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Long-term monitoring and management of grassland vernal pool plant assemblages

A dissertation submitted in partial satisfaction of the requirements

for the degree of Doctor of Philosophy

in Ecology, Evolution, and Marine Biology

by

Joanna Jiaying Tang

Committee in charge:

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September 2024

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August 2024

Long-term monitoring and management of grassland vernal pool plant assemblages

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by

Joanna Jiaying Tang

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Deo omnis gloria

Vita of Joanna Jiaying Tang

September 2024

Education
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Minor in Medieval & Early Modern Studies
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Teaching & Leadership Experience
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- Re-designed, developed, taught, & graded field lab for EEMB 128: Restoration Ecology
- Developed, taught, & graded discussion sections for ES 100: Environmental Ecology & EEMB 168: Conservation Ecology

Schimdt Mentorship Award   *$8,000*   2021
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Guest Lecturer   *UCSB, Westmont, Natural*   2021- 2024
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- INT 95B: Introduction to Undergraduate Research guest lecture on field research (2021- 2023)
- Westmont College biology seminar series invited speaker on vernal pool restoration ecology (October 2021)
- Quasar to Sea Star Santa Barbara Museum of Natural History Teen Summer Program guest lecture on urban biodiversity & conservation (June 2022)

- Westmont College Plant Classification guest lecturer on vernal pool plants (November 2022)
- Ocean Discovery Institute Science Leader (2023-2024)

Grants, Fellowships, & Awards

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Student Engagement & Leadership
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The Green Initiative Fund *UCSB* 2022
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California Native Plant Society Student Grant *$1,000* 2022
- Project title: Restoring vernal pools using ecotypic variation analysis

2nd Place Student Lightning Talk Award *California Invasive Plant Council* 2021
- Cal-IPC Symposium talk title: Increasing the Diversity of People and Ecosystems Through Urban Restoration Projects

Bloom-Hays Ecological Research Grant *$1,000* 2021
- Project title: Ecotypic variation in vernal pool communities
- Awarded to projects that "advance ecological research, particularly research related to avian species and the natural communities on which they depend"

Schimdt Research Accelerator Award *$8,000* 2021
- Project title: Resilient restoration strategies for endangered vernal pool communities
- Awarded to projects focusing on "advancing science that has direct application for environmental problem solving"

Schimdt Mentorship Award *$8,000* 2021
- Project title: Assessing success of restored vernal pool communities
- Awarded "to support the development of graduate and undergraduate research…through a mentoring program that pairs an undergraduate with a graduate student mentor" researching projects on "advancing science that has direct application for environmental problem solving"

CNGA Grassland Research Awards for Student Scholarship *$500* 2020, 2021
- 2021 project title: Ecotypic variation in Southern California grassland vernal pool communities
- 2020 project title: Investigating abiotic and biotic interactions in restored vernal pool grassland communities
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Student Presentation Award *California Invasive Plant Council* 2020

- Cal-IPC Symposium talk title: Positive feedback loops of invasive grasses: breaking the cycle

The Garden Club of Santa Barbara Grant *$4,995* 2020
- Project title: Long-term management of native species in Isla Vista's restored vernal pool communities
- Awarded to projects focusing on "the protection of our environment and native plants"

Faculty Research Assistance Program *$350* 2019
- Project title: Improving the long-term success of vernal pool restoration through thatch manipulation
- FRAP "seeks to enhance undergraduates' time at UCSB through participation in research and creative activities…to foster individuals who are prepared to apply their learned skills towards their future personal, academic, and professional goals"
- Funds go toward field & lab supplies to support research by undergraduate student intern

2nd Place Student Poster Award *California Invasive Plant Council* 2019
- Cal-IPC Symposium poster title: Exotic Species Invasion in Restored Vernal Pools

Cal-IPC Student Travel Award *California Invasive Plant Council* 2019
- Cal-IPC Symposium Poster Title: Exotic Species Invasion in Restored Vernal Pools
- Awarded to student symposium presenter who displays distinguished experience & goals aligned with Cal-IPC's mission of researching & "protecting California's environment & economy from invasive plants"
- Funds go toward travel expenses to present research at Cal-IPC Symposium

Coastal Fund Grants *$1,000-$16,000* 2019, 2022
- Project titles: Improving the long-term success of vernal pool restoration through thatch manipulation; Assessing success of restored ecosystems; Drone monitoring to inform habitat restoration; Enhancing native populations of vernal pool plants; Native vernal pool seed bank assessment through DNA and RNA extractions
- "The Coastal Fund's Mission [is] to preserve, protect, and enhance the terrestrial and marine habitats associated with the shoreline of the University of California Santa Barbara through preservation, education, open access, research, and restoration"
- Funds go toward stipend for undergraduate student intern & field supplies

Publications & Presentations

Tang, J., D'Antonio, CM. (2024) Restoring then and now: Long-term management to address reinvasion of restored grassland vernal wetlands. *Ecosphere*. In review.

Tang, J., Nolan, M., D'Antonio, CM, Cooper, SD, Stratton, L. (2023) Reinvasion of restored California vernal pools reveals the importance of long-term restoration planning. *Restoration Ecology*. DOI: http://doi.org/10.1111/rec.13991

Tang, J. (2023). The Journey of Restoration: A case study of vernal pools, plants, and people. Grasslands 33:3

Tang, J. (2022). Meet a native grassland: North Campus Open Space, Santa Barbara, California. Grasslands 23:3, 15-17

Supporting Ecologists Throughout their Careers   *Ecological Society of America*   2024

- Talk title: Detecting and addressing invasion of restored vernal pool wetlands via long-term monitoring and management

Urban Biodiversity and Design for Local Communities   *Urban Biodiversity and Design*   2024

- Talk title: Using vernal pool wetlands to restore both biodiversity and the relationship between people and place

Holistic Restoration: Restoring and Reconnecting People to Place   *California Society for Ecological Restoration*   2024

- Talk title: Thatch removal as a part of long-term, holistic stewardship in grassland vernal pools
- Poster title: California Rapid Assessment Method: Using vernal pool CRAM to evaluate past restoration success & prioritize future restoration goals

Merced Vernal Pool & Grassland Reserve Symposium   *10ᵗʰ Anniversary Symposium*   2024

- Talk title: Addressing reinvasion of restored vernal pools via thatch manipulation: it's a long-term relationship!
- Poster title: Long-term monitoring detects reinvasion in restored vernal pools

30x30 Partnership Gathering   *California Biodiversity Network*   2024

- Talk title: Restoration of vernal pool wetlands requires stewardship

Think Big, Start Small, Restore Now   *Society for Ecological Restoration -- California*   2023

- Talk title: What's the easiest way to take data? Survey 123!

Invasive Plant Management from Cities to Wildlands   *California Invasive Plant Council Symposium*   2022

- Talk title: Who's managing what, and for whom?

Rooting Together: Restoring Connections to Plants, Place & People   *California Native Plant Society Conference*   2022

- Talk title: Increasing native species in urban ecosystems

A Change is Gonna Come   *Ecological Society of America*   2022

- Talk title: We need to have the DTR talk

Grasslands Vol. 32, No. 3   *California Native Grasslands Association*   2022

- Article title: Meet a Grassland: North Campus Open Space, Santa Barbara, California

Ecesis Vol. 31, Issue 4   *California Society for Ecological Restoration*   2021
- Article title: Increasing the Diversity of People and Ecosystems through Restoration

Restoration in Our Backyard   *California Society for Ecological Restoration*   2021
- Talk title: Vernal Pools in Urban Mitigation

Vital Connections in Ecology   *Ecological Society of America*   2021
- Talk title: Environmental filters governing long-term invasion resistance in restored vernal pools

Living on the Edge – Plants in Extreme Environments   *Southern California Botanists*   2020
- Poster title: Extreme conditions in extreme environments: an extreme restoration challenge

Recovery and Resilience: Confronting Fire, Weeds, and Forest Pests   *California Invasive Plant Council*   2020
- Talk title: Positive feedback loops of invasive grasses: breaking the cycle

Evolving Management Perspectives in a Changing World   *California Invasive Plant Council*   2019
- Poster title: Exotic Species Invasion in Restored Vernal Pools

Graduate Student Symposium   *California Botanic Society*   2019
- Poster title: Exotic Species Invasion in Restored Vernal Pools

Beyond Recovery: Restoration for the Future   *California Society for Ecological Restoration*   2019
- Poster title: Exotic Species Invasion in Restored Vernal Pools

Abstract

Long-term monitoring and management of grassland vernal pool plant assemblages

by

Joanna Jiaying Tang

Vernal pools are temporary wetlands that only form when rainwater pools in depressions, often within a grassland landscape. Over 95% of California's vernal pool wetlands have been lost to land use change, and remaining pools are often invaded by European annual grasses. To counteract this degradation, efforts to restore vernal pools in Santa Barbara began in the 1980s, which involved intensive short-term restoration actions such as the excavation of pool basins and 1-3 years of seeding with endemic pool species. My research evaluates the resilience of native plant assemblages in restored pools over time, after short-term restoration actions were completed. In a survey of 69 restored pools along the coast Santa Barbara County, I found that native plants were abundant throughout pool bottoms, but that the edges of pools that had been restored decades ago had lower native plants and/or higher exotic plants than pools restored more recently. Vernal pool edges are often surrounded by exotic-dominated grasslands, and exotic grasses can invade restored pools over time in the absence of long-term management. After these exotic grasses are established, they produce large amounts of plant litter, or "thatch". This thatch allows for the germination of more exotic grasses but suppresses the germination of native species in subsequent years. I designed a long-term experiment to reduce exotic grass thatch in pool edges via annual raking to disturb or remove thatch. I coupled thatch raking with the addition of native plant seed to test whether the extant seed bank was also limiting native

plant populations. After three years of thatch removal and native seed addition, native plant abundance and diversity increased. However, not all seeded species were able to establish, suggesting that native seed germination or seedling survival was limiting populations of some native species. I hypothesized that the performance of native populations depends on characteristics of the source population. Intraspecific variation, e.g., phenotypic plasticity or local adaptation, may result in different populations responding differently to environmental stressors such as drought and invasive species. Invasive grasses are prevalent in and around Santa Barbara vernal pools, and Santa Barbara is also predicted to experience a shorter winter wet season and a longer summer/fall drought in the future. I set up a common garden greenhouse experiment to evaluate intraspecific differences in the drought and competition tolerance of the native rush, *Juncus bufonius*, from populations in Santa Barbara and San Diego Counties. When I subjected the populations to drought regimes and planted them in competition with the invasive species *Festuca perennis*, I found differences in plant performance among populations. Specifically, the Santa Barbara population exhibited the highest mortality and the lowest biomass production when subjected to drought, one San Diego population produced the greatest biomass under the drought and competition treatments, and the other San Diego population had the most significant negative effect on *F. perennis* when grown together in competition. This evidence of intraspecific plant performance can inform seed sourcing strategies for future restoration: because local Santa Barbara populations exhibit intolerance to drought and competition, and because drought and competition are prevalent threats in Santa Barbara, sourcing seed from a variety of other populations that exhibit higher tolerance, such as those from San Diego, may increase the performance of restored populations. Overall, my studies and research findings highlight the

need for long-term monitoring and adaptive management strategies to track the performance of restored assemblages over time and to address ongoing threats. My research demonstrates the need and opportunity for investing in long-term stewardship actions to increase the persistence of native plant assemblages.

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Introduction

Invasive species are one of the primary drivers of native biodiversity loss (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) 2019). Species moved outside of their historical range are categorized as invasive if they survive, reproduce, disperse, and become so abundant or have such large per-capita effects that they alter ecological structures and processes, such as habitat structure or primary productivity (Blackburn et al. 2011; Parker et al. 1999). Invasive plants that rapidly sequester water, light, or nutrients can out-compete their native counterparts (Levine et al. 2006).

There are over 1,000 invasive plant species in California (Rejmánek et al. 1991). Spanish colonists began introducing Eurasian plants to native California ecosystems in the 16th Century (Anderson 2005). Annual European grasses such as *Bromus diandrus* (ripgut brome), *Avena fatua* (wild oats), and *Festuca perennis* (Italian ryegrass) are generalist species that do not require specific ecological conditions (i.e., they have broad temperature tolerances and are not associated with specialist pollinators) and can rapidly germinate and sequester available resources to grow and reproduce at the start of each rainy season. They are now dominant in grassland settings throughout the state (Stromberg et al. 2007).

Historical studies suggest that indigenous communities in California regularly burned areas around their villages, and this cultural burning promoted native grassland plant assemblages (Timbrook et al. 1982). Indigenous communities used fire to achieve a variety of socio-ecological goals, including creating disturbance to cause germination and new growth of plants used for food and building materials. Yet, the arrival of Euro-American colonists, and

associated invasive plant and animal species, precipitated large land-use change and the

extirpation of indigenous tribes from most of their ancestral territories (Anderson

2005). Since Euro-American colonization, a majority of California's grasslands have been

invaded by European annual grasses such that there is little knowledge about prehistorical

plant assemblages or disturbance regimes other than likely regular burning (Barry et al.

2006). Indigenous management has been suggested to be the primary force counteracting

other forces such as succession that might have allowed for a gradual shift from native

herbaceous-dominated assemblages to native woody-dominated assemblages, which has been

seen in grasslands without regular disturbance (Van Auken 2000). Ultimately, the arrival of

Euro-American colonists and associated large-scale landscape transformations from tilling,

tree harvesting, and overgrazing, as well as the proliferation of invasive species in

California's native ecosystems, has caused local decreases in native herbaceous and woody

species and alterations in ecosystem functions and processes (e.g., nitrogen cycling, soil

erosion, fire regimes; D'Antonio et al. 2007; Stromberg et al. 2007).

Some invasive species establish near-monocultures and initiate positive feedbacks that

perpetuate their dominance (Molinari & D'Antonio 2020; Faist & Beals 2018). For example,

invasive annual grasses produce large amounts of dead plant matter, hereafter "thatch", that

accumulates over many years because of slow decomposition (Ogle et al. 2003). This

invasive thatch suppresses native plant species germination and growth, but exotic plant

seeds can germinate in their own thatch, generating a positive feedback that results in the

increased reproduction and biomass production of the invasive grasses and perpetuation of

invasive dominance (Chen et al. 2018; Molinari & D'Antonio 2020).

Since California's colonization by Europeans, grasslands have been invaded by exotic

species to the extent that we often do not know the native grass or forb assemblages that have

been lost (Stromberg et al. 2007). Yet, California's grasslands still harbor vernal pool

wetlands, which are temporary wetlands that, in California, form atop an impermeable

subsurface soil layer during cool, wet winters. They dry out during warm, dry summers.

Because many vernal pools exist as topographic depressions within an invaded grassland

landscape, the gradient from the pool center to the exotic-dominated upland grassland

showcases the invasion front of Eurasian annual grasses (Keeley & Zedler 1998). Over 40%

of species found in California's vernal pools are endemic because species require specific

adaptations to survive and reproduce under highly dynamic seasonal and interannual wetting

and drying cycles (Stone 1990). Iconic forbs such as *Lasthenia conjugens* (Contra Costa

goldfields), *Limnanthes floccosa* ssp. *californica* (Butte County meadowfoam), and

Pogogyne abramsii (San Diego mesa mint) are examples of unique regional species that

characterize natural vernal pools. However, 95% of pre-colonial vernal pool habitat has been

lost due to urbanization, agricultural development, and overgrazing, all of which promote

invasive species (Holland 1978).

The Society for Ecological Restoration (SER) defines ecological restoration as "the process

of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed"

(Gann et al. 2019). A litmus test of restoration is whether vernal pool restoration efforts can

actually disrupt or overcome positive feedbacks from invasive species, re-establish

dominance of native plant species, and subsequently allow or manage for the persistence of native assemblages (Bradshaw 1987).

This dissertation examines how different restoration actions influence the composition of vernal pool plant assemblages in Santa Barbara, California, USA, that are threatened by invasive species over time. Vernal pool restoration in the Santa Barbara region and California as a whole began in the 1980s, with restoration actions usually consisting of an intensive 1-3-year implementation phase involving pool basin excavation, exotic species weeding, and native species seeding, but these efforts have resulted in mixed success of restoring native plant assemblages that persist over time (Black & Zedler 1998). SER specifies that one major attribute of a restored plant assemblage is that threats to native species, such as clearcutting, overgrazing, agricultural development, and invasive species, are eliminated (Gann et al. 2019). However, invasive species continue to be a widespread threat to native species in vernal pools, and continued anthropogenic disturbances, such as increased urbanization and climate change causing warmer temperatures and drier conditions, can promote even more invasive species (Walther et al. 2009). Although the implementation phase is usually a short-term effort constrained by contracts, grant cycles, and limited resources, the ongoing threat of, and environmental modifications caused by, invasive species provide a persistent force undoing the initial implementation efforts and facilitating reversal of plant assemblages to dominance by exotic species. As a result, studies have shown that, although restored wetlands may attain high native species cover during the first few years following restoration implementation, it is common for native species cover to decrease and exotic species cover to increase over time (Gutrich et al. 2009).

The first chapter of this dissertation investigates whether restored vernal pool plant assemblages are resistant to the invasion of exotic plant species after the implementation phase has ceased. Here, I ask: Do restored native plant assemblages persist with relatively stable native plant cover, composition, and dominance after the cessation of pool construction and weeding? To address this question, I first tracked the vegetation composition of seven restored vernal pools at the University of California, Santa Barbara, for three years after the implementation phase had ceased. These pools were all restored using the same pool basin excavation and native plant seeding techniques, and all pools were intensively weeded for 1-3 years. I hypothesized that, without continued long-term management, the exotic annual grasses present around the restored pools would invade into the pools and cause exotic abundance and diversity to increase over time. I monitored plant species percent cover in quadrats distributed throughout three pool zones: central (i.e., the bottom, deepest part of the pool that experiences the longest inundation), transition (i.e., the ring around the central zone that experiences an inundation about half the duration of the central zone), and upland (i.e., the ring around the transition zone that is adjacent to the surrounding grassland matrix, which is only inundated during largest storm events). I found that native plant cover decreased and exotic plant cover increased over time, but only in the transition and upland zones of the vernal pools, supporting my hypothesis that invasive species were able to encroach into the pool from the surrounding exotic-dominated grassland landscape. Yet, central zones of the pools remained dominated by native species throughout the monitoring period. This suggests that the edges of restored vernal pools are susceptible

to invasion over time, but the long inundation of the central zone can exclude invasive grasses and favor native species.

I further hypothesized that certain pool characteristics (e.g., pool shape and depth) and climate conditions (e.g., annual precipitation) could influence native and exotic plant cover and richness in restored vernal pools. To test this hypothesis, I collected environmental and landscape variables, including pool shape, pool depth, pool size, pool basin topography, and historical annual precipitation, on 69 restored vernal pools in Santa Barbara County, California, and I investigated whether any of these variables correlated with higher native plant species richness and cover or lower exotic plant species richness and cover.   I found that more circular pools with less edge area (i.e. less proportional area exposed to the invasion front) had higher native cover and lower exotic cover in the central zone. I also found that the upland edges of vernal pools had lower native cover and higher exotic cover, suggesting that these areas are most susceptible to invasion by exotic annual grasses in the absence of long-term weed management. The timing and amount of annual rainfall also influenced plant cover and richness: pools that experienced higher rainfall the year before they were restored exhibited higher native cover in the central zone but lower native cover in the upland zone, and pools that experienced higher precipitation during the year they were restored experienced lower exotic richness. Thus, constructing more circular vernal pools during high-rainfall years may favor native plant species, and management can prioritize upland areas, especially during dry years, to moderate exotic species invasion.

The second chapter of this dissertation investigates a long-term management method targeted at destabilizing invasive species positive feedbacks. Studies have shown that exotic annual grasses produce large amounts of thatch that perpetuate exotic populations while suppressing the germination and growth of native species (Molinari & D'Antonio 2020). I hypothesized that thatch manipulation, particularly if repeated annually, would destabilize the invasive species feedback, decrease exotic plant cover, and open microsites for native species to colonize. However, degraded vernal pools often have a depleted native seed bank due to topsoil removal and disturbance, e.g., from agricultural operations. I hypothesized that, if the vernal pools have a depleted native seed bank, then native seed addition would be needed to restore native plant assemblages. I tested these hypotheses by subjecting 15 vernal pools in Isla Vista, California, to thatch manipulation and native seed addition treatments annually for four years in a full two-way factorial experiment (including unmanipulated pools without seeding as controls). I found that thatch removal opened up microsites (because bare ground consistently increased), but native diversity primarily increased in areas that also received native seed addition, and then only after at least three years of annual treatments. Moreover, plant diversity was moderated by annual precipitation, with plant diversity increasing during above-average rainfall years. These results highlight the importance of the long-term monitoring and management of restored plant assemblages to counteract the invasion pressure from exotic plants and to increase the capability of native plant assemblages to respond to favorable conditions.

The third chapter of this dissertation addresses the question of where to acquire seed for restoration projects. Restoration projects can have different goals, such as retaining genetic

or species diversity, and challenges, such as unstable environmental conditions and invasive species, and these considerations can influence seed selection. For example, if a restoration site is predicted to undergo climate change, theory predicts that restored populations will persist if they have adaptations to the predicted climate conditions (Breed et al. 2013). Along the south coast of California, climate models predict an increase in the duration of annual summer/fall drought, as well as more variable and episodic winter storm events resulting in pools intermittently drying out during the wet winter season (Feng et al. 2019). Thus, local vegetation will experience longer and more severe summer/fall drought. Intraspecific variation among native populations, such as phenotypic plasticity and local adaptation, may result in different stress tolerance among populations. Here, I ask: Is there intraspecific variation in *Juncus bufonius* (toad rush) in response to drought and competition? I hypothesized that local adaptation to historical climate regimes may cause a local population to exhibit greater tolerance to drought. To test this hypothesis, I set up a common garden experiment in Santa Barbara, California, to examine the performance of different populations of *J. bufonius*, a common facultative vernal pool native species, that were germinated from seed sourced from Santa Barbara and San Diego Counties. I subjected all the populations to two different drought regimes: an end-season drought regime wherein the populations experienced a short water inundation period modeled after the inundation period of a San Diego vernal pool during a drought year, and a mid-season drought regime wherein the populations experienced drying and rewetting modeled after intermittent inundation Santa Barbara vernal pools experience during episodic storm events. I then subjected all the populations to Competition x Drought treatments, wherein the populations of *J. bufonius* were grown with populations of *Festuca perenni*s (Italian ryegrass), an exotic grass that

commonly invades vernal pools, in addition to being grown in the two drought regimes. I found that the southernmost population of *J. bufonius*, which historically experienced more severe drought conditions, produced the most aboveground biomass when subjected to both drought regimes and competition x drought. This suggests that, as Santa Barbara faces threats of drought and invasive species, using one or more populations that exhibit higher drought and competition tolerance, such as the San Diego population, in future Santa Barbara restoration projects may increase the performance of the restored populations.

