptible to edge effects due to stressful environmental conditions and disturbances originating outside of the habitat patch (e.g. pollution, presence of exotic propagules; Laurance et al. 2002). For example reinvasion of *Phragmites australis* (common reed) from the surrounding landscape into wetlands is common, as is the encroachment of trees from forests into adjacent meadows (Wang et al. 2006; Halpern & Antos 2021). Several studies have shown that exotic species abundance increases closer to forest edges, where disturbance and exotic propagule supply is high (Dawson et al. 2015). It is, therefore, critical to evaluate and manage edges of restoration projects as they face unique pressures that can jeopardize native assemblages.

Management Recommendations to Increase Persistence of Native Species

Our results highlight the importance of both sustained inundation of central zones and active management of transition and upland zones of vernal pools to reduce invasion. Collinge et al. have similarly emphasized the role of both abiotic and biotic filters (including human management) in creating and sustaining restored native communities that are resistant to exotic invasion (Collinge et al. 2011; Gerhardt & Collinge 2007). Biotic filters that can decrease susceptibility to reinvasion include adaptive management strategies, such as planting with competitive native species and active control of exotic competitors through an array of long-term weed management techniques (D'Antonio & Meyerson 2002). In vernal pools, strategically planting suites of species at different elevation zones within pools can also increase native establishment and persistence. For example, in our studies, *E. macrostachya*, *J. mexicanus*, and *J. phaeocephalus* were able to dominate the central zone, while *Carex praegracilis*, *E. macrostachya*, *Distichlis spicata*, *J. mexicanus*, and *E. triticoides* performed well in the transition zone, and *Stipa pulchra*, *Cyperus eragrostis*, and *Hordeum brachyantherum* were able to establish and persist in the upland zone despite exotic invasion, so these species can be the foci of zonal planting palettes for future local restoration projects. Although intensive hand-weeding did not create resistance in the edges of the pools and may not be sustainable in the long run due to time and resource constraints, feasible long-term weeding strategies may focus more on large-scale contexts. For example, the upland and surrounding unrestored grassland matrix probably accounted for the exotic invasion of the transition and upland zones of the pools, so large-scale grassland management techniques such as grazing and prescribed fire disturbance may reduce exotic species dominance in both the grassland and the edges of the vernal pools (Pollak & Kan 1998; Marty 2005). Even periodic reductions of exotic species could help to sustain greater native abundance in the edge zones.

Overall, our studies evaluating the trajectories of plant assemblages post-implementation suggest that active management of restored habitats should persist beyond the implementation phase, which means projects need to be budgeted with long-term monitoring and adaptive management plans. Although 5 years of intensive restoration efforts can successfully reestablish native assemblages, our studies showed that native cover and richness decreased significantly in older pools. Other studies of restored wetlands similarly showed that restored wetlands initially achieving high native plant diversity can subsequently experience a decline in native diversity and an increase in exotic diversity 5–11 years post-implementation (Gutrich et al. 2009; Matthews & Spyreas 2010). Our long-term monitoring dataset provides unique insight into plant community trajectories over time by showing that, even when central zones of restored vernal pools can remain native-dominated, the drier pool edges exposed to the surrounding exotic grassland matrix can experience reinvasion over time, much like how forest edges and other edge habitats can experience reinvasion when not actively managed (McClain et al. 2011). Short-term success can be misleading, and long-term monitoring is important to evaluate the success of restoration and guide adaptive management over time.

Identifying drivers of reinvasion can be particularly useful for guiding adaptive management. In our study, the main abiotic variables that correlated with increased exotic diversity and/or decreased native diversity were the amount of edge area, relative