Overall, my dissertation on the long-term monitoring and management of vernal pool plant assemblages not only tests and develops our ecological knowledge of vernal pools, but also provides relevant management recommendations for restoration practitioners and land managers. Vernal pools in Santa Barbara, with only 3% of historical habitat still extant, are some of the most degraded and depauperate in the state, and they are also the most understudied (Bauder & McMillan 1998). However, their unique flora and position at the junction between northern and southern California has merited their own category in statewide vernal pool classifications (Keeler-Wolf et al. 1998). As these endemic and endangered ecosystems face threats from invasive species and climate change, restoration efforts that promote the performance of native plant assemblages are a top priority. My research evaluates the efficacy of innovative restoration strategies to establish and sustain native vernal pool plant assemblages. In particular, my research highlights the importance of investing in a long-term relationship with a restored ecosystem to track its stability and persistence over time, assess the impacts of restorative actions, and develop adaptive

strategies (such as long-term community engagement and stewardship) to safeguard these unique ecosystems for future generations.

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

A. Abstract

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.

B. 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 (Crouzeilles et al. 2016; Holl & Aide 2011; Naveh 1994). 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 six 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

(Walther et al. 2009; Mack & D'Antonio 1998). 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 (Cox & Allen 2011; Stromberg et al. 2007). 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 shallower 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 (Bliss & Zedler 1998; Zedler 1987). Gerhardt & Collinge (2007) showed that, even when native species were abundant, 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 & 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 (Gieselman et al. 2013; Laurance et al. 2002). 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 three-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 (Gorchov et al. 2014; Bauder 2000; Platenkamp 1998). 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?

C. 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. (Figure 1). This land is part of unceded ancestral territory of the Chumash people. The study areas lie within one mile of the Pacific Ocean and experience a Mediterranean climate with cool (13.3ºC average) and wet conditions from November to April and warm (15.6ºC average) and dry conditions during the remainder of the year (PRISM 2019). Rainfall averages approximately 43.18cm 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 32ºC) 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: Multi-Year Monitoring Study

We monitored seven 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 $67m^2$ to $425m^2$ in area and 14-18cm
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 mainly were 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 five-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 (Figure 2A). Within each of these
zones, we haphazardly placed three $1m^2$ quadrats, for a total of nine 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 three years allowed us

to evaluate the vegetation community in pools ages two to nine 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 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).

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 66m^2 to 1,367m^2 and a maximum depth ranging from 53.5cm to 80cm, planting of

locally-sourced native plant species via seeding and transplanting, and hand-weeding and

herbicide treatments of exotic species during a 2-5-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 two transects bisecting the

pool along its elliptical major and minor axes (Figure 2B). Every other meter along each

transect, we laid down a 1m^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 used a laser level to calculate the elevation of each quadrat

above the deepest point of the pool. To determine pool hydroperiod, we installed 0.8m 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).

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 (Brookes 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 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: Multi-Year 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 treated time since restoration (years), the pool edge ratio (ratio of pool perimeter, in m, to the pool area, m^2; see, e.g., Figure 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 pool name and in 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.

D. Results

Approach 1: Multi-Year Monitoring Study

<u>Q1: How does exotic plant abundance and richness change in restored vernal pools over time?</u>

In the multi-year 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; Figure 4). Exotic plant species richness did not significantly change over time, but ranged from 1 to 11 species between pools (Table S2; Figure S1). Dominant 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).

<u>Q2: How does native plant abundance and richness change in restored vernal pools over time?</u>

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; Figure 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; Figure 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), *Stipa pulchra, Juncus mexicanus*, *Carex praegracilis* (clustered field sedge), *Distichlis spicata*

(saltgrass), *Eleocharis macrostachya*, *Eryngium vaseyi* (coyote thistle), *Cyperus eragrostis* (tall flatsedge), *Juncus bufonius* (toad rush), *Schoenoplectus pungens*, and *Alopecurus saccatus* (Pacific foxtail). Dominant native species in the upland zone included *Stipa pulchra*, *Epilobium canum* (California fuchsia), *Hordeum brachyantherum* (meadow barley), *Lepidium nitidum* (peppergrass), and *Juncus bufonius*.

Approach 2: Chronosequence Survey

<u>Q3: What abiotic factors correlate with higher exotic plant abundance and richness in restored pools over time?</u>

Exotic cover did not significantly correlate with time since restoration (Table S6; Figure 6). Yet, the central zone had significantly lower average cover (mean = 11.49±0.81%) than the transition zone (mean = 39.93±1.65%; $p < 0.001$) and upland zone (mean = 68.50±2.36%; $p < 0.001$). Exotic plant species richness also did not significantly correlate with time since restoration (Table S7; Figure S3). Yet, the central zone had significantly lower average richness (mean = 2.03±0.05 species) than the transition zone (mean = 3.78±0.09 species; $p < 0.001$) and upland zone (mean = 5.03±0.12 species; $p < 0.001$).

The most abundant exotic invasive species was *Festuca 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 *Festuca myuros*, *Polypogon monspeliensis*, *Bromus diandrus*, *Bromus hordeaceus*, *Avena*

fatua (wild oats), *Hordeum marinum* (seaside barley), *Plantago lanceolata* (English

plantain), and *Lythrum hyssopifolia* (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 upon the pool zone. The

native cover was significantly lower in older pools, but only in the upland zone ($p < 0.001$;

Table S9; Figure 7). In addition, the upland zone had significantly lower native cover (mean

= 34.90±1.85%) compared to the central zone (mean = 74.52±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 pool 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; Figure 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 *Eleocharis macrostachya*, *Eryngium*

vaseyi, and *Eleocharis acicularis*. Dominant native species in the upland zone included *Eleocharis macrostachya* and *Stipa pulchra*.

E. 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 into the pool centers (Javornik & Collinge 2016; Bliss & Zedler 1998). 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 multi-year 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 (Lesage et al. 2018; McClain et al. 2011). 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 2021). Other studies

have reported higher invasive species in drier parts of the pools and during drier years

(Gerhardt & Collinge 2003; Bauder 2000). 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 (Halpern & Antos 2021; Wang et al. 2006). Several studies

have shown that exotic species abundance increases closer to forest edges, where disturbance

and exotic propagule supply is high (Dawson et al. 2014). 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

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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 and colleagues 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, *Eleocharis macrostachya*, *Juncus mexicanus*, and *Juncus phaeocephalus* were able to dominate the central zone, while *Carex praegracilis*, *Eleocharis macrostachya*, *Distichlis spicata*, *Juncus mexicanus*, and *Elymus 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

(Marty 2005; Pollack & Kan 1998). 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 (Matthews & Spyreas 2010; Gutrich et al. 2009). 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 (Lulow 2006;

Dukes 2002). 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.

F. Figures and Tables

Figure 1. Map showing 69 surveyed pools (highlighted in yellow) throughout 9 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).
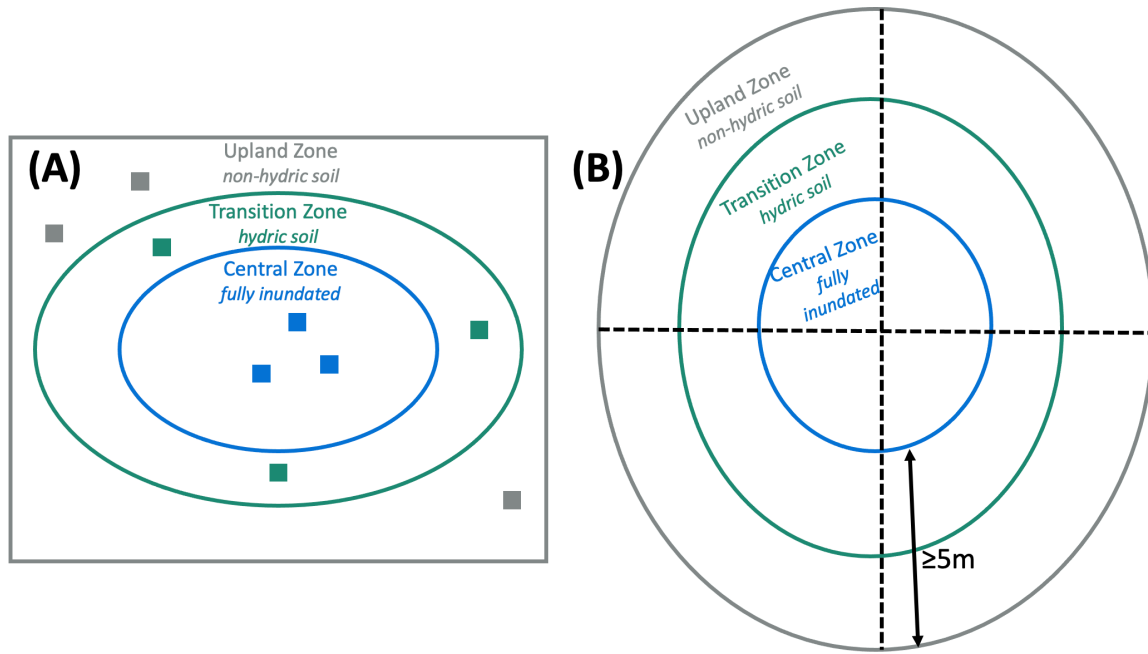
Figure 2. (A) Schematic of the sampling design for the multi-year monitoring study. Each

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; 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. Two sampling transects

bisected each pool, along which quadrats were placed every other meter; exact location of the

transects varied for each pool.
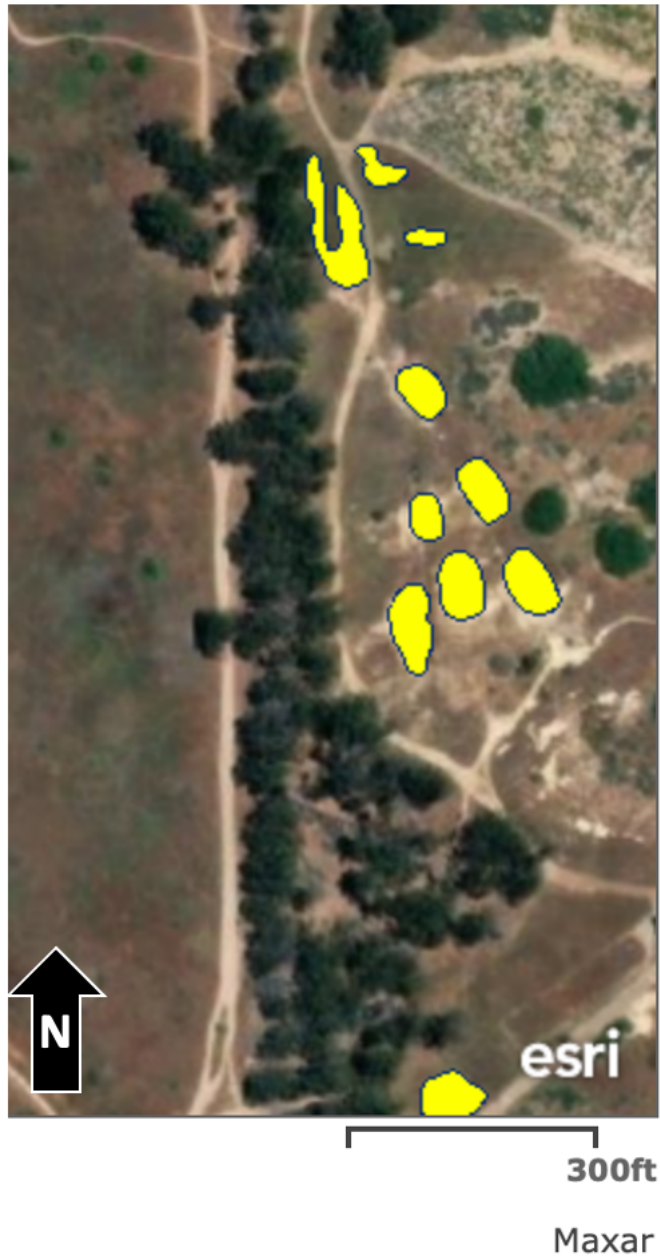
Figure 3. Close-up map of vernal pools (highlighted in yellow) in South Parcel restoration site, with examples of pools with high pool edge ratio (top) and low pool edge ratio (middle, bottom).
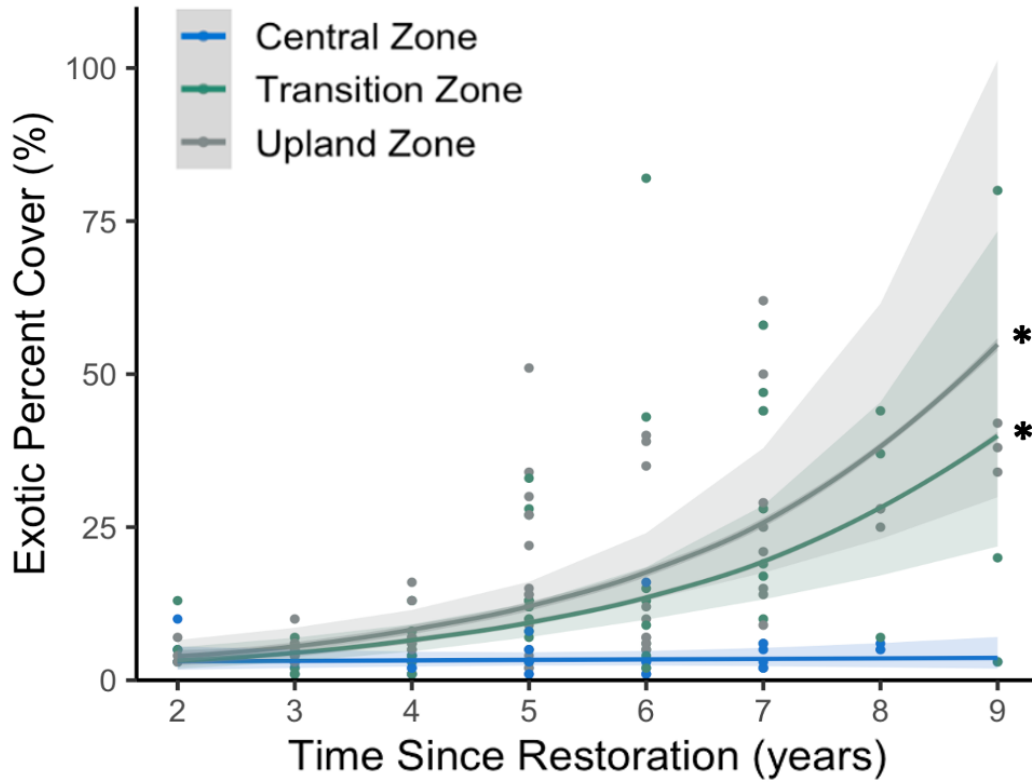
Figure 4. Total exotic species percent cover in restored vernal pool zones over time for multi-year monitoring study, plotted with GLMER predictions and 95% confidence intervals as linear models. Asterisks indicate significant interaction between zone and time since restoration for exotic percent cover (p <0.05).
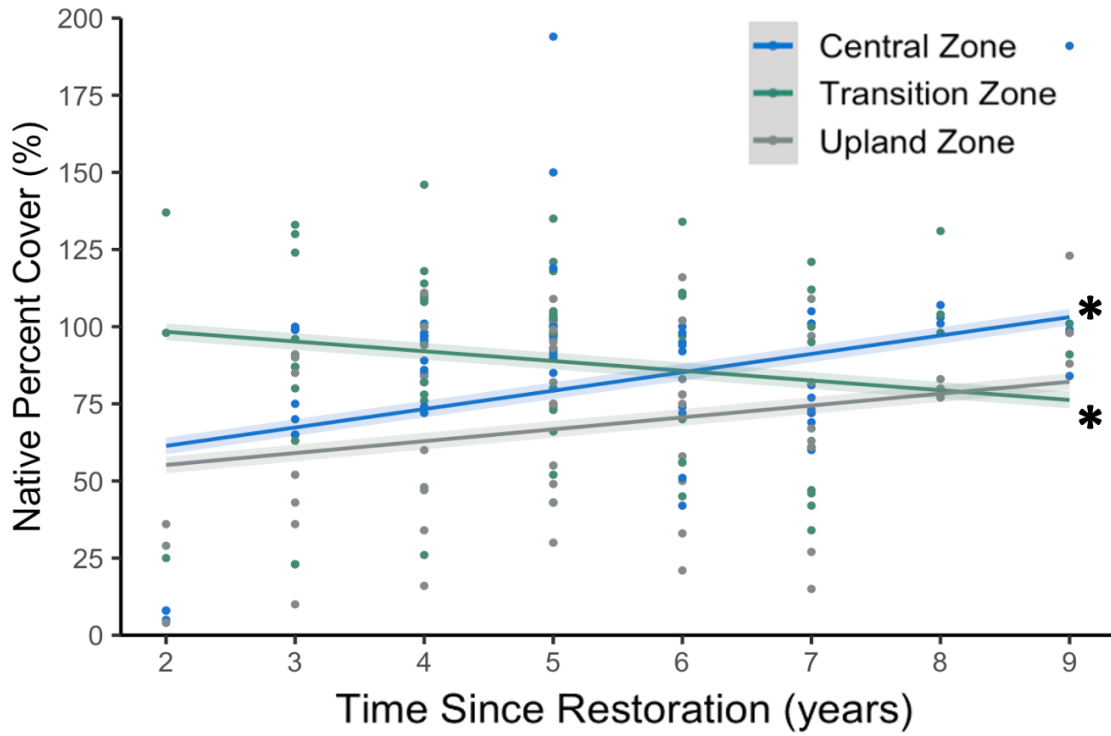
Figure 5. Total native species percent cover in restored vernal pool zones over time for multi-year monitoring study, plotted with LMER predictions and standard error as linear models. Asterisks indicate significant interaction between zone and time since restoration for native percent cover ($p <0.05$).
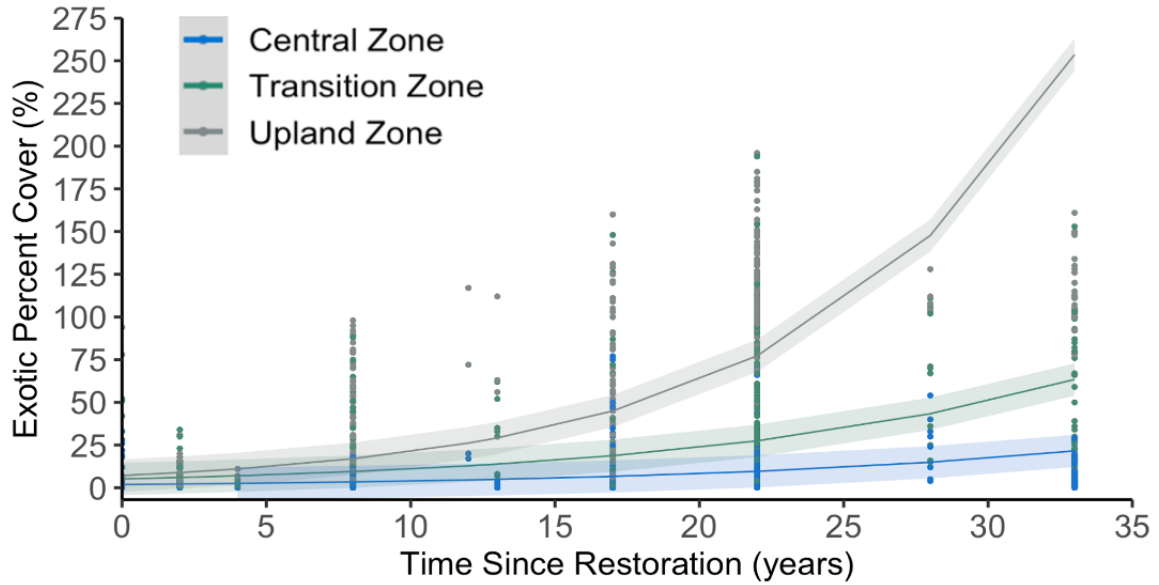
Figure 6. Average total exotic species percent cover per pool zone over time in 2019 chronosequence, shown with GLMER estimates and standard error as linear models. Asterisks indicate significant interaction between zone and time since restoration for exotic percent cover ($p < 0.05$).
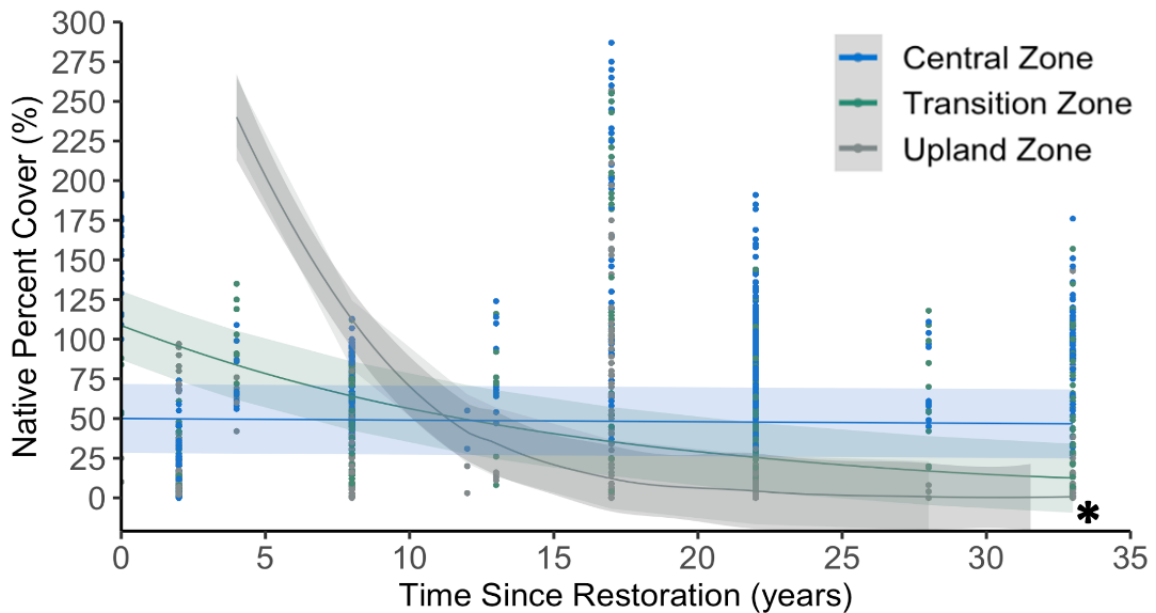
Figure 7. Average total native species percent cover per pool zone over time in 2019 chronosequence, shown with GLMER estimates and standard error as linear models. Asterisks indicate significant interaction between zone and time since restoration for native percent cover ($p < 0.05$).

	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													

Table 1. Significant fixed effects from GLMERs for exotic cover, exotic richness, native cover, and native richness ($p < 0.05$). Sign indicates 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.

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H. Appendix A

Supporting Information

Supplement S1. Restoration Actions for Vernal Pools in Multi-Year Monitoring Study

All vernal pool restoration was conducted by the Cheadle Center for Biodiversity and Ecological Restoration at UCSB (CCBER; https://ccber.ucsb.edu). We monitored 7 restored vernal pools within the management unit named North Parcel (Figure i). The pools were created between 2011 and 2014, and varied in size and depth (Table S1), but all 7 pools were managed in a similar fashion.

Restoration of the vernal pools began by grading to deepen vernal pool basins. As vernal pools were constructed with adjacent upland area to facilitate soil restoration, sifted compost from the Santa Barbara County was distributed throughout the area at approximately 6 inches in depth. A tractor tilled the compost into dry soil to a depth of approximately 8-12 inches. No organic material was incorporated into the wetland basins. Additionally, a humate

product called Live Earth Soil Conditioner (1.50% sulfur, 2.25% iron, 45% humic acid) and Live Earth First Green (4% calcium, 5% sulfur, 1% iron, and 5% nitrogen, 3% phosphorous, and 1% potassium) was equally distributed one time, across both wetland and upland soils, at a depth of approximately 5 inches.

After the site was physically manipulated and amended, the individual pools were planted, and to a lesser degree seeded, with approximately 70 species of locally-sourced native plants from vernal pool, vernal marsh, coastal prairie, and coastal sage scrub assemblages. Vegetation was purposely planted in patches to mimic landscape patterns generally observed in nature, according to soil types, hydrology, and other site factors. Planting continued throughout the summer months in some cases. Installed plantings were watered-in using mainly moveable drip irrigation until establishment was achieved.

After the initial planting was completed, the site was actively maintained in a number of ways. First, native annual thatch was periodically removed in the late summer and fall months, to simulate clearing likely done by historically indigenous burning practices. Species whose thatch was removed include *Centromadia parryi* ssp. *australis* (southern tarplant), *Symphyotrichium sublatum* (Eastern annual saltmarsh aster), *Dienandra fasciculata* (clustered tarweed). Thatch material from perennial natives, such as *Stipa pulchra* (purple needlegrass), was also removed annually in places for the same effect. Additionally, certain native species are removed periodically to maintain landscape variability, facilitate the colonization of novel or desirable native species, and avoid homogenization of common species (e.g., *Baccharis pilularis* (coyote brush), *Typha* spp., *Schoenoplectus californicus*

(California bulrush), and *Salix* spp.). Exotic species were controlled mainly by hand-weeding, although solarization, herbicide, and green flaming were also employed to a lesser degree. This implementation phase of this restoration project lasted 5 years.

Figure i. North Parcel vernal pools (highlighted in purple). #3, 7, 9, 14, 16, 19, and PH1 monitored in this experiment.

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

Figures ii-viii show close-up maps of vernal pools surveyed across 9 restoration sites. Table i provides a summary of the restoration actions performed on each pool during the indicated restoration year. Table ii lists the native and exotic plant species found during the 2019 vegetation surveys.

Figure ii. Map of vernal pools (highlighted in yellow) in South Parcel restoration site.

Figure iii. Map of vernal pools (highlighted in yellow) in Manzanita Village restoration site.

Figure iv. Map of vernal pools (highlighted in yellow) in North Parcel restoration site.
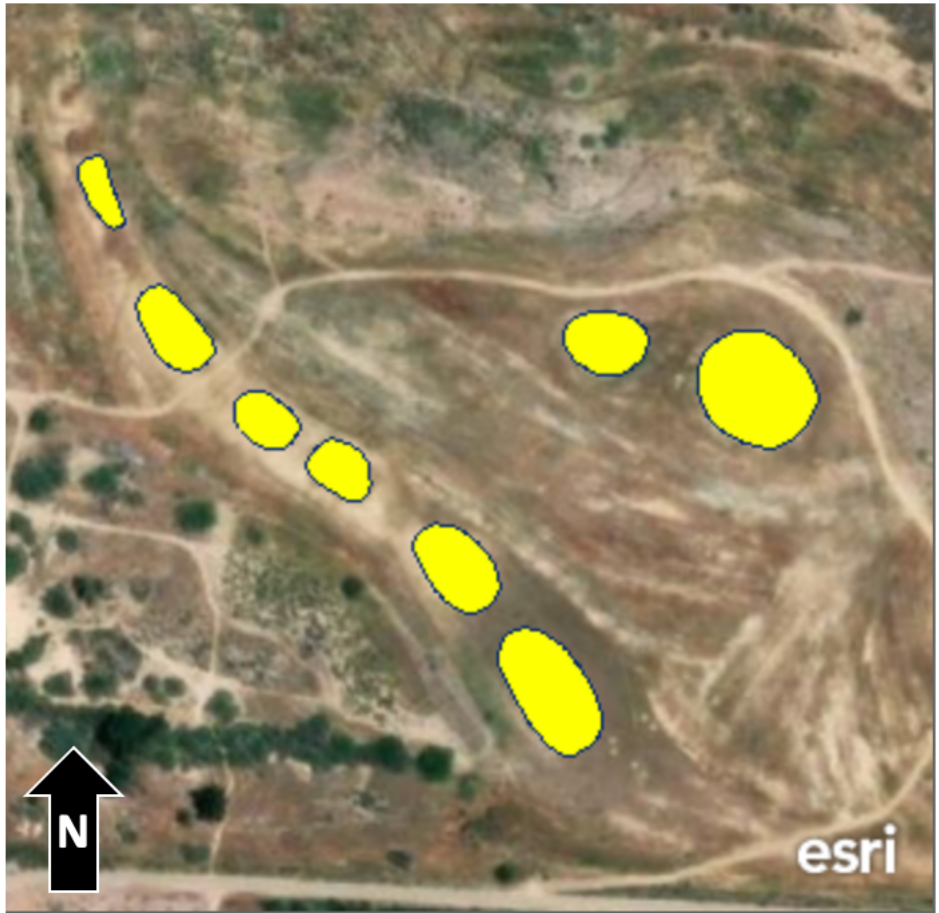
Figure v. Map of vernal pools (highlighted in yellow) in North Campus Open Space restoration site.
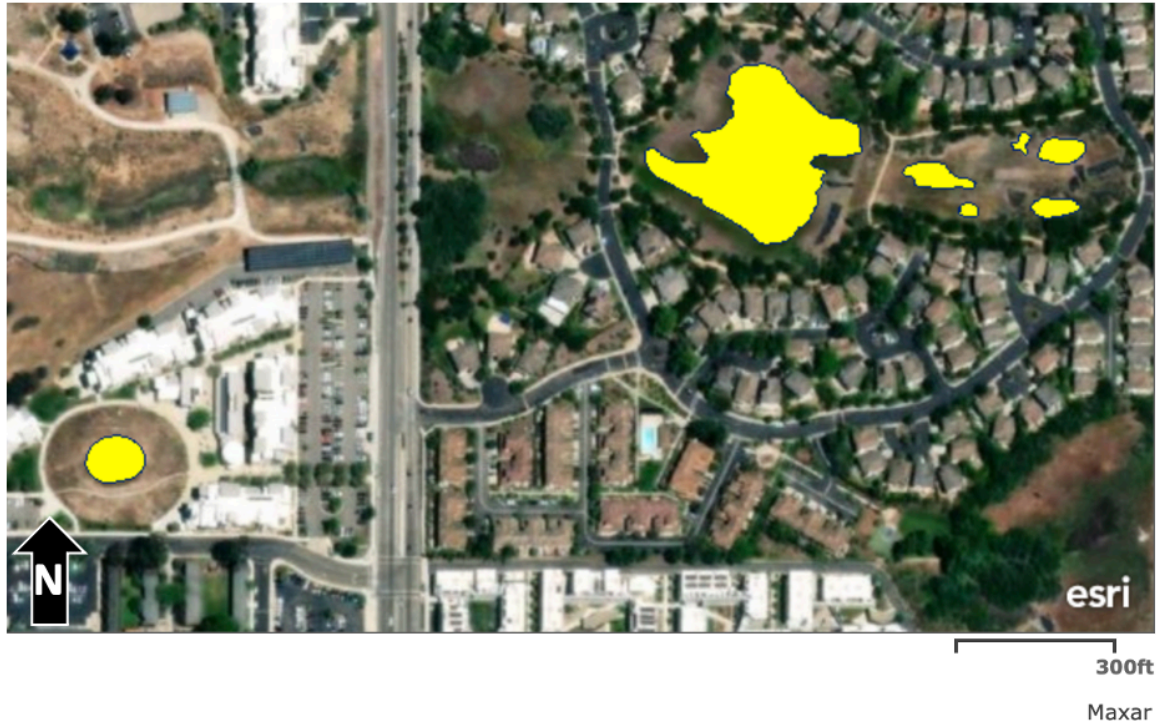
Figure vi. Map of vernal pools (highlighted in yellow) in Sierra Madre (left) and Storke Ranch (right) restoration sites.

Figure vii. Map of vernal pools (highlighted in yellow) in West Campus Bluffs restoration site.

Figure viii. Map of vernal pools (highlighted in yellow) in Camino Corto Open Space (left) and Del Sol Vernal Pool Preserve (right) restoration sites.

Table i. Summary of characteristics and monitoring of 69 vernal pools surveyed in 2019 chronosequence.

Restoration Site	Vernal Pool ID	Restoration Year	Area (square meters)	Restoration Actions	2019 Monitoring Date
Camino Corto Open Space	2	1997	578.25149	Enhancement of pool edge: berm enhancement, seeding of edges	5/24, 7/1
	3	1997	282.98003	Enhancement of pool edge: berm enhancement, seeding of edges	5/16, 6/28
	4	1997	215.82577	Enhancement of pool edge: berm enhancement, seeding of edges	5/24, 6/28

	5	1997	205.04528	Enhancement of pool edge: berm enhancement, seeding of edges	5/22, 6/28
	6	1997	841.86376	Enhancement of pool edge: berm enhancement, seeding of edges	5/22, 7/5
	7	1997	1297.04083	Enhancement of pool edge: berm enhancement, seeding of edges	5/10, 7/1
	8	1997	115.48721	Enhancement of pool edge: berm enhancement, seeding of edges	5/29, 6.28

Del Sol Vernal Pool Preserve	E	1986	1461.22026	Restoration of pool basin: excavation of pool basin, seeding of pool basin	5/20, 7/3
	F	1991	196.49584	Enhancement of pool edge: berm enhancement, seeding of edges	6/67/2,
	G	1986	420.91006	Restoration of pool basin: excavation of pool basin, seeding of pool basin	5/20, 6/27
	H	1986	66.97073	Created: excavation of pool basin,	5/13, 6/26

				seeding of pool basin	
	M	1986	74.00052	Created: excavation of pool basin, seeding of pool basin	5/13, 6/24
	N	1986	1267.18599	Enhancement of pool edge: berm enhancement, seeding of edges	5/3, 5/8
	S	1997	571.45015	Enhancement of pool edge: berm enhancement, seeding of edges	5/23, 7/3
	T	1997	158.80983	Enhancement of pool edge: berm	4/29-5/2

				enhancement, seeding of edges	
	U	1997	444.76421	Enhancement of pool edge: berm enhancement, seeding of edges	6/3, 6/27
	V	1997	945.26530	Enhancement of pool edge: berm enhancement, seeding of edges	5/30, 7/8
	W	1986	964.58172	Enhancement of pool edge: berm enhancement, seeding of edges	5/23, 7/2
Ellwood Mesa Open Space	1	1980	473.09113	Grazed	7/9
	2	1980	185.55477	Grazed	5/9

	3	1980	202.30872	Grazed	5/9
	4	1980	64.95253	Grazed	7/9
	5	1980	214.93384	Grazed	5/9
Manzanita Village	San Miguel	2002	279.81479	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 6 years	5/29
	Santa Barbara	2002	195.94477	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 6 years	6/19-6/20

	Santa Ca talina	2002	186.90141	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 6 years	6/18-6/19
	Santa Cr uz	2002	129.53654	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 6 years	6/13-6/14
	Santa Ro sa	2002	272.70344	Created: excavation of pool basin, seeding & planting of pool	5/29, 6/3

			basin, weeding for 6 years	
North Campus Open Space	1	2017	1367.0923 3	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 2 years	7/19
	2	2017	544.07430	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 2 years	7/2
	3	2017	1081.2805 7	Created: excavation of pool basin,	5/6

				seeding & planting of pool basin, weeding for 2 years	
4		2017	669.13452	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 2 years	6/27
5		2017	362.43625	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 2 years	5/7

	6	2017	355.67991	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 2 years	5/7
	7	2017	540.88420	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 2 years	5/7
	8	2017	247.33571	Created: excavation of pool basin, seeding & planting of pool	5/8

				basin, weeding for 2 years	
North Parcel	14	2014	432.89275	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 2 years	7/16
	16	2014	424.18353	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 2 years	7/16
	19	2013	359.35838	Created: excavation of pool basin,	7/17, 7/22

				seeding & planting of pool basin, weeding for 2 years	
3		2012	67.80549	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 2 years	7/31
4		2012	85.28026	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 2 years	7/30

	6	2012	79.45495	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 2 years	7/11
	7	2012	346.78561	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 2 years	7/9
	9	2015	160.07318	Created: excavation of pool basin, seeding & planting of pool	7/11

				basin, weeding for 2 years	
	PH1	2010	173.12680	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 3 years	7/22
Sierra Madre	Central Wetland	2015	678.64330	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 3 years	7/16-7/17
South Parcel	1	2011	322.58988	Created: excavation of pool basin,	5/14-5/15

				seeding & planting of pool basin, weeding for 5 years	
2		2011	330.63380	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 5 years	5/15
3		2011	366.71542	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 5 years	5/15

	4	2011	172.63579	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 5 years	6/11
	5	2011	283.08781	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 5 years	6/20
	6	2011	245.20166	Created: excavation of pool basin, seeding & planting of pool	6/11

				basin, weeding for 5 years	
	7	2011	532.95060	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 5 years	7/22-7/23
	8	2011	139.53243	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 5 years	6/20-6/21
	9	2011	78.35054	Created: excavation of pool basin,	7/22

				seeding & planting of pool basin, weeding for 5 years	
	SWW 1	2011	344.68195	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 5 years	5/16
Storke Ranch	2007	2007	66.98034	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 11 years	7/18

	2017	2017	68.58075	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 2 years	5/15-5/16
	East	2006	379.64773	Enhancement of pool edge: planting of pool edge	5/3, 5/10, 5/12, 5/13
	North	2006	306.16317	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 12 years	5/16, 5/24

	South	2006	233.48607	Created: excavation of pool basin, seeding & planting of pool basin, weeding for 12 years	6/7, 6/28
West Campus Bluffs	1	2015	838.63646	Restoration of pool basin: excavation of pool basin, seeding & planting of pool basin, weeding for 3 years	5/1, 5/6
	10	2002	98.54318	Created: excavation of pool basin, seeding &	7/8

				planting of pool basin	
	11	2002	105.14194	Created: excavation of pool basin, seeding & planting of pool basin	7/10
	13	2002	56.54870	Created: excavation of pool basin, seeding & planting of pool basin	7/10
	4	1997	1017.73074	Enhancement of pool edge: berming of pool	5/8

				edge, planting of pool edge	
6		1997	237.47864	Enhancement of pool edge: berming of pool edge, planting of pool edge	7/9
8		2002	114.68265	Enhancement of pool edge: berming of pool edge, planting of pool edge	7/10
9		2002	341.98304	Enhancement of pool edge: berming of pool edge, planting of pool edge	7/8

Table ii. List of plant species found throughout pools. Species denoted with an asterisk were planted by CCBER during restoration. N = native; E = exotic

Species	Native Status
*Acmispon glaber**	N
Acmispon species	E
Alisma lanceolatum	E
*Alopecurus saccatus**	N
Ambrosia psilostachya	N
*Anemopsis californica**	N
*Artemisia californica**	N
*Artemisia douglasiana**	N
*Asclepias fascicularis**	N
*Atriplex californica**	N
*Atriplex lentiformis**	N
Atriplex semibaccata	E
*Baccharis douglasii**	N
Baccharis pilularis	N
*Baccharis plummerae**	N
*Baccharis salicifolia**	N
Bolboschoenus maritimus	N
Brachypodium distachyon	E
Brassica nigra	E
*Bromus carinatus**	N

Bromus diandrus	E
Bromus hordeaceus	E
Bromus madritensis	E
Calystegia macrostegia	N
Carduus pycnocephalus	E
Carex praegracilis	N
Centaurium tenuiflorum	E
Centromadia parryi ssp. australis	N
Corethrogyne filaginifolia	N
Cotula coronopifolia	E
Crassula aquatica	N
Cressa truxillensis	N
Croton setigerus	N
Crypsis schoenoides	E
Cyperus eragrostis	N
Deinandra fasciculata	N
Diplacus aurantiacus*	N
Distichlis spicata*	N
Eleocharis acicularis*	N
Eleocharis machrostachya*	N
Elymus condensatus*	N
Elymus glaucus*	N
Elymus triticoides*	N

*Encelia californica**	N
Epilobium brachycarphum	N
*Epilobium canum**	N
Erigeron bonariensis	E
Erigeron canadensis	N
Erigeron sumatrensis	E
*Eriogonum parvifolium**	N
*Eriophyllum confertiflorum**	N
Erodium cicutarium	E
*Eryngium armatum**	N
*Eryngium vaseyi**	N
*Eschscholzia californica**	N
Euphorbia peplus	E
Euphorbia serpens	E
Extriplex californica	N
Festuca myuros	E
Festuca perennis	E
Foeniculum vulgare	E
*Frankenia salina**	N
Geranium dissectum	E
Grindelia camporum	N
*Hazardia squarrosa**	N
Helminthotheca echiodes	E

*Heteromeles arbutifolia**	N
Heterotheca grandifolia	N
*Hordeum brachyantherum**	N
Hordeum murinum	E
Hypochaeris glabra	E
Isocoma menziesii	N
Isolepis cernua	N
*Jaumea carnosa**	N
*Juncus acutus**	N
*Juncus bufonius**	N
*Juncus mexicanus**	N
*Juncus occidentalis**	N
*Juncus patens**	N
*Juncus phaeocephalus**	N
*Juncus textilis**	N
Lactuca serriola	E
Laennecia coulteri	N
Lepidium nitidum	N
Logfia gallica	E
*Lonicera subspicata**	N
Lupinus microcarpus	N
Lupinus succulentus	N
Lysimachia arvensis	E

Lythrum hyssopifolia	E
Malacothrix saxatilis*	N
Malva parviflora	E
Malvella leprosa	N
Medicago lupulina	E
Medicago polymorpha	E
Melilotus indicus	E
Melilotus species	E
Monanthechloe littoralis*	N
Oxalis californica	N
Paraphalis incurva	E
Phalaris lemmonii*	N
Plagiobothrys undulatus*	N
Platanus racemose	N
Plantago coronopus	E
Plantago lanceolata	E
Poa annua	E
Polycarpon tetraphyllum	E
Polygonum aviculare ssp.depressum	E
Polypogon interruptus	E
Polypogon monospeliensis	E
Pseudognaphalium californicum*	N
Pseudognaphalium canescens*	N

Pseudognaphalium luteoalbum	E
*Psilocarphus brevissimus**	N
*Quercus agrifolia**	N
Raphanus sativus	E
*Rhamnus californica**	N
*Rhus integrifolia**	N
*Ribes speciosum**	N
*Rosa californica**	N
Rumex crispus	E
*Rumex salicifolius**	N
Salsola tragus	E
*Salvia mellifera**	N
*Salvia leucophylla**	N
*Salvia spathacea**	N
*Sambucus mexicana**	N
*Schoenoplectus americanus**	N
*Schoenoplectus californicus**	N
*Schoenoplectus pungens**	N
*Scrophularia californica**	N
Senecio vulgaris	E
*Sisyrinchium bellum**	N
*Solanum douglasii**	N
Sonchus asper	E

Sonchus oleraceus	E
Spergularia species	E
Stipa pulchra*	N
Symphoricarpos mollis*	N
Symphyotrichum chilense*	N
Symphyotrichum subulatum	N
Taraxacum officinale	E
Trifolium hirtum	E
Typha domingensis	N
Verbena lasiostachys*	N
Vicia sativa	E
Vicia villosa	E
Zeltnera muehlenbergii*	N

Table S1. ANOVA table of total exotic species percent cover GLMER for multi-year monitoring study. "Time Since" is years since restoration began; "Zone" is zone of sampling quadrat, either central (baseline), transition, upland; "sampling year" is year of sampling; "pool depth" is depth of deepest point in each pool in cm; "pool area" is area of each pool in square meters; "quadrat name" is the unique identifier of each quadrat; "annual precip" is annual total amount of precipitation in cm. Bolded values have a significance of $p < 0.05$.