elevation, and precipitation. For example, less precipitation during restoration implementation can correlate with higher exotic richness, although a wet year before restoration may promote higher exotic cover and lower native cover in the upland zone, perhaps due to competition from exotics taking advantage of higher winter water resources (Prevéy & Seastedt 2014). Although the precipitation that a restoration site experiences cannot be manipulated, knowing whether it is a particularly wet or dry year at a restoration site can inform management decisions, e.g., resources should be allocated to weeding exotic species out of pool edges during wet years. In addition, the invasion front of vernal pools may be reduced by creating circular pools with less edge area exposed to the surrounding exotic grassland matrix and associated edge effects. Because surrounding invasive grassland populations contribute propagules that invade pool edges, restoration efforts can also prioritize creating or restoring vernal pools in smaller grassland sites with fewer invasive species. For example, vernal pools may be constructed in smaller greenspaces within urban areas that are traditionally deemed too small for other habitat restoration projects. However, manipulation of these abiotic environmental variables alone cannot be relied upon to maintain high native cover and low exotic cover, especially in the higher-elevation transition and upland zones that are more hospitable to generalist species. These edge zones experienced an increase in exotic diversity and/or a decrease in native diversity over time, possibly due to the overwhelming propagule pressure from the surrounding unrestored grassland. These propagules likely take advantage of the higher-elevation edge zones of the vernal pools that, when not seeded with native species, provide hospitable open niche space for generalist grasses and forbs to inhabit (Dukes 2002; Lulow 2006). Other studies have shown that abiotic manipulation can lead to incomplete restoration, especially in hospitable environments that are easily colonized by exotic species (Osazuwa et al. 2021). Sengl et al. (2015) showed that retired farmland passively restored to grassland (i.e., farmland was plowed and unfertilized to make it hospitable for secondary succession, but no native propagules were added) did not achieve the same native species richness as reference sites and were instead colonized by invasive grasses. Our study aligns with these studies in recommending active long-term management to enhance native populations and resist invasive populations.

Instead of viewing restoration projects primarily as short-term implementation efforts with only an auxiliary "maintenance phase," the implementation phase of restoration could be primarily focused on establishing the biophysical conditions needed for native plant species establishment (e.g., vernal pool excavation and initial seeding or planting). This initiation of restoration is best followed by a long-term commitment to site stewardship, where community engagement could help defray long-term costs while providing ecosystem services. This directly aligns with indigenous land management practices, wherein humans are viewed as part of the annual and interannual dynamic of ecosystems (e.g., Anderson 2005). We suggest that "restoration" entails not only the initial restoration of native plants and animals and the exclusion of undesirable species but also the restoration of the symbiotic relationship between humans and nature via long-term human stewardship to create desirable ecosystems. Long-term adaptive management plans require ongoing monitoring so that management can pivot to address rising challenges. When funds are limited, engaging local community groups to help with ongoing restoration efforts can achieve both ecological goals (e.g., enhanced adaptive capacity; Dudney et al. 2022) and social goals (e.g., engaging a diversity of people in maintaining biodiversity; Reyes 2011). Shifting the focus toward viewing restoration as a long-term relationship with the land may thus allow us to realize more resilient and resistant socioecological systems.

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Supporting Information

The following information may be found in the online version of this article:

Supplemental S1. Restoration actions for vernal pools in multiyear monitoring study.

Supplement S2. Background information for vernal pools surveyed in 2019 chronosequence.

Table S1. ANOVA table of total exotic species percent cover GLMER for multiyear monitoring study.

Table S2. ANOVA table of exotic species richness GLMER for multiyear monitoring study.

Figure S1. Exotic species richness in restored vernal pool zones over time for multiyear monitoring study, plotted with GLMER predictions and 95% confidence intervals as linear models.

Table S3. ANOVA table of total native species percent cover LMER for multiyear monitoring study.

Table S4. ANOVA table of native species richness GLMER for multiyear monitoring study.

Figure S2. Native species richness in restored vernal pool zones over time for multiyear monitoring study, plotted with GLMER predictions and 95% confidence intervals as linear models.

Table S5. ANOVA table of binomial exotic species percent cover GLMER hurdle model for 2019 chronosequence.

Table S6. ANOVA table of gamma exotic species percent cover GLMER hurdle model for 2019 chronosequence.

Table S7. ANOVA table of exotic species richness GLMER model for 2019 chronosequence.

Figure S3. Average total exotic species richness per pool zone over time in 2019 chronosequence, shown with GLMER estimates and 95% confidence intervals as linear models.

Table S8. ANOVA table of binomial native species percent cover GLMER hurdle for 2019 chronosequence.

Table S9. ANOVA table of gamma native species percent cover GLMER hurdle for 2019 chronosequence.

Table S10. ANOVA table of native species richness GLMER for 2019 chronosequence.

Figure S4. Average total native species richness per pool zone over time in 2019 chronosequence, shown with GLMER estimates and 95% confidence intervals as linear models.