	Exotic Percent Cover		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	1.08	0.23 – 1.93	**0.013**

Time Since	0.02	-0.13 – 0.18	0.752
Zone [Transition]	-0.65	-1.74 – 0.45	0.248
Zone [Upland]	-0.48	-1.57 – 0.61	0.390
Time Since * Zone [Transition]	0.34	0.14 – 0.53	**0.001**
Time Since * Zone [Upland]	0.35	0.16 – 0.55	**<0.001**

Random Effects

σ^2	0.33
τ_{00} sampling year	0.01
τ_{00} pool depth	0.00
τ_{00} pool area	0.00
τ_{00} quadrat name:Zone:pool name	0.20
τ_{00} Zone:pool name	0.02
τ_{00} pool name	0.00
τ_{00} annual precip	0.00
N sampling year	3
N pool depth	6
N pool area	7
N quadrat name	62
N pool name	7
N annual precip	3
Observations	163
Marginal R^2 / Conditional R^2	0.649 / NA

Table S2. ANOVA table of exotic species richness GLMER for multi-year monitoring study. "Time Since" is years since restoration began; "Zone" is zone of sampling quadrat, either central (baseline), transition, upland; "sampling year" is year of sampling; "pool depth" is depth of deepest point in each pool in cm; "pool area" is area of each pool in m^2; "quadrat name" is the unique identifier of each quadrat; "annual precip" is annual total amount of precipitation in cm. Bolded values have a significance of $p < 0.05$.

Exotic Species Richness

Predictors	Log-Mean	CI	p
(Intercept)	0.36	-0.28 – 0.99	0.270
Time Since	0.09	-0.03 – 0.21	0.128
Zone [Transition]	0.78	0.09 – 1.47	**0.027**
Zone [Upland]	0.50	-0.18 – 1.19	0.150
Time Since * Zone [Transition]	-0.05	-0.17 – 0.08	0.467
Time Since * Zone [Upland]	0.03	-0.09 – 0.15	0.638

Random Effects

σ^2	0.27
τ_{00} quadrat name:Zone:pool name	0.00
τ_{00} Zone:pool name	0.00
τ_{00} pool name	0.00
τ_{00} pool area	0.00
τ_{00} pool depth	0.00
τ_{00} annual precip	0.01
τ_{00} sampling year	0.00
N sampling year	4
N pool depth	6
N pool area	7
N quadrat name	62
N pool name	7
N annual precip	4
Observations	184
Marginal R^2 / Conditional R^2	0.256 / 0.294
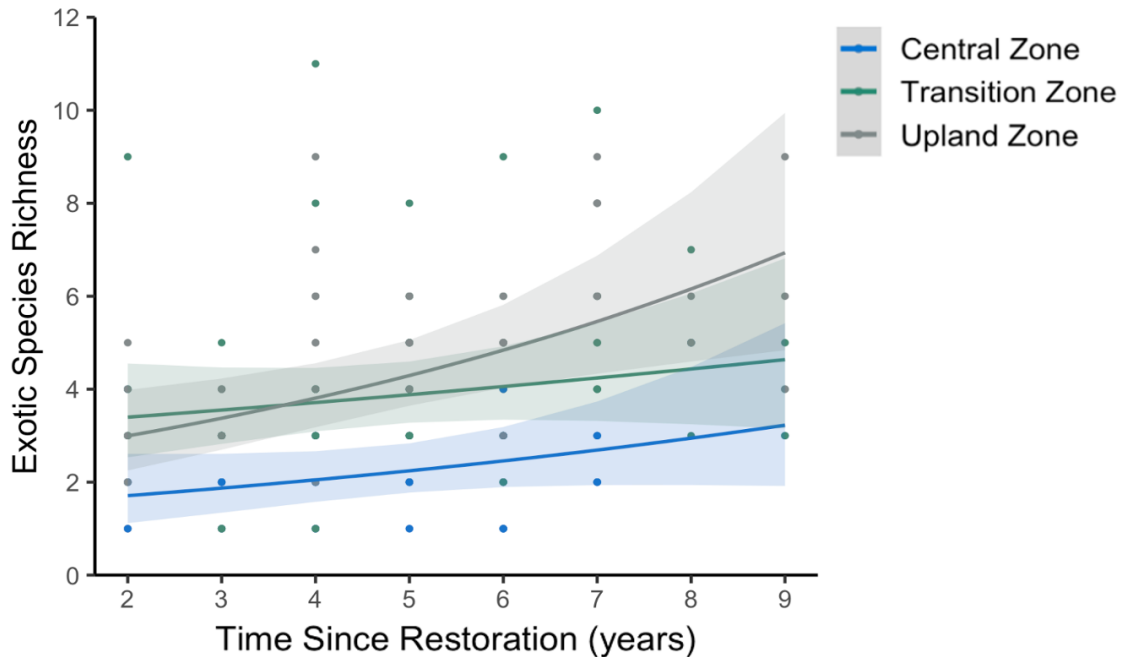
Figure S1. Exotic species richness in restored vernal pool zones over time for multi-year monitoring study, plotted with GLMER predictions and 95% confidence intervals as linear models. Asterisks indicate significant interaction between zone and time since restoration for exotic richness (p <0.05).

Table S3. ANOVA table of total native species percent cover LMER for multi-year monitoring study. "Time Since" is years since restoration began; "Zone" is zone of sampling quadrat, either central (baseline), transition, upland; "sampling year" is year of sampling; "pool depth" is depth of deepest point in each pool in cm; "pool area" is area of each pool in m^2; "quadrat name" is the unique identifier of each quadrat; "annual precip" is annual total amount of precipitation in cm. Bolded values have a significance of $p < 0.05$.

	Native Percent Cover		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	49.43	15.94 – 82.91	**0.004**

Time Since	5.96	0.58 – 11.35	**0.030**
Zone [Transition]	55.24	21.03 – 89.45	**0.002**
Zone [Upland]	-1.95	-36.12 – 32.21	0.910
Time Since * Zone [Transition]	-9.12	-15.26 – -2.99	**0.004**
Time Since * Zone [Upland]	-2.11	-8.24 – 4.02	0.497

Random Effects

σ^2	361.12
τ_{00} quadrat name:Zone:pool name	233.41
τ_{00} Zone:pool name	0.00
τ_{00} pool area	0.00
τ_{00} pool depth	381.82
τ_{00} annual precip	5.09
τ_{00} sampling year	5.89
N pool area	7
N pool depth	6
N sampling year	3
N pool name	7
N quadrat name	62
N annual precip	3
Observations	163
Marginal R^2 / Conditional R^2	0.283 / NA

Table S4. ANOVA table of native species richness GLMER for multi-year monitoring study. "Time Since" is years since restoration began; "Zone" is zone of sampling quadrat, either central (baseline), transition, upland; "sampling year" is year of sampling; "pool depth" is depth of deepest point in each pool in cm; "pool area" is area of each pool in m²; "quadrat name" is the unique identifier of each quadrat; "annual precip" is annual total amount of precipitation in cm. Bolded values have a significance of $p < 0.05$.

	Native Species Richness		
Predictors	*Log-Mean*	*CI*	*p*
(Intercept)	0.58	0.14 – 1.02	**0.009**
Time Since	0.10	0.02 – 0.18	**0.012**
Zone [Transition]	1.29	0.81 – 1.77	**<0.001**
Zone [Upland]	0.61	0.10 – 1.11	**0.019**
Time Since * Zone [Transition]	-0.10	-0.19 – -0.01	**0.030**
Time Since * Zone [Upland]	-0.02	-0.12 – 0.07	0.630

Random Effects

σ^2	0.20
τ_{00} quadrat name:pool name	0.01
τ_{00} pool name	0.01
τ_{00} pool size	0.00
τ_{00} pool depth	0.00
τ_{00} annual precip	0.00
τ_{00} sampling year	0.00
ICC	0.11
N sampling year	4
N pool area	7
N pool depth	6
N quadrat name	63
N pool name	7
N annual precip	4
Observations	225
Marginal R^2 / Conditional R^2	0.370 / 0.436
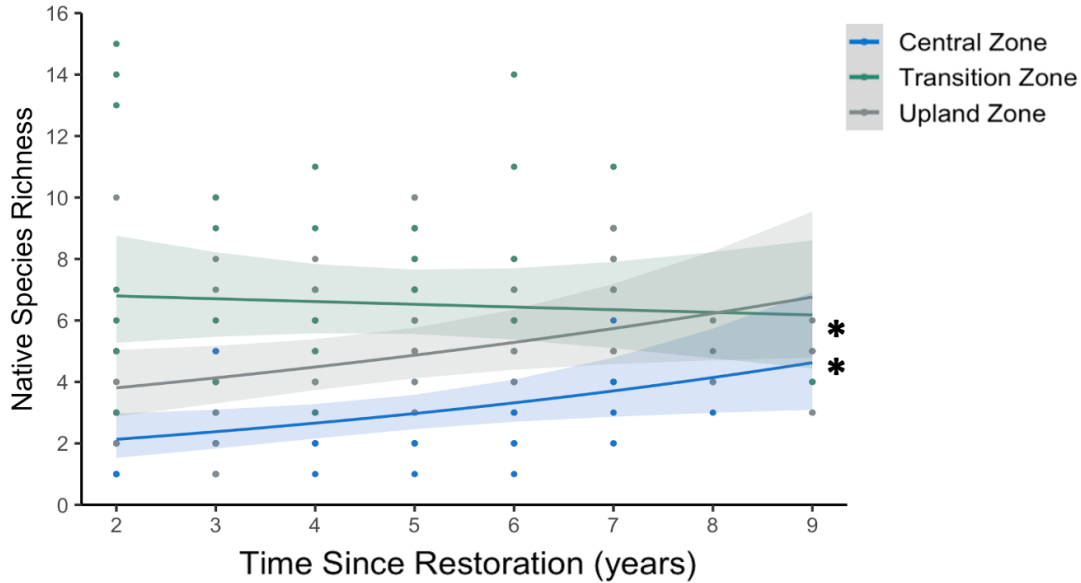
Figure S2. Native species richness in restored vernal pool zones over time for multi-year monitoring study, plotted with GLMER predictions and 95% confidence intervals as linear models. Asterisks indicate significant interaction between zone and time since restoration for native richness (p <0.05).

Table S5. ANOVA table of binomial exotic species percent cover GLMER hurdle model for 2019 chronosequence. "Zone" is zone of sampling quadrat, either central (baseline), transition, upland; "time since restoration" is years since restoration began; "pool edge ratio" is perimeter-to-area ratio of each pool, in m/m^2; "distance embedded in grassland" is distance of each pool from the edge of the restoration site, in m; "inundation period" is the number of days each pool was inundated, in cm; "elevation" is relative elevation of each quadrat above the deepest point of each pool, in cm; "historical precip" is the average annual precipitation that each pool experienced after it was restored, in cm; "previous year precip" is the total precipitation that each pool experienced the year before restoration began, in cm; "restoration year precip" is the total precipitation that each pool experienced the year that restoration

began, in cm; "next year precip" is the total precipitation that each pool experienced the year

after restoration began, in cm; "site" is the restoration site the pool is located in; "pool name"

is the unique identifier for each pool. Bolded values have a significance of $p < 0.05$.

	Predictors	Means	CI	p
	Exotic Percent Cover: Binomial			
	Count Model			
	(Intercept)	4.16	2.36 – 5.97	**<0.001**
	zone [upland]	5.51	-9.25 – 20.27	0.464
	zone [transition]	2.24	0.27 – 4.22	**0.026**
Central Zone	time since restoration	3.33	-0.40 – 7.06	0.080
	pool edge ratio	0.62	-0.36 – 1.59	0.214
	distance embedded in grassland	0.55	-1.49 – 2.59	0.594
	inundation period	-0.29	-1.54 – 0.96	0.649
	elevation	3.24	1.93 – 4.55	**<0.001**
	historical precip	-1.75	-4.78 – 1.28	0.259
	previous year precip	1.08	-1.85 – 4.01	0.470
	restoration year precip	0.75	-0.80 – 2.30	0.342
	next year precip	-0.81	-2.86 – 1.24	0.440
Transition Zone	time since restoration	1.35	-4.83 – 7.54	0.668
	pool edge ratio	-0.60	-2.43 – 1.22	0.516
	distance embedded in grassland	-0.55	-3.63 – 2.53	0.728
	inundation period	-1.49	-4.88 – 1.90	0.388

	elevation	-1.62	-3.48 – 0.25	0.089
	historical annual precip	-1.51	-7.36 – 4.33	0.612
	previous year precip	3.17	-2.25 – 8.59	0.251
	restoration year precip	1.99	-0.78 – 4.76	0.160
	next year precip	-0.13	-3.26 – 2.99	0.933
Upland Zone	time since restoration	1.94	-10.11 – 13.99	0.752
	pool edge ratio	-0.50	-1.96 – 0.96	0.502
	distance embedded in grassland	-0.88	-4.83 – 3.08	0.664
	inundation period	-3.09	-6.00 – -0.19	**0.037**
	elevation	-0.92	-1.72 – -0.12	**0.025**
	historical annual precip	0.91	-9.98 – 11.80	0.870
	previous year precip	4.00	-3.48 – 11.48	0.294
	restoration year precip	1.26	-4.91 – 7.43	0.690
	next year precip	0.73	-4.35 – 5.81	0.778

Zero-Inflated Model

(Intercept)   -4.38   -5.42 – -3.34   **<0.001**

Random Effects

σ^2 3.29

$\tau_{00 \; location}$ 1.55

$\tau_{00 \; site:pool \; name:zone}$ 4.35

ICC	0.64
N $_{site}$	7
N $_{pool\_name}$	34
N $_{zone}$	3
Observations	1432
Marginal R^2 / Conditional R^2	0.779 / 0.921

Table S6. ANOVA table of gamma exotic species percent cover GLMER hurdle model for 2019 chronosequence. "Zone" is zone of sampling quadrat, either central (baseline), transition, upland; "time since restoration" is years since restoration began; "pool edge ratio" is perimeter-to-area ratio of each pool, in m/m^2; "distance embedded in grassland" is distance of each pool from the edge of the restoration site, in m; "inundation period" is the number of days each pool was inundated, in cm; "elevation" is relative elevation of each quadrat above the deepest point of each pool, in cm; "historical precip" is the average annual precipitation that each pool experienced after it was restored, in cm; "previous year precip" is the total precipitation that each pool experienced the year before restoration began, in cm; "restoration year precip" is the total precipitation that each pool experienced the year that restoration began, in cm; "next year precip" is the total precipitation that each pool experienced the year after restoration began, in cm; "site" is the restoration site the pool is located in; "pool name" is the unique identifier for each pool. Bolded values have a significance of $p < 0.05$.

	Exotic Percent Cover: Gamma		
Predictors	*Estimates*	*CI*	*p*

	Count Model			
	(Intercept)	1.86	1.16 – 2.56	**<0.001**
	zone [upland]	1.90	1.58 – 2.22	**<0.001**
	zone [transition]	1.04	0.74 – 1.34	**<0.001**
Central Zone	time since restoration	0.75	-0.35 – 1.85	0.179
	pool edge ratio	0.26	0.05 – 0.47	**0.016**
	distance embedded in grassland	0.30	-0.22 – 0.81	0.262
	inundation period	-0.15	-0.47 – 0.17	0.357
	elevation	0.63	0.44 – 0.82	**<0.001**
	historical precip	-0.61	-1.59 – 0.37	0.223
	previous year precip	0.38	-0.69 – 1.45	0.488
	restoration year precip	0.26	-0.36 – 0.87	0.411
	next year precip	-0.02	-0.64 – 0.60	0.941
Transition Zone	time since restoration	0.02	-1.13 – 1.18	0.969
	pool edge ratio	-0.26	-0.56 – 0.05	0.101
	distance embedded in grassland	-0.39	-0.96 – 0.17	0.171
	inundation period	0.05	-0.37 – 0.46	0.825
	elevation	-0.20	-0.44 – 0.04	0.104
	historical annual precip	0.29	-0.90 – 1.48	0.637
	previous year precip	0.09	-1.15 – 1.34	0.884

	restoration year precip	0.01	-0.57 – 0.59	0.963
	next year precip	-0.01	-0.85 – 0.83	0.973
Upland Zone	time since restoration	0.35	-0.80 – 1.50	0.550
	pool edge ratio	-0.22	-0.51 – 0.07	0.135
	distance embedded in grassland	-0.30	-0.87 – 0.26	0.294
	inundation period	0.13	-0.29 – 0.54	0.544
	elevation	-0.66	-0.89 – -0.43	**<0.001**
	historical annual precip	-0.10	-1.28 – 1.09	0.874
	previous year precip	0.35	-0.88 – 1.59	0.574
	restoration year precip	-0.14	-0.73 – 0.45	0.646
	next year precip	-0.02	-0.85 – 0.82	0.970
(Intercept)		0.77	0.74 – 0.80	

Zero-Inflated Model

(Intercept)		-21.64	-2914.90 – 2871.63	0.99

Random Effects

σ^2	0.59
$\tau_{00\ location}$	0.60
$\tau_{00\ site:pool\ name:zone}$	0.35
ICC	0.62
N_{site}	7

N $_{pool\_name}$	34
N $_{zone}$	3
Observations	1144
Marginal R^2 / Conditional R^2	0.457 / 0.791

Table S7. ANOVA table of exotic species richness GLMER model for 2019 chronosequence. "Zone" is zone of sampling quadrat, either central (baseline), transition, upland; "time since restoration" is years since restoration began; "pool edge ratio" is perimeter-to-area ratio of each pool, in m/m^2; "distance embedded in grassland" is distance of each pool from the edge of the restoration site, in m; "inundation period" is the number of days each pool was inundated, in cm; "elevation" is relative elevation of each quadrat above the deepest point of each pool, in cm; "historical precip" is the average annual precipitation that each pool experienced after it was restored, in cm; "previous year precip" is the total precipitation that each pool experienced the year before restoration began, in cm; "restoration year precip" is the total precipitation that each pool experienced the year that restoration began, in cm; "next year precip" is the total precipitation that each pool experienced the year after restoration began, in cm; "site" is the restoration site the pool is located in; "pool name" is the unique identifier for each pool. Bolded values have a significance of $p < 0.05$.

	Exotic Species Richness		
Predictors	*Log-Mean*	*CI*	*p*
Count Model			
(Intercept)	0.26	-0.24 – 0.75	0.305
zone [upland]	1.03	0.82 – 1.24	**<0.001**
zone [transition]	0.73	0.53 – 0.93	**<0.001**

Central Zone	time since restoration	-0.24	-1.09 – 0.62	0.587
	pool edge ratio	0.11	-0.04 – 0.26	0.164
	distance embedded in grassland	0.08	-0.33 – 0.48	0.711
	inundation period	-0.23	-0.46 – 0.01	0.057
	elevation	0.37	0.26 – 0.48	**<0.001**
	historical precip	0.16	-0.54 – 0.85	0.660
	previous year precip	-0.35	-1.10 – 0.40	0.359
	restoration year precip	-0.01	-0.48 – 0.46	0.962
	next year precip	0.07	-0.34 – 0.47	0.754
Transition Zone	time since restoration	0.19	-0.62 – 1.00	0.648
	pool edge ratio	-0.02	-0.24 – 0.19	0.821
	distance embedded in grassland	0.05	-0.36 – 0.47	0.796
	inundation period	0.29	-0.02 – 0.59	0.066
	elevation	-0.11	-0.25 – 0.04	0.147
	historical annual precip	-0.18	-0.96 – 0.60	0.660
	previous year precip	0.39	-0.40 – 1.18	0.335
	restoration year precip	-0.05	-0.46 – 0.36	0.796
	next year precip	0.05	-0.48 – 0.58	0.854
Upland Zone	time since restoration	-0.09	-0.86 – 0.69	0.823
	pool edge ratio	-0.02	-0.22 – 0.18	0.819

distance embedded in grassland	-0.05	-0.44 – 0.35	0.820
inundation period	0.27	-0.03 – 0.57	0.080
elevation	-0.30	-0.44 – -0.17	**<0.001**
historical annual precip	-0.12	-0.52 – 0.28	0.561
previous year precip	0.16	-0.59 – 0.92	0.672
restoration year precip	-0.25	-0.44 – -0.07	**0.008**
next year precip	0.12	-0.39 – 0.63	0.645

Zero-Inflated Model

(Intercept)	-21.49	-4320.06 – 4277.08	0.992

Random Effects

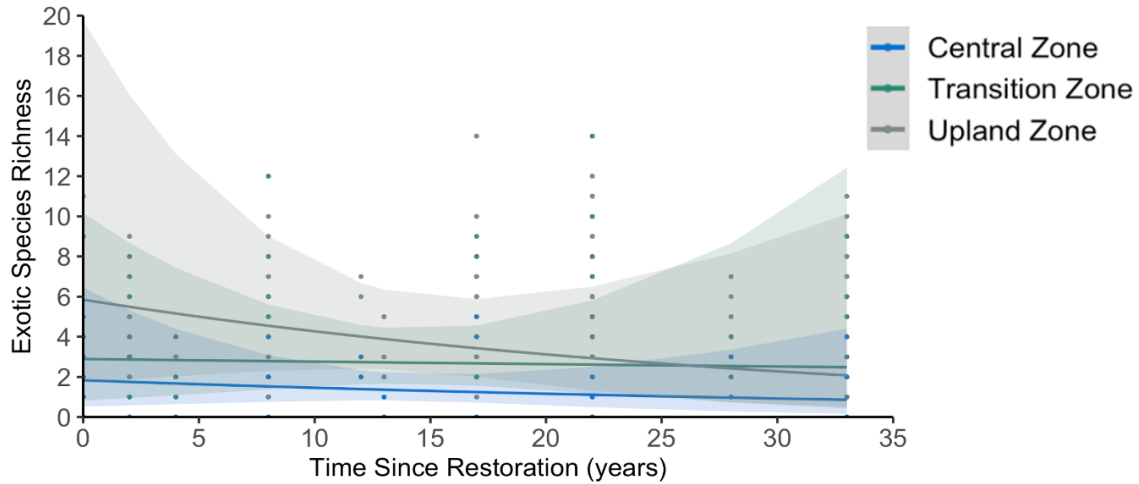|	
σ^2	0.42
$\tau_{00 \text{ location}}$	0.34
$\tau_{00 \text{ site:pool name:zone}}$	0.16
ICC	0.55
N_{site}	7
$N_{\text{pool\_name}}$	34
N_{zone}	3
Observations	1432
Marginal R^2 / Conditional R^2	0.342 / 0.701

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. Asterisks indicate significant interaction between zone and time since restoration for

exotic richness (p <0.05).

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

chronosequence. "Zone" is zone of sampling quadrat, either central (baseline), transition,

upland; "time since restoration" is years since restoration began; "pool edge ratio" is

perimeter-to-area ratio of each pool, in m/m^2; "distance embedded in grassland" is distance

of each pool from the edge of the restoration site, in m; "inundation period" is the number of

days each pool was inundated, in cm; "elevation" is relative elevation of each quadrat above

the deepest point of each pool, in cm; "historical precip" is the average annual precipitation

that each pool experienced after it was restored, in cm; "previous year precip" is the total

precipitation that each pool experienced the year before restoration began, in cm; "restoration

year precip" is the total precipitation that each pool experienced the year that restoration

began, in cm; "next year precip" is the total precipitation that each pool experienced the year after restoration began, in cm. Bolded values have a significance of $p < 0.05$.

	Predictors	Mean	CI	p
	Native Percent Cover: Binomial			
	Predictors	*Mean*	*CI*	*p*
	Count Model			
	(Intercept)	9.04223	-15.37313 – 27.54758	0.142
	zone [upland]	1.55086	-23.19663 – 31.72504	0.732
	zone [transition]	1.42748	-25.73761 – 29.07315	0.610
Central Zone	time since restoration	4.78947	1.61879 – 8.49290	**<0.001**
	pool edge ratio	1.11717	0.03759 – 2.00970	**0.012**
	distance embedded in grassland	-1.11757	-3.26250 – 1.00078	0.320
	inundation period	0.65498	-0.05415 – 1.46264	**0.074**
	elevation	1.65116	0.57705 – 2.67358	**0.018**
	historical precip	-4.26909	-7.49447 – -0.77878	**0.012**
	previous year precip	6.11911	2.76560 – 9.51989	**<0.001**
	restoration year precip	1.87811	-0.22930 – 4.16728	0.102
	next year precip	-2.95220	-4.84364 – -1.07405	**0.010**
Transition Zone	time since restoration	-5.31431	-10.45701 – 0.23571	**0.024**
	pool edge ratio	-1.23963	-3.06792 – 0.23250	0.146
	distance embedded in grassland	2.12546	-1.21948 – 5.01633	0.242
	inundation period	-0.68580	-2.69333 – 0.87768	0.520

Zone		Estimate	CI	p
	elevation	-2.60510	-4.33396 – -0.37565	**<0.001**
	historical annual precip	5.01426	-0.40212 – 9.24000	**0.076**
	previous year precip	-6.32312	-10.69518 – -0.29651	**0.026**
	restoration year precip	-2.98524	-6.10681 – -0.34058	**0.078**
	next year precip	3.84848	0.26788 – 8.12612	**0.054**
Upland Zone	time since restoration	-4.08752	-8.32025 – 0.43464	0.104
	pool edge ratio	-0.48752	-1.56560 – 0.56106	0.522
	distance embedded in grassland	1.68989	-0.87900 – 4.38219	0.306
	inundation period	-0.17828	-1.34087 – 0.80886	0.768
	elevation	-1.70174	-3.10811 – -0.49518	**0.044**
	historical annual precip	9.65058	4.16921 – 15.85588	**<0.001**
	previous year precip	-6.00498	-10.40049 – -0.77729	**0.018**
	restoration year precip	-2.14443	-5.36670 – 0.88978	0.244
	next year precip	3.54362	-0.13493 – 6.39765	**0.068**

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

chronosequence. "Zone" is zone of sampling quadrat, either central (baseline), transition,

upland; "time since restoration" is years since restoration began; "pool edge ratio" is perimeter-to-area ratio of each pool, in m/m²; "distance embedded in grassland" is distance of each pool from the edge of the restoration site, in m; "inundation period" is the number of days each pool was inundated, in cm; "elevation" is relative elevation of each quadrat above the deepest point of each pool, in cm; "historical precip" is the average annual precipitation that each pool experienced after it was restored, in cm; "previous year precip" is the total precipitation that each pool experienced the year before restoration began, in cm; "restoration year precip" is the total precipitation that each pool experienced the year that restoration began, in cm; "next year precip" is the total precipitation that each pool experienced the year after restoration began, in cm; "site" is the restoration site the pool is located in; "pool name" is the unique identifier for each pool. Bolded values have a significance of $p < 0.05$.

		Native Percent Cover: Gamma		
	Predictors	*Estimates*	*CI*	*p*
	Count Model			
	(Intercept)	3.88	3.18 – 4.58	**<0.001**
	zone [upland]	-0.81	-1.05 – -0.58	**<0.001**
	zone [transition]	-0.20	-0.41 – 0.01	0.066
Central Zone	time since restoration	-0.02	-1.09 – 1.04	0.968
	pool edge ratio	-0.81	-1.05 – -0.58	**<0.001**
	distance embedded in grassland	-0.20	-0.41 – 0.01	0.066
	inundation period	0.01	-0.15 – 0.17	0.927
	elevation	-0.30	-0.73 – 0.13	0.175
	historical precip	0.15	-0.07 – 0.38	0.183

	previous year precip	0.12	0.01 – 0.23	**0.039**
	restoration year precip	-0.31	-1.14 – 0.52	0.465
	next year precip	0.34	-0.53 – 1.21	0.438
Transition Zone	time since restoration	-0.66	-1.56 – 0.24	0.149
	pool edge ratio	-0.10	-0.34 – 0.13	0.386
	distance embedded in grassland	0.07	-0.37 – 0.51	0.745
	inundation period	-0.05	-0.37 – 0.26	0.742
	elevation	-0.23	-0.39 – -0.07	**0.005**
	historical precip	0.49	-0.37 – 1.35	0.267
	previous year precip	-0.19	-0.62 – 0.25	0.406
	restoration year precip	-0.16	-0.39 – 0.07	0.184
	next year precip	0.15	-0.44 – 0.74	0.613
Upland Zone	time since restoration	-2.20	-3.19 – -1.22	**<0.001**
	pool edge ratio	-0.27	-0.50 – -0.04	**0.019**
	distance embedded in grassland	-0.49	-0.95 – -0.03	**0.035**
	inundation period	-0.22	-0.54 – 0.10	0.171
	elevation	-0.33	-0.47 – -0.19	**<0.001**
	historical precip	1.40	0.45 – 2.36	**0.004**
	previous year precip	-1.74	-2.69 – -0.78	**<0.001**
	restoration year precip	0.19	-0.30 – 0.67	0.450

next year precip	0.56	-0.09 – 1.22	0.092
(Intercept)	0.67	0.65 – 0.70	
Zero-Inflated Model			
(Intercept)	-22.01	-3224.01 – 3179.99	0.989
Random Effects			
σ^2	0.45		
$\tau_{00 \ location}$	0.73		
$\tau_{00 \ site:pool \ name:zone}$	0.19		
ICC	0.67		
N_{site}	7		
N_{pool_name}	34		
N_{zone}	3		
Observations	1357		
Marginal R^2 / Conditional R^2	0.258 / 0.756		

Table S10. ANOVA table of native species richness GLMER for 2019 chronosequence. "Zone" is zone of sampling quadrat, either central (baseline), transition, upland; "time since restoration" is years since restoration began; "pool edge ratio" is perimeter-to-area ratio of each pool, in m/m^2; "distance embedded in grassland" is distance of each pool from the edge of the restoration site, in m; "inundation period" is the number of days each pool was inundated, in cm; "elevation" is relative elevation of each quadrat above the deepest point of each pool, in cm; "historical precip" is the average annual precipitation that each pool experienced after it was restored, in cm; "previous year precip" is the total precipitation that each pool experienced the year before restoration began, in cm; "restoration year precip" is the total precipitation that each pool experienced the year that restoration began, in cm; "next year precip" is the total precipitation that each pool experienced the year after restoration

began, in cm; "site" is the restoration site the pool is located in; "pool name" is the unique identifier for each pool. Bolded values have a significance of $p < 0.05$.

	Predictors	Log-Mean	CI	p
		Native Species Richness		
	Count Model			
	(Intercept)	1.31	1.10 – 1.53	**<0.001**
	zone [upland]	-0.45	-0.63 – -0.28	**<0.001**
	zone [transition]	0.02	-0.13 – 0.16	0.833
Central Zone	time since restoration	0.12	-0.38 – 0.63	0.637
	pool edge ratio	0.07	-0.04 – 0.18	0.204
	distance embedded in grassland	-0.05	-0.29 – 0.18	0.664
	inundation period	0.07	-0.09 – 0.23	0.364
	elevation	0.19	0.11 – 0.27	**<0.001**
	historical precip	-0.11	-0.55 – 0.33	0.631
	previous year precip	0.29	-0.15 – 0.74	0.196
	restoration year precip	-0.14	-0.41 – 0.13	0.301
	next year precip	-0.14	-0.41 – 0.14	0.325
Transition Zone	time since restoration	-0.45	-1.07 – 0.17	0.154
	pool edge ratio	-0.02	-0.18 – 0.15	0.851
	distance embedded in grassland	-0.09	-0.40 – 0.21	0.550
	inundation period	-0.05	-0.27 – 0.18	0.679
	elevation	-0.20	-0.31 – -0.08	**0.001**

	historical precip	0.13	-0.45 – 0.72	0.652
	previous year precip	-0.19	-0.78 – 0.40	0.531
	restoration year precip	0.09	-0.22 – 0.39	0.573
	next year precip	-0.01	-0.40 – 0.39	0.969
Upland Zone	time since restoration	-0.70	-1.36 – -0.04	**0.037**
	pool edge ratio	-0.11	-0.28 – 0.06	0.220
	distance embedded in grassland	-0.08	-0.40 – 0.25	0.649
	inundation period	-0.06	-0.29 – 0.17	0.610
	elevation	-0.25	-0.36 – -0.13	**<0.001**
	historical precip	0.06	-0.56 – 0.68	0.849
	previous year precip	-0.29	-0.91 – 0.34	0.365
	restoration year precip	0.25	-0.09 – 0.58	0.147
	next year precip	-0.11	-0.53 – 0.32	0.623

Zero-Inflated Model

(Intercept)	-22.10	-3829.45 – 3785.24	0.991

Random Effects

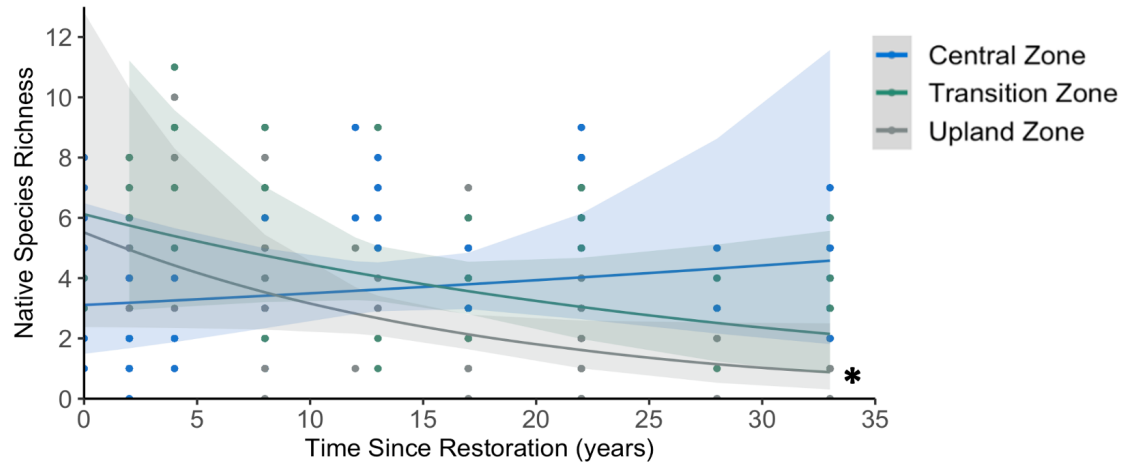|	
σ^2	0.27
$\tau_{00 \ location}$	0.04
$\tau_{00 \ site:pool \ name:zone}$	0.09
ICC	0.33
N_{site}	7
N_{pool_name}	34
N_{zone}	3
Observations	1432
Marginal R^2 / Conditional R^2	0.270 / 0.509

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. Asterisks indicate significant interaction between zone and time since restoration for

native richness (p <0.05).

II. Restoring then and now: Long-term management to address reinvasion of restored grassland vernal wetlands

A. Abstract

Invasive plant species are a widespread and persistent threat to many native plant assemblages. Exotic annual grasses can dominate ecosystems by producing a thick layer of dead plant litter, hereafter "thatch", that promotes the regeneration of exotic grasses and inhibits native species. These processes have resulted in the degradation of most of California's grasslands, including those that were restored in the past. In particular, restored vernal pool wetlands that are surrounded by exotic grasses are susceptible to the encroachment of exotic grasses into the edges of the pools during dry years. We investigated whether this invasion can be reversed by reducing the accumulation of invasive thatch around the edges of the pools. Summer thatch removal successfully reduced thatch accumulation and increased bare ground, but it did not result in a consistent increase in native plant species abundance or richness. Instead, the effects of thatch manipulation on plant composition were modulated by annual precipitation, with exotic species increasing during dry years and native species increasing during wet years. Yet, when thatch removal was coupled with the addition of native plant seed in a factorial design, native plant species richness increased, but only after three years of annual thatch removal and native seed addition. These results indicate that the restoration of native vernal pool plants can be limited by invasive species, native seed availability, and annual precipitation. Our findings also highlight the importance of long-term management and monitoring. By engaging the

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local community in our experimental restoration, we were able see how repeated annual restoration treatments built up capacity for native plant populations to increase over time.

B. Introduction

The proliferation of invasive species that have the capacity to quickly disperse and dominate landscapes is a major reason why restoration projects are both initiated and stymied (Funk et al. 2008). In particular, exotic annual grasses have the capacity to dominate and transform many vegetation formations around the world, including grasslands, shrublands, deserts, forests, and wetlands (Brooks et al. 2016; D'Antonio & Vitousek 1992). Much of that transformation can be ascribed to the accumulation of dead annual grass material, hereafter "thatch", that can promote fire and create a positive feedback that favors exotic plant species and reduces native plant species (Bradley et al. 2019; Faist & Beals 2018; D'Antonio & Vitousek 1992). Exotic annual grasses exhibit fast initial growth when seasonal rains begin and are capable of annually producing large amounts of biomass and seeds prior to death. The slow decomposition of this typically high-C:N thatch results in its accumulation over time, which can suppress the germination and growth of native species while enhancing the performance of the next cohort of exotic grasses (Molinari & D'Antonio 2020).

Because this invasive thatch layer can hinder or even reverse efforts to restore native species, several studies have explored methods for reducing thatch (e.g., Marty 2015*a*; Marty 2015*b*). Grazing by sheep and cattle has been shown to decrease invasive thatch cover and depth and decrease exotic seed production, seed rain, and seedling recruitment, resulting in lower abundance of exotic annual grasses (e.g., Evans et al. 2023; Skaer et al. 2013;

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DiTomaso et al. 2008; Jackson & Bartolome 2002). Prescribed burns also can reduce the amount of thatch (Pollak & Kan 1998). Similar to grazing, fire reduces thatch, but it also can kill exotic seeds, resulting in lower overall exotic annual grass cover and lower cover and germination of specific invasive grasses such as *Aegilops triuncialis* (barbed goatgrass; Keeley et al. 2023; Marty et al. 2015). Additionally, prescribed burns can stimulate the germination of some native plant species, resulting in higher overall native plant cover and the recovery of target native species (Young et al. 2015; Pollak & Kan 1998). Although fire and grazing can pose logistical challenges (e.g., in small, urban restoration sites) or cause unwanted changes in nutrient cycling and plant communities, mechanical mowing also can be used to remove or fragment thatch (Croel & Kneitel 2011; D'Antonio et al. 2002; Davison & Kindscher 1999). However, vegetation responses to different disturbances can be variable, with some native assemblages responding more favorably to mowing than to grazing, some sites showing equally favorable outcomes of burning and mowing, and some sites showing minimal to no effect of burning and mowing on native or exotic plant assemblages (Stahlheber & D'Antonio 2013; MacDougall & Turkington 2007; Meyer & Schiffman 1999; Collins et al. 1998). This variation in plant responses to thatch disturbance is likely due to interactions of seasonality, interannual variation in precipitation, species, specific site conditions, and the abundance of native species in the seed bank that can respond to disturbance.

Vernal pool wetlands have unique site conditions that can moderate the effect of invasive thatch on native plant assemblages. Vernal pools are temporary wetlands that form in depressions in grassland landscapes where there is a subsurface impermeable soil layer (Keeley & Zedler 1998). Rainwater accumulates and then persists in these depressions for

months before evaporating or being transpired, leaving a completely dry landscape for the remainder of the year. Only a few species with special adaptations can grow in the deeper parts of vernal pools, leading to high rates of endemism especially in the deeper parts of vernal pools (Stone 1990). In California, USA, most grassland vernal pools are surrounded by exotic annual grasses that were historically excluded from vernal pools because they could not tolerate inundation (Gerhardt & Collinge 2007). However, drought and land use change can shorten the inundation period of vernal pools, resulting in an environment drier than historical pool conditions and thus amenable to the invasion of exotic annual grasses (Gosejohan et al. 2017; Marty 2015*b*). This drier environment initiates a feedback whereby the growth and accumulation of exotic annual grasses and their thatch engender even drier conditions (Marty 2015*b*). Faist (2015) found that the decomposition rates of invasive thatch were slower than those for native grass thatch, resulting in the accumulation of a dense invasive thatch layer that suppressed native species. Several studies have shown that grazing and fire can decrease thatch and increase native species in vernal pools (e.g., Michaels et al. 2022; Merriam et al. 2016; Marty 2015*a*; Marty 2005). However, Marty et al. (2007) stressed that repeated reduction of the thatch (via annual grazing at their study sites) was necessary to ensure long-term restoration success. In addition, previous studies assume that native species are able to regenerate from the seed bank because vernal pools are known to have long-lived native seed banks, with native species germinating primarily during years of sufficient precipitation that can occur decades apart (Faist & Collinge 2015).

Because the regeneration of native species is dictated by the availability of suitable microsites, precipitation conditions, the seed bank of target species, and the reduction of invasive plants and thatch, restoration efforts will only be successful if native propagules are

also present (Piessens et al. 2004; Eriksson & Ehrlen 1992). Disturbed exotic grasslands, which comprise the surrounding landscape matrix for many vernal pools in California, often suffer from a depleted native seed bank (Seabloom et al. 2003; Hutchings & Booth 1996). Seed bank depletion can be particularly important in abandoned agricultural land or in grasslands that experienced fragmentation decades in the past (Pywell et al. 2002). Plue & Cousins (2013) showed that, even though seed banks can postpone the local extirpation of a species, seed banks eventually become depleted over time if not replenished by local production or dispersal. If the native species seed bank is depleted, then any open microsites created by thatch removal may be colonized by undesirable dispersive species (e.g., invasive annual grasses dispersing from nearby fields; Vandvik et al. 2006).

This study investigates the effectiveness of invasive thatch removal and native seed addition in restoring degraded grassland vernal pool plant assemblages in California, USA. The study sites are small remnant grasslands along the south coast of California that were cultivated by farmers or ranchers in the 1940s and subsequently restored in the 1980s, which included the re-excavation and creation of vernal pools. However, the lack of long-term management (e.g., annual weeding) of both the pools and the surrounding grassland matrix has resulted in the dominance of grasslands by invasive annual grasses such as *Festuca perennis* (Italian ryegrass), *Bromus diandrus* (ripgut brome), and *Avena fatua* (wild oat). These annual grasses can invade the drier edges of pools, especially during successive years of low precipitation. This invasion can initiate a positive feedback: Marty (2015*b*) reported that higher abundance of exotic species was correlated with pools being inundated for a shorter amount of time, and we might expect these drier conditions to allow for the encroachment of annual grasses deeper into the pool and subsequent declines in native species. To investigate

whether appropriate vegetation management can mitigate such invasions, we asked: 1) How does annual thatch manipulation influence exotic plant cover? 2) Can native plants regenerate from the seed bank after the reduction of thatch, or does seed limitation inhibit the recovery of native assemblages?

To explore these questions, we evaluated the outcome of two different methods for manipulating thatch: directly removing thatch from experimental plots using rakes and indirectly reducing thatch by disturbing the thatch (to break it up and potentially expose it to enhanced photodegradation and increased soil microbial activity) to promote faster decomposition. If the accumulation of thatch promotes the regeneration of exotic species, we predicted that removing the thatch would result in lower exotic plant cover. We also hypothesized that thatch removal would open suitable microsites and allow for greater germination of dormant native seeds and native plant establishment and growth. However, because the study sites have been extensively altered and experienced several disturbances to topsoil, they may not have retained a robust native seed bank. In this case, thatch manipulations may reduce thatch without enhancing native diversity or abundance. To test this hypothesis, we also added native seed to half of the experimental plots to create a factorial thatch manipulation-by-seeding design. If there is no remnant native seed bank, we would only expect native cover and richness to increase in the seeded plots (assuming we are adding enough seed to overcome loss to seed predators and other factors).   Identifying whether there are multiple factors limiting the re-establishment of native plant assemblages can help managers develop comprehensive long-term plans to restore native habitat threatened by invasive species.

C. Methods

Study Sites

We performed annual of thatch manipulation and seed addition in created vernal pools at Del Sol Vernal Pool Preserve and Camino Corto Open Space in the unincorporated community of Isla Vista, Santa Barbara County, California, USA, from 2019 to 2022. These sites are located on the ancestral unceded territory of the kaswa'a coastal band of the Chumash tribe, who have historically used fire in managing their land (Timbrook et al. 1982). These lands are currently managed by the Isla Vista Recreation and Parks District, but were originally restored in the 1980s under the supervision of personnel from the University of California, Santa Barbara (UCSB). In 1986, six pools were created and three pools were restored at Del Sol (Figure 1). In 1997, five existing pools at Camino Corto and one existing pool at Del Sol were restored (Figure 1). During restoration efforts, pools received topsoil grading, basin excavation, and enhancement of berms around the basins by tractors to enhance vernal pool topography, as well as native seed addition (Ferren & Pritchett 1988). After the completion of the pools' creation or restoration, there has been no sustained invasive or native species management. As a consequence, invasive annual grasses are prevalent around and in the pools, thus providing appropriate systems for testing the effects of thatch removal on ecosystem recovery.

All the pools are located within 1 km of the Pacific Ocean and are subject to a Mediterranean climate characterized by a cool, wet season from November to April and warm, dry conditions the remainder of the year, moderated by sporadic summertime fog. The area receives an average of 43.2 cm of rainfall each year, but interannual variability is very high

(PRISM 2014). Annual precipitation data were taken from the California Nevada River

Forecast Center, which records total annual precipitation per water year from the previous

year's October through the recorded year's September (California Nevada River Forecast

Center 2023). In this mild maritime climate, frost is rare, and summer fog can reduce

temperatures in the summer. "Sundowner" winds can bring extreme heat and dry conditions

during the late summer and fall. Soil formation is governed by the weathering of uplifted

marine shale and mountain sandstone formations that results in a prevalence of Mollisol soils

with a high clay content. Dominant soil series are Concepción fine sandy loam and Diablo

clay (Soil Survey Staff 2019).

Thatch Manipulation Treatments

To test our hypothesis that thatch removal will decrease exotic plant species cover and

richness and allow for the regeneration of native plant species, we performed three thatch

manipulation treatments on 15 restored vernal pools (5 pools per treatment). The three

raking treatments were: 1) raking and removal of thatch from the pool, 2) disturbance of

thatch by raking without direct removal, 3) no raking or removal. The raking and removal of

thatch treatment can precipitate similar effects of grazing or prescribed fire, which have been

shown to decrease exotic species cover and increase native species cover in Central Valley

vernal pools (Marty 2005; Cox & Austin 1990). The raking treatment was performed using

hard rakes, with the vegetation being scraped down to < 1 cm-tall standing vegetation and

thatch. This raking treatment is based on Faist & Beals (2018), who found that removing all

thatch down to 1 cm after summer senescence significantly reduced exotic grass abundance

over their two-year study. The thatch disturbance by raking (no direct removal) treatment

assesses the feasibility of thatch reduction without direct removal, thus testing the impact of

disturbance on thatch decomposition rate (i.e., by exposing more thatch to photodegradation or soil microbes). The disturbance treatment also physically breaks up the thatch to some extent, potentially allowing light to pass through, which may stimulate germination and seedling emergence (Romich 2020).

The thatch manipulation treatments were applied to the edges of each pool. All of the pool centers support dominant *Eleocharis palustris* populations that create visually distinct vegetation boundaries on the pool bottoms. These central bottom areas contain almost no exotic grasses (Tang et al. 2023). Upland of the *E. palustris* zone, native species become intermixed with exotic species, with exotic species increasing to 100% cover toward the pool edges. The treatment zone consisted of the transition zone, a 3 m-wide band extending upward from the upper elevational boundary of *E. palustris*. Thatch manipulation treatments were performed during the summer (July-August), after all seed had dropped, for four years (2019-2022). We performed thatch manipulations in the summer season, after species had senesced, to both minimize collateral damage to native plants and to test the efficacy of targeting thatch management at a time more convenient for land managers (i.e., after the busy spring field season).

Seed Addition Treatments

Because the study sites were extensively degraded between the 1940s and late 1980s, we hypothesized that seed bank depletion might limit the regeneration of native plant assemblages even where invasive thatch was removed. Thus, we crossed our thatch manipulation treatments with native seed additions in a fully factorial design. Each of the 15 selected pools were divided in half along their longest axis, with one half receiving one of the

three thatch manipulation treatments, and the other half receiving the same treatment plus native seed addition to permanent quadrats. Native seeds of *Juncus bufonius*, *Juncus occidentalis*, *Stipa pulchra*, *Grindelia camporum*, *Phalaris lemmonii*, and *Hordeum brachyantherum* (all species that historically inhabit the edges of local vernal pools) was collected from local vernal pools (< 3 km from experimental sites) during the spring of each year. Seeds were stored at room temperature until the first winter rains of each year. Consistent amounts of seed of each species were sown into six randomly-placed 1 m^2 quadrats in each pool half (Table S1). These permanent quadrats were marked and seeded every year. The amount of seed varied from year to year based on seed availability, but each quadrat received the same amount of seed within each year (see Table S1 for annual seeding rates of each species). Seed was sown into the quadrats using hand rakes during the autumn seasons of 2019 through 2022, before the first winter rains.

Species Composition Surveys

Plant species cover and richness were monitored annually between June and August. Before the first treatment year, species percent cover and richness were measured in August 2019 to determine baseline vegetation composition (all species were distinct so they were identifiable even after senescence). Percent cover of each native and exotic species was measured in 12 permanent 1 m^2 quadrats in each pool, including the six quadrats that were seeded. In the spring seasons from 2020 to 2023, we monitored the cover and richness of native and exotic species in all quadrats.

Additionally, we measured the richness of native and exotic plant species in the seed bank prior to experimental manipulations. We collected and mixed three 8 cm-deep soil cores

from each of the quadrats using a 4 cm-diameter auger in July 2019. We spread 50g of each

homogenized sample over PRO-MIX© BX Biofungicide^{TM} potting soil in germination

trays. Trays were set up outside in November 2019 and hand-watered weekly. Mauchamp et

al. (2002) concluded that only identifying species that germinated from field soil cores in a

controlled environment were inadequate in capturing the total seed bank diversity in

wetlands; therefore, we assessed seed bank diversity via soil DNA sequencing according to

protocols developed by Stephanie Ma Lucero and colleagues (pers. comm.). We sieved each

homogenized soil sample through a 4 mm sieve, then mixed 5 g of the homogenized soil

with liquid nitrogen and extracted DNA using the Qiagen DNeasy® PowerSoil® Pro

Kit. Extracted DNA was amplified using standard polymerase chain reaction (PCR)

protocols, using the rbcL forward and reverse primers. Samples underwent two PCR

amplification cycles to attain sufficient DNA for analysis, and amplicons were then cleaned

using AMPure beads. Amplicons were sequenced using Illumina's 600-cycle MiSeq

Reagent Kit V3. Sequences were cleaned using the "dada2" coding package and then

matched with family, genus, and species using the National Center for Biotechnology

Information's Basic Local Alignment Search Tool (BLAST), BLAST+, and the "annotate"

coding package (Gentry 2024; Callahan et al. 2016). Sequences were matched to taxa based

on the BLAST Maximum Score metric.

Data Analysis

All analyses and visualization were performed in RStudio version 1.4.1106 (R Core Team

2023). The **aov** and **anova** functions from the "stats" package were used to perform analyses

of variance. Generalized linear mixed effects models were generated using the "glmmTMB"

and "lme4" packages (Brooks et al. 2017; Bates et al. 2014). The **emmeans** function from

the "emmeans" package was used to perform post-hoc Tukey's least-squares mean tests to examine the effects of treatments on plant response variables (Lenth 2023). All graphs were generated using the functions in the package "ggplot2".

We compared the cumulative effects of treatments on diversity metrics using an analysis of variance. We summed the percent cover of every exotic or native species to obtain the total exotic or native cover for each quadrat at each sampling time. We calculated native richness by counting all the unique native species found in each quadrat at each time. We also used the "vegan" package to calculate the Simpson's Index for each quadrat at each time to assess how treatments affected species evenness in addition to richness.

Most of the datasets were not normally distributed based on diagnostic residual tests, which thus required the use of models that accounted for the particular distributions that best fit the datasets. We constructed repeated measures generalized linear mixed-effects models (GLMM) with sampling year, thatch manipulation treatment, and seeding treatment, and their interaction effects, included as fixed effects, and quadrat included as a random effect to account for repeated measures. The thatch percent cover dataset followed a beta distribution based on diagnostic residual tests. The bare ground percent cover and total native plant percent cover datasets were zero-inflated, so we constructed hurdle models with gamma distributions. In addition, the percent bare ground dataset exhibited unequal variances, so percent bare ground was log-transformed using Box-Cox transformations (Osborne 2019). Total exotic plant percent cover among quadrats also followed a gamma distribution and exhibited unequal variances, so total exotic plant percent cover was square-root-transformed using appropriate Box-Cox transformations. Native and exotic plant species

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richness datasets followed a Poisson distribution. Post-hoc Tukey's Honestly Significant Difference tests were performed on GLMM outputs to delineate significant interactions among year, thatch treatment, and seeding addition on dependent variables.

We also used species community matrices of percent cover to conduct non-metric multidimensional scaling using the "vegan" package (Oksanen et al. 2022). Differences in community composition among thatch and seeding treatments were determined using a permutational multivariate analysis of variance (PERMANOVA), and post-hoc pairwise comparisons between two-way factorial thatch manipulation and seeding treatments were evaluated using the **pairwise.adonis** function of the "pairwiseAdonis" package (Martinez Arbizu 2017).

D. Results

Influence of thatch manipulations on exotic plant species cover

There were no consistent effects of either Thatch Disturbance or Thatch Removal on the total cover of exotic plant species (excluding thatch) throughout the four years of the experiment (Figure 2(a)). In 2021 (which was a dry year, with total rainfall of 18.6 cm), Thatch Removal quadrats had significantly higher exotic cover than Control quadrats ($p = 0.005$; Table S2), but that difference did not persist through subsequent years. In 2023 (which was a wet year, with total rainfall of 73.5 cm), Thatch Disturbance quadrats had higher exotic cover than both Control quadrats ($p = 0.019$) and Thatch Removal quadrats ($p < 0.001$; Table S2). In 2023, Thatch Disturbance quadrats also had lower Simpson's Index values than those for Control quadrats ($p = 0.02$; Table S3), indicating that exotic species were dominating

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Thatch Disturbance quadrats. PERMANOVA analysis on non-metric multidimensional scaling (NMDS) of plant species percent cover did not reveal any differences between two-way factorial thatch manipulation and seeding treatments in any given year, indicating that all quadrats had similar species composition (Figure S1). This suggests that higher total exotic cover was a result of the increasing abundance of all exotic species that were present in all the pools. The most abundant exotic species in all pools included *Festuca perennis*, *Erodium botrys*, *Bromus hordeaceus*, *Festuca bromoides*, *Vicia villosa*, *Bromus diandrus*, *Plantago lanceolata*, *Spergularia* spp., *Lythrum hyssopifolia*, and *Festuca myuros*. Total exotic species richness from all aboveground surveys was 34 (see Table S10 for full species list).

Although thatch manipulation treatments did not decrease total exotic plant cover, Thatch Removal was successful in reducing thatch and increasing bare ground (Figure 2). However, Thatch Disturbance did not decrease thatch cover. In the 2019 pre-treatment survey, percent thatch cover was lower in quadrats randomly assigned to the Control treatment than in quadrats randomly assigned to the Thatch Removal treatment ($p = 0.007$; Table S4). Despite this initial disparity, in 2020 after the first year of treatments, Thatch Removal quadrats had lower percent thatch cover than Control quadrats, regardless of native seed addition ($p < 0.0001$; Table S4). Thatch Removal quadrats also had lower percent thatch cover than Thatch Disturbance quadrats, regardless of whether or not they received native seed addition ($p < 0.0001$; Table S4). Percent thatch cover in Thatch Removal quadrats remained lower than both Control and Thatch Disturbance quadrats during all post-treatment years ($p < 0.0001$; Table S4).

As a result of thatch reduction, microsite availability increased. Thatch Removal quadrats had higher bare ground cover than Thatch Disturbance and Control quadrats during all post-treatment years ($p < 0.003$; Tables S5-S6; Figure 2(c)).

Native plant regeneration

Although Thatch Removal reduced thatch cover and increased bare ground throughout the four years of the experiment, native plants did not consistently take advantage of the bare ground. There was no impact of thatch manipulation treatments on total native plant species cover during the first three years of the experiment (Figure 3). Native seed addition resulted in higher native cover in Thatch Disturbance quadrats compared to Control quadrats in 2021 ($p = 0.018$; Table S8). However, after the fourth year of treatments (2023, which was a wet year with total annual rainfall of 73.5 cm), Thatch Removal quadrats had significantly higher native cover than Thatch Disturbance quadrats ($p = 0.0003$) and Control quadrats ($p = 0.026$; Table S8).

Native plant species richness also only increased after multiple years of native seeding treatments. Native species richness was higher in quadrats that received native seed addition than quadrats that did not receive native seed addition in 2022 ($p = 0.003$) and in 2023 ($p = 0.0001$), regardless of thatch manipulation treatment (Table S9; Figure 4).

Total native species richness from all aboveground surveys was 29 (see Table S10 for full species list). PERMANOVA analyses on NMDS of plant species percent cover did not reveal any differences among treatments in any given year, indicating that all quadrats had similar covers by component species (Figure S1). The most abundant native species in all pools included *Grindelia camporum*, *Distichlis spicata*, *Eleocharis acicularis*, *Eleocharis*

palustris, *Juncus bufonius*, *Eryngium vaseyi*, *Hordeum brachyantherum*, *Ambrosia psilystachya* and *Stipa pulchra*. Out of the seven native species added in the seeding treatment, only *Grindelia camporum* seedlings were found in seeded quadrats in all four years, and *Phalaris lemmonii* seedlings were only found in seeded quadrats in 2023 (which was a wet year).

Seed bank composition

To further investigate whether seed bank depletion was limiting the restoration of native species, we assessed seed bank diversity by germinating seed from soil samples and by performing eDNA analysis on soil samples. In the germination grow-out experiment, we found a native species richness of 8 and an exotic species richness of 17. All of the species that germinated from soil samples were also found in the above-ground surveys. In contrast, we found a native species richness of 33 and an exotic species richness of 88 from the eDNA analysis of soil samples (see Table S10 for full species list). All the species found in above-ground surveys were found in the seed bank. Most of the additional exotic species in the seed bank that were not seen in surveys were ornamental species. Of the additional native species found in the seed bank, two were endemic vernal pool species that were assumed to have been locally extirpated due to their absence in surveys, suggesting that the ideal environmental conditions for their germination did not occur during this study.

E. Discussion

We found that thatch reduction could only be achieved by directly mechanically removing thatch rather than by just disturbing thatch. Our results do not support our hypothesis that

thatch disturbance can promote increased decomposition (indirect thatch removal) because our thatch disturbance treatments did not affect thatch cover. Our results showed that only direct thatch removal altered the landscape by increasing the amount of bare ground, providing potential microsites for species to colonize. Whether or not this bare ground was colonized by native or exotic plant species depended upon other factors besides thatch manipulations, such as seeding and annual precipitation.

This study spanned five years that encompassed large interannual climatic variation. Three of the years were historic drought years, whereas intense El Niño storms occurred during the other two years. Annual precipitation directly affects the hydrology and inundation period of vernal pools, which, in turn, influences the vegetation community. Different native vernal pool species and exotic grassland species are adapted to withstand different inundation periods, such that dry years can result in low germination of native species and a subsequent shift in community composition from native wetland species to exotic grassland species (Gosejohan et al. 2017). Drought years can even cause a reduction in both native and exotic species cover, as we saw in our 2021 survey when pools only remained inundated for about one month. In contrast, after the El Niño storms during the last year of the experiment in 2023, pools were inundated for over four months, and native plant cover was highest in Thatch Removal quadrats in that year. Because of interannual climatic variability, we cannot determine whether the increased native plant cover in the Thatch Removal quadrats was due to the cumulative effects of four years of thatch removal or to the effects of thatch removal during a wet year. Notwithstanding, in either case, this increase in native plant cover shows the importance of repeated thatch removal over multiple years to allow for native species to respond after either repeated removal or during favorable climatic conditions. If thatch

removal had only occurred during one or two dry years, we would not have been able to detect any effect of thatch removal on native plants, but continued management and monitoring allowed us to detect treatment impacts.

Our study also found that consistent annual addition of native seed increased native species richness. This supports our hypothesis that the establishment of native plant populations is limited by a depleted seed bank and corroborates the findings of other studies that stress the importance of both opening colonization microsites (e.g., by removing thatch) and bolstering the native seed bank (Valliere et al. 2018; Seabloom et al. 2003). However, of the seven species that were added, only *Grindelia camporum* consistently germinated in significant numbers every year. Yet, another added species, *Phalaris lemmonii*, also germinated in 2023, after four years of seeding treatments. We do not know if its presence in 2023 is due to the accumulation of seeds to detectable germination levels or due to above-average rainfall in 2023; however, these results suggest that investing in repeated annual seeding treatments builds capacity for the ecosystem to respond to favorable conditions when they arise.

Native species can only take advantage of favorable conditions if they have a robust seed bank, and our eDNA analysis of the seed bank showed that vernal pools in coastal Santa Barbara County harbor relatively few native plant species but many exotic plant species. However, there were several native and exotic species found in the eDNA analysis of soil samples that were not observed in quadrat surveys. For example, a few native species found in the eDNA analysis were only observed during additional surveys in deeper parts of the pool or in the upland grassland matrix, indicating that inundation is a primary abiotic filter determining which native species are found in vernal pools. This corroborates other

studies that have shown that inundation period affects which species are found in different portions of pools or during different climatic conditions (Tang et al. 2023; Torres-Martínez et al. 2019). However, the majority of exotic species in the seed bank that were not observed in vernal pool surveys were cultivated or horticultural species, likely unintentionally dispersed by humans from the surrounding residential area. This shows that exotic species introduction is a constant threat to our study system and, although only a few introduced species become invasive, interannual precipitation variability and climate change may provide conditions favorable for the proliferation of some introduced exotic species (Richardson & Pyšek 2006).

The prevalent anthropogenic influences on our study system, including the abundance of introduced species, climate change-induced droughts, the history of human disturbances, and the surrounding urban landscape, provide an interesting context for studying the effects of exotic grass thatch removal and native seed addition on native plant restoration. In this context, mechanical thatch removal did not confer the same ecosystem benefits as other thatch reduction methods in other contexts. For example, fire and grazing have been used to reduce thatch in remnant pools in northern California, enhancing native species abundance and richness without native seed addition (Marty et al. 2007). These pools likely had a history of less severe soil disruption and a larger native seed bank, and both the pool basins and surrounding protected land were magnitudes larger than our urban study sites (Keeler-Wolf et al. 1998). Pools in Santa Barbara County are known to have a relatively depauperate species pool, which, combined with a history of soil disruption, likely explains the lack of an abundant native seed bank. Because remnant pools and restoration land parcels in coastal Santa Barbara County are relatively small, they also have lost the capacity to achieve the beta

and landscape-scale native diversity found in northern California pools (Michaels et al. 2021).

The mere presence of native seed, however, may not necessarily increase native species cover even if exotic species thatch is reduced (Henning et al. 2017). Plant community composition and abundance are strongly influenced by interannual variability in precipitation. Seabloom et al. (2003) found that mowing and native seeding had the strongest positive effects on native species abundance during a wet year and strongest negative effects on exotic species cover during a dry year. Our study, which was conducted across dry and wet years, suggests that ecosystems can exhibit stronger increases in native species cover and richness in wet years. In addition, other methods of thatch manipulation may influence other abiotic conditions that may favor native species. For example, ungulate grazing can create microtopographic variation and highly localized disturbances that can favor native plant germination, particularly when soils are moist (Michaels et al. 2022). Burning of thatch can cause temporary increases in mineral nitrogen that may promote native species (D'Antonio et al. 2002). Although our current experiment isolated the effects of physical thatch removal on plant assemblages, we suggest that further research should be conducted to examine how other methods of thatch removal alter biogeochemical conditions affecting plant diversity. For example, indigenous stewardship of grassland vernal pools involved regular cultural burns to consume unwanted plant material and promote culturally valuable plant species (Timbrook et al. 1982). Indeed, because of this present study, experiments investigating the effects of cultural burns on native plant regeneration have been proposed with the goals of simultaneously restoring indigenous practices and native species. Such

restoration can be viewed as restoring the relationship between people and nature in order to safeguard native ecosystems.

Traditional indigenous land stewardship practices centered around humans having a longstanding, continual relationship with their surrounding ecosystems (Anderson 2005). Although the close proximity of our study site to residential areas created unique challenges for native species restoration (e.g., littering, sources of exotic species), it also allowed for the involvement of myriad people who are now invested in vernal pool restoration. This small and accessible restoration site benefited from over 40 undergraduate students who participated in restoration activities, which also garnered the support of local funding agencies and community members. This type of community engagement has allowed us to invest in this restoration site for such a prolonged period of time, which in turn has allowed us to detect the benefits of long-term management.

F. Conclusions

Our results indicate that mechanical thatch removal can be a useful tool for reducing accumulated thatch produced by invasive annual grasses, but that the restoration of native vernal pool plants can be limited by invasive species, native seed availability, and annual precipitation. Although reintroducing historical disturbance regimes to reduce thatch may promote the regeneration of native species, native species may not be able to take advantage of suitable microsites due to unfavorable changing climate conditions (Svenning et al. 2013). A suite of restorative actions is needed in settings where native seed banks are depleted and exotic species are abundant, and desired responses may not occur every year

due to climatic variation. Our study shows the importance of ongoing, long-term monitoring and management in restoration projects. The pools in our study area had been restored in the 1980s but had already suffered reinvasion and domination by exotic species by 2019, when we began this study. Continual monitoring after the restoration of vernal pool vegetation could have triggered adaptive management that may have prevented domination by exotic species. Early detection and rapid response (EDRR) to invasion is the most effective method of managing invasion, whereas attempting to reverse widespread invasion is difficult and costly (Reaser et al. 2020). The complex results of our study highlight the cost of foregoing long-term monitoring and adaptive management. Four years of thatch manipulation and seeding did not result in consistent trends; however, sustained management techniques can moderate the effects of invasion over time. Although no effects of thatch manipulation or seeding treatments on native plant assemblages were seen after the first two years, continued investment in management practices and monitoring did increase native cover and richness after three years, particularly during a wet year. Annual investment in management can add up over time, allowing ecosystems to become more resilient and building up the capacity for ecosystems to respond to favorable conditions, such as high-precipitation years, when they occur. Our study shows that the restoration of the relationship between people and nature, involving continual annual monitoring and management, can confer long-term benefits to native plant assemblages.

Acknowledgements

Figures

1986: H, I, J, K, L, M created
1986: E, G, W restored
1997: 2-8, U restored

Thatch Removal: 4, 5, W, I, L
Thatch Disturbance 2: 3, 8, G, H, M
Control: 2, U, E, J, K

lat 34.417160
long -119.866358

Figure 1. Vernal pools (highlighted in purple) of Del Sol Vernal Pool Preserve and Camino Corto Open Space, Santa Barbara, California, USA with experimental treatment pools labeled.

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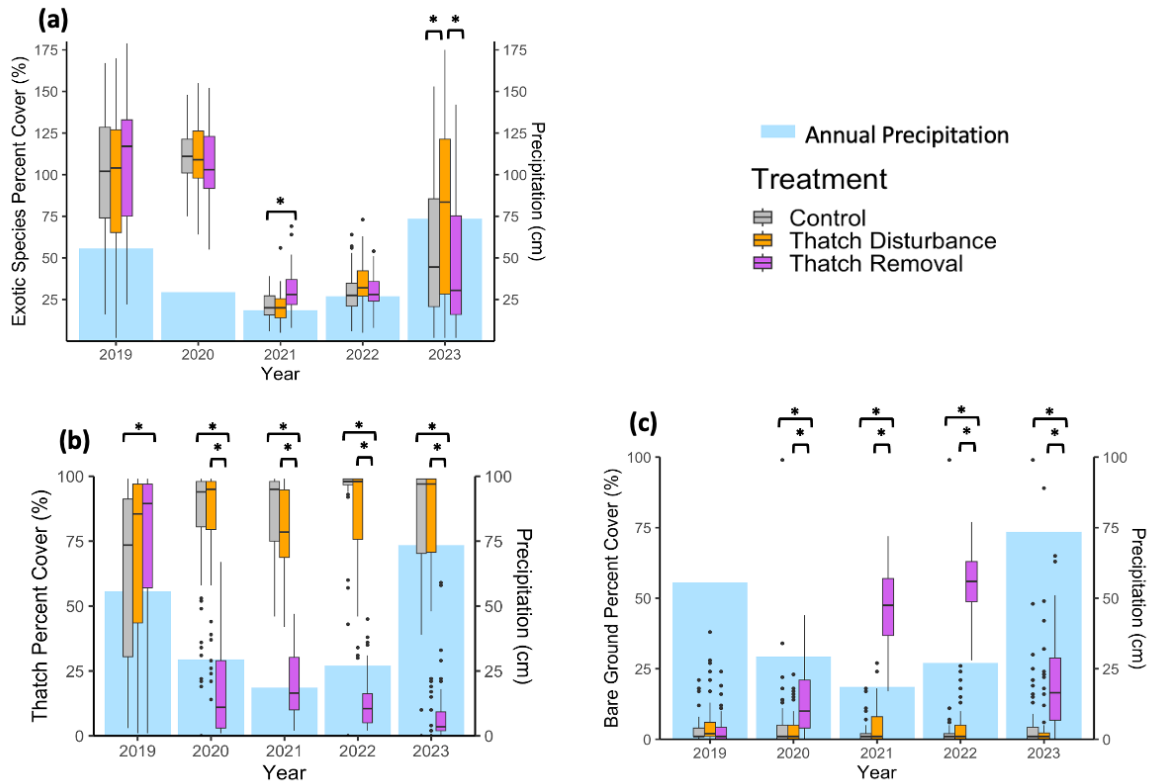
Figure 2. Boxplots showing medians and interquartile ranges of (a) total exotic plant species cover, (b) thatch percent cover, and (c) bare ground percent cover, with whiskers extending 1.5*IQR and outliers shown as solid points. Pre-treatment (2019) data and data collected after annual treatments (2020-2023) shown. Total annual precipitation is represented by blue bars. Asterisks indicate significant post-hoc Tukey's HSD pairwise comparisons of values across thatch manipulation treatments from generalized linear mixed-effects models ($p <$ 0.05).
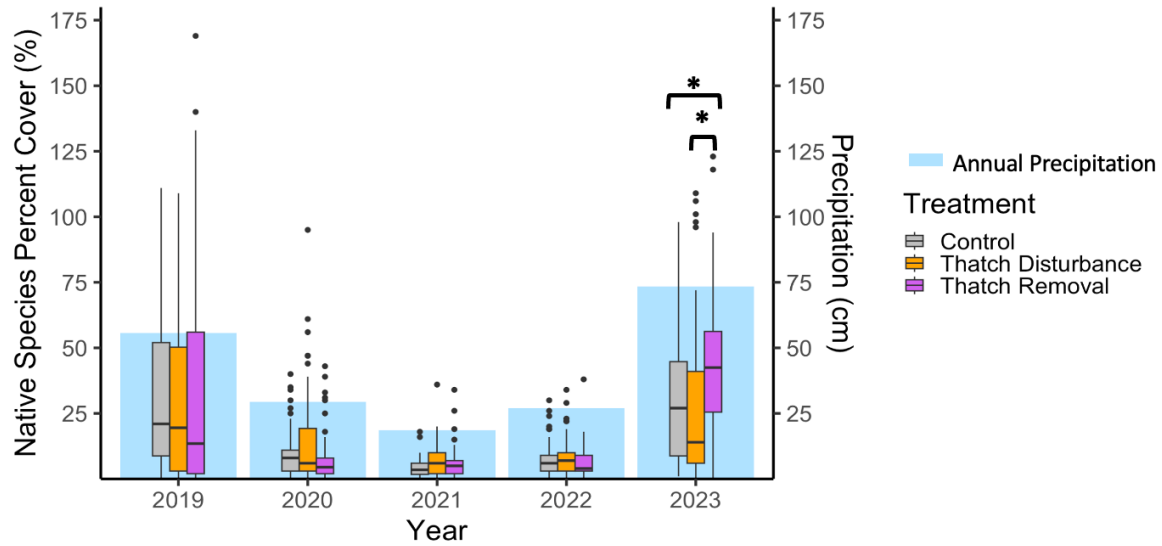
Figure 3. Boxplots showing medians and interquartile ranges of total native plant species percent cover, with whiskers extending 1.5*IQR and outliers shown as solid points. Pre-treatment (2019) data and data collected after annual treatments (2020-2023) shown. Total annual precipitation is represented by blue bars. Asterisks indicate significant post-hoc Tukey's HSD pairwise differences among thatch manipulation treatments from generalized linear mixed-effects models ($p < 0.05$).
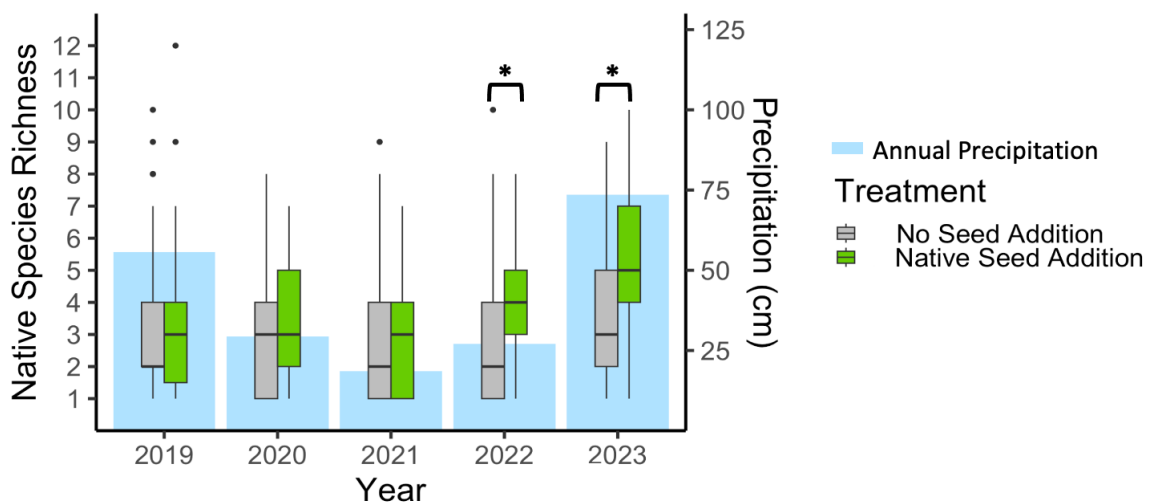
Figure 4. Boxplots showing medians and interquartile ranges of native plant species percent cover, with whiskers extending 1.5*IQR and outliers shown as solid points. Pre-treatment (2019) data and data collected after annual treatments (2020-2023) shown. Total annual precipitation is represented by blue bars. Asterisk indicate significant post-hoc Tukey's HSD pairwise differences between native seeding treatments from generalized linear-mixed effects models ($p < 0.05$).

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I. Appendix B

Supporting Information

Table S1. Seeding rates of native plant species per quadrat. Approximate seed counts were determined by counting seeds in 6 x 1 g samples.

Species	2019		2020		2021		2022	
	Grams	Approx. Seed Count	Grams	Approx. Seed Count	Grams	Approx. Seed Count	Grams	Approx. Seed Count
Eryngium vaseyi	17.99	18,482	17.99	14,260	17.99	14,413	17.99	14,320
Grindelia camporum	6.77	1,986	12.6	2,234	11.30	2,213	11.3	2,504
Hordeum brachyantherum	9.11	2,399	9.13	2,260	9.13	2,401	9.13	2,500
Juncus bufonius	1.40	85,714	1.00	25,816	0	0	0.41	2,152
Juncus occidentalis	0.95	35,625	0.71	7,986	0.63	17,772	0.19	10,867
Phalaris lemmonii	0.17	103	0.44	240	0.17	93	0.17	86
Stipa pulchra	1.32	752	1.32	622	1.32	652	1.32	698

Table S2. ANOVA table of gamma distribution GLMM (logarithmic link) of treatment and year effects on total exotic species percent cover, compared to 2019 Control plots.

	sqrt-transformed Total Exotic Plant Species Cover		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	2.29	2.19 – 2.40	**<0.001**
year [2020]	0.08	-0.02 – 0.17	0.103
year [2021]	-0.77	-0.86 – -0.68	**<0.001**
year [2022]	-0.62	-0.71 – -0.53	**<0.001**

year [2023]	-0.43	-0.53 – -0.34	**<0.001**
treatment [Thatch Disturbance]	-0.06	-0.21 – 0.10	0.470
treatment [Thatch Removal]	-0.01	-0.16 – 0.14	0.946
seeded [No Seed Addition]	-0.03	-0.18 – 0.12	0.682
year [2020] × treatment [Thatch Disturbance]	0.02	-0.09 – 0.14	0.705
year [2021] × treatment [Thatch Disturbance]	0.00	-0.11 – 0.12	0.973
year [2022] × treatment [Thatch Disturbance]	0.08	-0.03 – 0.19	0.172
year [2023] × treatment [Thatch Disturbance]	0.17	0.06 – 0.29	**0.003**
year [2020] × treatment [Thatch Removal]	-0.07	-0.18 – 0.04	0.230
year [2021] × treatment [Thatch Removal]	0.14	0.03 – 0.26	**0.014**
year [2022] × treatment [Thatch Removal]	-0.03	-0.15 – 0.08	0.594
year [2023] × treatment [Thatch Removal]	-0.16	-0.28 – -0.05	**0.006**
year [2020] × seeded [No Seed Addition]	0.00	-0.09 – 0.09	0.997
year [2021] × seeded [No Seed Addition]	-0.01	-0.10 – 0.08	0.819
year [2022] × seeded [No Seed Addition]	0.01	-0.08 – 0.11	0.808
year [2023] × seeded [No Seed Addition]	0.06	-0.04 – 0.15	0.229
treatment [Thatch Disturbance] × seeded [No Seed Addition]	0.05	-0.13 – 0.24	0.576

treatment [Thatch Removal] × seeded [No Seed Addition]	0.07	-0.12 – 0.26	0.479

Random Effects

σ^2	0.05
$\tau_{00\ \text{quadrat\_id}}$	0.02
ICC	0.25
N $_{\text{quadrat\_id}}$	180
Observations	900
Marginal R^2 / Conditional R^2	0.601 / 0.703

Notes: "year" is the year of sampling; "quadrat _id" is the unique identifier for each quadrat.

Bold values are significant at $p < 0.05$. Total cover was square-root transformed to fit a gamma distribution with a logarithmic link.

Table S3. ANOVA table of beta distribution GLMM of treatment and year effects on Simpson's Index, compared to 2019 Control plots.

	Simpson's Index		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.49	0.26 – 0.71	**<0.001**
year [2020]	-0.45	-0.72 – -0.17	**0.001**
year [2021]	0.44	0.15 – 0.73	**0.003**
year [2022]	0.14	-0.14 – 0.42	0.324
year [2023]	-0.06	-0.33 – 0.22	0.690
treatment [Thatch Disturbance]	-0.14	-0.45 – 0.18	0.391
treatment [Thatch Removal]	-0.24	-0.55 – 0.08	0.137
seeded [x Native Seed Addition]	-0.22	-0.53 – 0.09	0.167

year [2020] × treatment [Thatch Disturbance]	0.13	-0.25 – 0.52	0.507
year [2021] × treatment [Thatch Disturbance]	0.13	-0.27 – 0.53	0.524
year [2022] × treatment [Thatch Disturbance]	0.09	-0.30 – 0.48	0.664
year [2023] × treatment [Thatch Disturbance]	-0.04	-0.42 – 0.35	0.849
year [2020] × treatment [Thatch Removal]	0.25	-0.13 – 0.64	0.196
year [2021] × treatment [Thatch Removal]	0.19	-0.21 – 0.59	0.362
year [2022] × treatment [Thatch Removal]	0.35	-0.04 – 0.75	0.082
year [2023] × treatment [Thatch Removal]	0.28	-0.10 – 0.67	0.150
year [2020] × seeded [x Native Seed Addition]	-0.06	-0.44 – 0.32	0.767
year [2021] × seeded [x Native Seed Addition]	0.21	-0.18 – 0.61	0.291
year [2022] × seeded [x Native Seed Addition]	0.43	0.04 – 0.82	**0.031**
year [2023] × seeded [x Native Seed Addition]	0.38	-0.00 – 0.77	0.052
treatment [Thatch Disturbance] × seeded [x Native Seed Addition]	0.15	-0.28 – 0.59	0.491
treatment [Thatch Removal] × seeded [x Native Seed Addition]	0.24	-0.20 – 0.68	0.280
(year [2020] × treatment [Thatch Disturbance]) × seeded [x Native Seed Addition]	0.01	-0.52 – 0.55	0.956

(year [2021] × treatment [Thatch Disturbance]) × seeded [x Native Seed Addition]	-0.16	-0.72 – 0.40	0.584
(year [2022] × treatment [Thatch Disturbance]) × seeded [x Native Seed Addition]	-0.29	-0.84 – 0.26	0.307
(year [2023] × treatment [Thatch Disturbance]) × seeded [x Native Seed Addition]	-0.39	-0.93 – 0.15	0.160
(year [2020] × treatment [Thatch Removal]) × seeded [x Native Seed Addition]	0.14	-0.40 – 0.68	0.605
(year [2021] × treatment [Thatch Removal]) × seeded [x Native Seed Addition]	-0.24	-0.80 – 0.32	0.393
(year [2022] × treatment [Thatch Removal]) × seeded [x Native Seed Addition]	-0.42	-0.98 – 0.13	0.132
(year [2023] × treatment [Thatch Removal]) × seeded [x Native Seed Addition]	-0.43	-0.98 – 0.11	0.121

Random Effects

σ^2	0.00
$\tau_{00 \ quadrat\_id}$	0.08
ICC	1.00
$N_{quadrat\_id}$	180
Observations	899
Marginal R^2 / Conditional R^2	0.568 / 1.000

Notes: "year" is the year of sampling; "quadrat _id" is the unique identifier for each quadrat.

Bold values are significant at $p < 0.05$.

Table S4. ANOVA table of gamma distribution GLMM (logarithmic link) of treatment and year effects on thatch percent cover (as a proportion), compared to 2019 Control plots.

	Thatch Percent Cover (as a proportion)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.37	-0.00 – 0.75	0.052
year [2020]	1.18	0.71 – 1.66	**<0.001**
year [2021]	1.37	0.88 – 1.86	**<0.001**
year [2022]	1.86	1.36 – 2.36	**<0.001**
year [2023]	1.20	0.72 – 1.68	**<0.001**
treatment [Thatch Disturbance]	0.43	-0.11 – 0.96	0.118
treatment [Thatch Removal]	0.92	0.37 – 1.47	**0.001**
seeded [No Seed Addition]	0.27	-0.28 – 0.81	0.336
year [2020] × treatment [Thatch Disturbance]	-0.58	-1.25 – 0.09	0.092
year [2021] × treatment [Thatch Disturbance]	-0.87	-1.57 – -0.18	**0.014**
year [2022] × treatment [Thatch Disturbance]	-0.99	-1.68 – -0.30	**0.005**
year [2023] × treatment [Thatch Disturbance]	-0.60	-1.27 – 0.07	0.079
year [2020] × treatment [Thatch Removal]	-3.82	-4.52 – -3.11	**<0.001**
year [2021] × treatment [Thatch Removal]	-3.75	-4.47 – -3.04	**<0.001**

year [2022] × treatment [Thatch Removal]	-4.59	-5.32 – -3.86	**<0.001**
year [2023] × treatment [Thatch Removal]	-4.21	-4.93 – -3.49	**<0.001**
year [2020] × seeded [No Seed Addition]	-0.37	-1.06 – 0.32	0.292
year [2021] × seeded [No Seed Addition]	-0.42	-1.12 – 0.29	0.247
year [2022] × seeded [No Seed Addition]	-0.52	-1.22 – 0.19	0.149
year [2023] × seeded [No Seed Addition]	-0.12	-0.81 – 0.57	0.728
treatment [Thatch Disturbance] × seeded [No Seed Addition]	-0.13	-0.90 – 0.64	0.737
treatment [Thatch Removal] × seeded [No Seed Addition]	-0.64	-1.42 – 0.15	0.111
(year [2020] × treatment [Thatch Disturbance]) × seeded [No Seed Addition]	0.52	-0.45 – 1.49	0.296
(year [2021] × treatment [Thatch Disturbance]) × seeded [No Seed Addition]	0.35	-0.65 – 1.35	0.496
(year [2022] × treatment [Thatch Disturbance]) × seeded [No Seed Addition]	0.46	-0.53 – 1.44	0.365
(year [2023] × treatment [Thatch Disturbance]) × seeded [No Seed Addition]	-0.09	-1.05 – 0.87	0.853
(year [2020] × treatment [Thatch Removal]) × seeded [No Seed Addition]	0.65	-0.34 – 1.63	0.197

(year [2021] × treatment [Thatch Removal]) × seeded [No Seed Addition]	0.63	-0.37 – 1.62	0.217
(year [2022] × treatment [Thatch Removal]) × seeded [No Seed Addition]	0.87	-0.12 – 1.87	0.086
(year [2023] × treatment [Thatch Removal]) × seeded [No Seed Addition]	0.27	-0.72 – 1.27	0.590

Random Effects

σ^2	0.00
$\tau_{00 \text{ quadrat\_id}}$	0.31
ICC	1.00
N $_{\text{quadrat\_id}}$	180
Observations	900
Marginal R^2 / Conditional R^2	0.850 / 1.000

Notes: "year" is the year of sampling; "quadrat _id" is the unique identifier for each quadrat.

Bold values are significant at $p < 0.05$.

Table S5. ANOVA table of binomial hurdle GLMM of treatment and year effects on bare ground, compared to 2019 Control plots.

	Probability of Bare Ground Presence		
Predictors	*Log-Odds*	*CI*	*p*
Count Model			
(Intercept)	1.45	0.36 – 2.55	**0.009**
year [2020]	-0.58	-1.72 – 0.56	0.318
year [2021]	-0.60	-1.75 – 0.55	0.307
year [2022]	-0.58	-1.73 – 0.58	0.329
year [2023]	-0.75	-1.87 – 0.36	0.183

treatment [Thatch Disturbance]	-0.19	-1.66 – 1.28	0.801
treatment [Thatch Removal]	-0.68	-2.19 – 0.82	0.374
seeded [No Seed Addition]	0.81	-0.62 – 2.24	0.267
year [2020] × treatment [Thatch Disturbance]	-0.25	-1.66 – 1.16	0.724
year [2021] × treatment [Thatch Disturbance]	0.36	-1.06 – 1.79	0.616
year [2022] × treatment [Thatch Disturbance]	0.80	-0.63 – 2.23	0.271
year [2023] × treatment [Thatch Disturbance]	-0.04	-1.45 – 1.37	0.954
year [2020] × treatment [Thatch Removal]	5.20	3.07 – 7.33	**<0.001**
year [2021] × treatment [Thatch Removal]	35.06	-3961135.63 – 3961205.75	1.000
year [2022] × treatment [Thatch Removal]	35.76	-4281473.28 – 4281544.81	1.000
year [2023] × treatment [Thatch Removal]	3.30	1.79 – 4.82	**<0.001**
year [2020] × seeded [No Seed Addition]	-1.01	-2.31 – 0.29	0.127
year [2021] × seeded [No Seed Addition]	-0.75	-2.11 – 0.61	0.280
year [2022] × seeded [No Seed Addition]	-1.45	-2.81 – -0.09	**0.037**
year [2023] × seeded [No Seed Addition]	-1.09	-2.29 – 0.11	0.075
treatment [Thatch Disturbance] × seeded [No Seed Addition]	0.69	-0.93 – 2.31	0.405

Predictors	Estimates	CI	p
treatment [Thatch Removal] × seeded [No Seed Addition]	-0.73	-2.64 – 1.17	0.449
Zero-Inflated Model			
(Intercept)	-22.77	-10393.55 – 10348.01	0.997
Random Effects			
σ^2	3.29		
$\tau_{00\ quadrat\_id}$	3.37		
ICC	0.51		
$N_{quadrat\_id}$	180		
Observations	900		
Marginal R^2 / Conditional R^2	0.952 / 0.976		

Notes: "year" is the year of sampling; "quadrat _id" is the unique identifier of each quadrat.

Bolded values have a significance of $p < 0.05$.

Table S6. ANOVA table of gamma distribution hurdle GLMM of treatment and year effects on bare ground percent cover, compared to 2019 Control plots.

	Log-transformed Percent Bare Ground Cover		
Predictors	*Estimates*	*CI*	*p*
Count Model			
(Intercept)	-0.30	-0.67 – 0.08	0.123
year [2020]	0.38	-0.07 – 0.84	0.095
year [2021]	-0.23	-0.69 – 0.22	0.313
year [2022]	-0.10	-0.56 – 0.35	0.663
year [2023]	0.43	-0.02 – 0.89	0.061
treatment [Thatch Disturbance]	0.61	0.14 – 1.09	**0.011**

treatment [Thatch Removal]	0.42	-0.06 – 0.90	0.085
seeded [No Seed Addition]	0.42	-0.01 – 0.85	0.057
year [2020] × treatment [Thatch Disturbance]	-0.45	-1.00 – 0.11	0.114
year [2021] × treatment [Thatch Disturbance]	0.17	-0.37 – 0.71	0.547
year [2022] × treatment [Thatch Disturbance]	-0.23	-0.78 – 0.32	0.419
year [2023] × treatment [Thatch Disturbance]	-0.63	-1.21 – -0.05	**0.032**
year [2020] × treatment [Thatch Removal]	0.32	-0.22 – 0.86	0.246
year [2021] × treatment [Thatch Removal]	1.48	0.94 – 2.01	**<0.001**
year [2022] × treatment [Thatch Removal]	1.39	0.85 – 1.93	**<0.001**
year [2023] × treatment [Thatch Removal]	0.48	-0.08 – 1.03	0.094
year [2020] × seeded [No Seed Addition]	-0.12	-0.56 – 0.32	0.586
year [2021] × seeded [No Seed Addition]	-0.07	-0.51 – 0.36	0.736
year [2022] × seeded [No Seed Addition]	-0.05	-0.49 – 0.38	0.809
year [2023] × seeded [No Seed Addition]	-0.04	-0.49 – 0.41	0.868
treatment [Thatch Disturbance] × seeded [No Seed Addition]	-0.58	-1.06 – -0.11	**0.017**
treatment [Thatch Removal] × seeded [No Seed Addition]	-0.33	-0.78 – 0.12	0.150

(Intercept)	0.86	0.81 – 0.91	

Zero-Inflated Model

(Intercept)	-22.75	-6666.89 – 6621.39	0.995

Random Effects

σ^2	0.74
$\tau_{00 \ quadrat\_id}$	0.15
ICC	0.17
$N_{\ quadrat\_id}$	172
Observations	660
Marginal R^2 / Conditional R^2	0.287 / 0.408

Notes: "year" is the year of sampling; "quadrat _id" is the unique identifier for each quadrat.

Bold values are significant at $p < 0.05$. Bare ground was log-transformed to fit a gamma

distribution with a logarithmic link.

Table S7. ANOVA table of binomial hurdle GLMM of treatment and year effects on total

native species cover, compared to 2019 Control plots.

	Probability of Native Species Presence		
Predictors	*Log-Odds*	*CI*	*p*
Count Model			
(Intercept)	9.03	5.09 – 12.97	**<0.001**
year [2020]	6.54	0.77 – 12.32	**0.026**
year [2021]	0.05	-3.17 – 3.27	0.976
year [2022]	4.61	-0.25 – 9.46	0.063
year [2023]	32.96	-66075.76 – 66141.69	0.999
treatment [Thatch Disturbance]	0.69	-4.60 – 5.99	0.798

treatment [Thatch Removal]	0.70	-5.30 – 6.70	0.819
seeded [No Seed Addition]	-0.07	-5.43 – 5.29	0.979
year [2020] × treatment [Thatch Disturbance]	-7.17	-13.37 – -0.97	**0.023**
year [2021] × treatment [Thatch Disturbance]	0.96	-3.60 – 5.51	0.680
year [2022] × treatment [Thatch Disturbance]	-1.09	-6.51 – 4.34	0.695
year [2023] × treatment [Thatch Disturbance]	3.33	-88471.97 – 88478.63	1.000
year [2020] × treatment [Thatch Removal]	-4.02	-9.29 – 1.25	0.135
year [2021] × treatment [Thatch Removal]	0.93	-4.41 – 6.27	0.733
year [2022] × treatment [Thatch Removal]	-2.25	-7.30 – 2.80	0.383
year [2023] × treatment [Thatch Removal]	-11.00	-62721.29 – 62699.28	1.000
year [2020] × seeded [No Seed Addition]	-3.32	-7.77 – 1.13	0.144
year [2021] × seeded [No Seed Addition]	7.42	1.47 – 13.38	**0.014**
year [2022] × seeded [No Seed Addition]	-0.68	-4.78 – 3.43	0.746
year [2023] × seeded [No Seed Addition]	-9.15	-20980.39 – 20962.09	0.999
treatment [Thatch Disturbance] × seeded [No Seed Addition]	2.55	-5.48 – 10.58	0.533
treatment [Thatch Removal] × seeded [No Seed Addition]	-1.15	-8.86 – 6.57	0.771

Zero-Inflated Model

(Intercept)	-6.61	-8.58 – -4.63	**<0.001**

Random Effects

σ^2	3.29
$\tau_{00\ quadrat\_id}$	132.11
ICC	0.98
$N_{quadrat\_id}$	180
Observations	900
Marginal R^2 / Conditional R^2	0.450 / 0.987

Notes: "year" is the year of sampling; "quadrat _id" is the unique identifier of each quadrat.

Bolded values have a significance of $p < 0.05$.

Table S8. ANOVA table of gamma distribution hurdle GLMM (logarithmic link) of treatment and year effects on total native species percent cover, compared to 2019 Control plots.

	Total Native Plant Percent Cover		
Predictors	*Estimates*	*CI*	*p*
Count Model			
(Intercept)	3.08	2.74 – 3.43	**<0.001**
year [2020]	-1.18	-1.47 – -0.89	**<0.001**
year [2021]	-1.92	-2.22 – -1.63	**<0.001**
year [2022]	-1.39	-1.68 – -1.09	**<0.001**
year [2023]	0.03	-0.25 – 0.31	0.846
treatment [Thatch Disturbance]	0.14	-0.34 – 0.61	0.572
treatment [Thatch Removal]	0.25	-0.23 – 0.73	0.299

seeded [No Seed Addition]	0.41	-0.05 – 0.86	0.084
year [2020] × treatment [Thatch Disturbance]	0.33	-0.03 – 0.69	0.072
year [2021] × treatment [Thatch Disturbance]	0.63	0.26 – 0.99	**0.001**
year [2022] × treatment [Thatch Disturbance]	0.24	-0.12 – 0.60	0.197
year [2023] × treatment [Thatch Disturbance]	-0.04	-0.39 – 0.31	0.833
year [2020] × treatment [Thatch Removal]	-0.21	-0.57 – 0.16	0.267
year [2021] × treatment [Thatch Removal]	0.31	-0.06 – 0.67	0.100
year [2022] × treatment [Thatch Removal]	-0.13	-0.49 – 0.24	0.494
year [2023] × treatment [Thatch Removal]	0.57	0.20 – 0.93	**0.002**
year [2020] × seeded [No Seed Addition]	-0.04	-0.33 – 0.26	0.808
year [2021] × seeded [No Seed Addition]	0.04	-0.26 – 0.34	0.804
year [2022] × seeded [No Seed Addition]	-0.05	-0.35 – 0.25	0.731
year [2023] × seeded [No Seed Addition]	-0.13	-0.42 – 0.17	0.401
treatment [Thatch Disturbance] × seeded [No Seed Addition]	-0.70	-1.29 – -0.11	**0.020**
treatment [Thatch Removal] × seeded [No Seed Addition]	-0.67	-1.26 – -0.07	**0.028**
(Intercept)	0.66	0.62 – 0.69	

Zero-Inflated Model

(Intercept)	-21.81	-3688.22 – 3644.60	0.991

Random Effects

σ^2	0.43
$\tau_{00 \ quadrat\_id}$	0.58
ICC	0.57
$N_{quadrat\_id}$	179
Observations	850
Marginal R^2 / Conditional R^2	0.368 / 0.730

Notes: "year" is the year of sampling; "quadrat _id" is the unique identifier for each quadrat.

Bold values are significant at $p < 0.05$.

Table S9. ANOVA table of Poisson distribution GLMM of treatment and year effects on native species richness, compared to 2019 Control plots.

	Native Plant Species Richness		
Predictors	*Log-Mean*	*CI*	*p*
(Intercept)	1.12	0.90 – 1.35	**<0.001**
year [2020]	0.02	-0.21 – 0.24	0.875
year [2021]	-0.38	-0.62 – -0.13	**0.003**
year [2022]	0.15	-0.07 – 0.37	0.177
year [2023]	0.42	0.22 – 0.63	**<0.001**
treatment [Thatch Disturbance]	-0.01	-0.32 – 0.29	0.931
treatment [Thatch Removal]	-0.06	-0.37 – 0.24	0.681
seeded [No Seed Addition]	0.02	-0.27 – 0.31	0.876
year [2020] × treatment [Thatch Disturbance]	-0.06	-0.33 – 0.22	0.698

year [2021] × treatment [Thatch Disturbance]	0.24	-0.06 – 0.54	0.119
year [2022] × treatment [Thatch Disturbance]	-0.05	-0.33 – 0.23	0.734
year [2023] × treatment [Thatch Disturbance]	0.04	-0.22 – 0.30	0.760
year [2020] × treatment [Thatch Removal]	0.13	-0.15 – 0.41	0.379
year [2021] × treatment [Thatch Removal]	0.51	0.21 – 0.80	**0.001**
year [2022] × treatment [Thatch Removal]	0.15	-0.12 – 0.43	0.275
year [2023] × treatment [Thatch Removal]	0.12	-0.14 – 0.39	0.351
year [2020] × seeded [No Seed Addition]	-0.10	-0.33 – 0.13	0.413
year [2021] × seeded [No Seed Addition]	-0.07	-0.31 – 0.17	0.551
year [2022] × seeded [No Seed Addition]	-0.33	-0.56 – -0.10	**0.005**
year [2023] × seeded [No Seed Addition]	-0.32	-0.54 – -0.11	**0.003**
treatment [Thatch Disturbance] × seeded [No Seed Addition]	-0.06	-0.41 – 0.30	0.746
treatment [Thatch Removal] × seeded [No Seed Addition]	-0.17	-0.52 – 0.19	0.360

Random Effects

σ^2	0.28
$\tau_{00 \ quadrat\_id}$	0.18
ICC	0.39
$N_{\ quadrat\_id}$	180

Observations		900			
Marginal R^2 / Conditional R^2		0.094 / 0.448			

Notes: "year" is the year of sampling; "quadrat _id" is the unique identifier for each quadrat.

Bold values are significant at $p < 0.05$.

Table S10. Plant species found in aboveground vegetation surveys and seed bank analyses.

Name	Native Status	Present in Survey	Present in seed bank germination	BLAST Max Score match from seed bank eDNA
Allium sativum	exotic			x
Ambrosia psilostachya	native	x	x	x
Anacardium occidentale	exotic			x
Apodolirion lanceolatum	exotic			x
Astragalus sp.	exotic			x
Austrostipa ramosissima	exotic			x
Austrostipa stipoides	exotic			x
Avena fatua	exotic	x	x	x
Baccharis pilularis	native	x	x	
Begonia purpureofolia	exotic			x
Berberis kansuensis	exotic			x
Berberis longibracteata	exotic			x
Berberis thunbergii	exotic			x
Berberis vulgaris	exotic			x
Bocconia arborea	exotic			x
Bromus sp.	exotic	x	x	x
Bromus diandrus	exotic	x	x	
Bromus hordeaceus	exotic	x	x	
Calotropis gigantea	exotic			x
Capsicum anuum	exotic			x
Carduus pycnocephalus	exotic	x		
Centaurium tenuiflorum	exotic	x		
Centromadia parryi ssp. *australis*	native	x	x	
Chrysitrix dodii	exotic			x
Clerodendrum yunnanense	exotic			x

Clintonia andrewsian	native			x
Clintonia udensis	native			x
Convolvulus arvensis	exotic	x		
Cornus kousa	exotic			x
Cotula coronopifolia	exotic	x		
Crassula aquatica	native	x	x	x
Croton setiger	native	x		
Crypsis schoenoides	exotic	x		
Cyperus sp.	native	x	x	x
Cyperus eragrostis	native		x	
Cyrtopodium macrobulbon	exotic			x
Deinandra fasciculata	native	x		
Deinandra increscens	native	x		
Delosperma sp.	exotic			x
Distichlis spicata	native	x		x
Echium vulgare	exotic			x
Elatine sp.	native			x
Eleocharis sp.	native	x		x
Eleocharis acicularis	native	x		x
Eleocharis palustris	native	x		x
Eleocharis parvula	native	x		x
Eleusine indica	exotic			x
Epilobium brachycarpum	native	x	x	
Erigeron bonariensis	exotic	x		
Erigeron canadensis	native	x		
Erodium sp.	exotic	x	x	x
Erodium botrys	exotic	x	x	x
Eryngium armatum	native	x		
Eryngium vaseyi	native	x		x
Eschscholzia californica	native			x
Euonymus lichiangensis	exotic			x
Festuca bromoides	exotic	x	x	x
Festuca myuros	exotic	x	x	
Festuca perennis	exotic	x	x	x
Ficus sp.	exotic			x
Foeniculum vulgare	exotic	x		x
Gastridium phleoides	exotic	x	x	
Geranium dissectum	exotic	x	x	x
Gossypium herbaceum	exotic			x

Gossypium raimondii	exotic			x
Gossypium turneri	exotic			x
Greenwayodendron suaveolens	exotic			x
Grindelia camporum	native	x		
Gunnera herteri	exotic			x
Hedychium flavum	exotic			x
Heliconia paka	exotic			x
Heliotropium marifolium	exotic			x
Helminthotheca echioides	exotic	x		
Hirschfeldia incana	exotic	x		
Hordeum brachyantherum	native	x		
Hordeum marinum	exotic	x		
Humenaea verrucosa	exotic			
Hypochaeris glabra	exotic	x	x	
Indigofera linifolia	exotic			x
Isocoma menziesii	native	x		x
Isoetes sp.	native			x
Isoetes nuttallii	native			x
Isolepis tenuissima	native			x
Juncus sp.	native	x	x	x
Juncus alpinoarticulatus	exotic			x
Juncus bufonius	native	x	x	x
Juncus occidentalis	native	x		x
Juncus phaeocephalus	native	x		
Lactuca serriola	exotic	x		x
Lasthenia sp.	native			x
Laurus nobilis	exotic			x
Linnaea borealis	native			x
Litsea cubeba	exotic			x
Lourtella resinosa	exotic			x
Lysimachia arvensis	exotic	x	x	x
Lysimachia minima	native	x		x
Lythrum hyssopifolia	exotic	x	x	x
Madia sativa	native	x		x
Malus robusta	exotic			x
Medicago polymorpha	exotic	x	x	
Musa rosea	exotic			x
Nepenthes rafflesiana	exotic			x

Nicotiana tomentosifor	exotic			x
Nigella damascena	exotic			x
Ocimum basilicum	exotic			x
Oxalis pilosa	native	x		
Pelargonium tragacanthoides	exotic			x
Phalaenopsis equestris	exotic			x
Phalaris lemmonii	native	x		
Phaseolus lunatus	exotic			x
Phoebe attenuata	exotic			x
Phoenix dactylifera	exotic			x
Piptatherum songaricum	native			x
Plagiobothrys sp.	native	x		x
Plagiobothrys undulatus	native	x		
Plantago sp.	exotic	x		x
Plantago coronopus	exotic	x		
Plantago lanceolata	exotic	x		x
Plantago major	exotic			x
Platanus racemosa	native			x
Poa annua	exotic		x	
Polypogon monspeliensis	exotic	x	x	x
Potentilla anserina	exotic			x
Pseudognaphalium californicum	native	x		
Psilocarphus brevissimus	native	x		
Raphanus sativus	exotic	x		x
Rheum sp.	exotic			x
Rheum tanguticum	exotic			x
Rubia cordifolia	exotic			x
Rubus sp.	exotic			x
Rubus odoratus	exotic			x
Rumex acetosella	exotic	x		x
Rumex crispus	exotic	x		x
Salvia apiana	native			x
Salvia brandegeei	native			x
Sandbergia perplexa	exotic			x
Sarcococca conzattii	exotic			x
Setaria intermedia	exotic			x
Solanum lycopersicum	exotic			x
Sonchus sp.	exotic	x		x

Sonchus asper	exotic	x		
Sonchus oleraceus	exotic	x		
Sorbaria sorbifolia	exotic			x
Spergula arvensis	exotic			x
Spergula marina	native			x
Spergularia sp.	native	x	x	
Spergularia sp.	exotic	x	x	
Spiraea media	native			x
Stipa brachychaeta	exotic			x
Stipa pulchra	native	x		x
Symphyotrichum subulatum	native	x	x	x
Timouria saposhnikowii	exotic			x
Triticum aestivum	exotic			x
Triticum monococcum	exotic			x
Umbilicus rupestris	exotic			x
Vaccinium sp.	native			x
Vateria macrocarpa	exotic			x
Vicia sativa	exotic			x
Vicia villosa	exotic	x	x	x
Whipplea modesta	native			x
Zea mays	exotic			x
Ziziphus jujuba	exotic			x
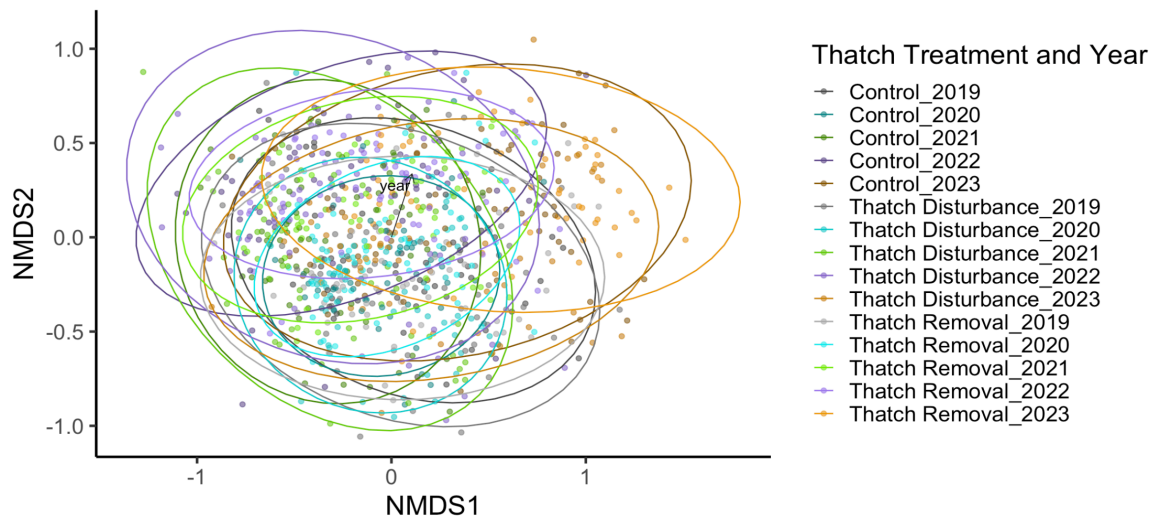
Figure S1. NMDS of plant species percent cover, by thatch treatment and year of sampling, shown with significant year effect ($p < 0.05$).

III. Interpopulation variation in *Juncus bufonius* performance in response to imposed drought regimes and competition

A. Abstract

Selection of genotypes to use in habitat restoration projects requires consideration of specific restoration goals, such as retaining genetic or species diversity, as well as challenges, such as climate change and the location and quality of extant source populations. If local source populations are readily available, restoration projects may choose to use local material to prioritize local genetic integrity and local adaptation. If the climate in the restoration site is predicted to change, restoration projects may prioritize genotypes that can adapt to and persist under changing conditions. Along the south coast of California, USA, climate change is predicted to shorten the annual wet season, with larger but fewer winter storm events, resulting in prolonged summer/fall drought and episodic dry periods during the rainy season. Drought conditions may favor invasive species such as exotic annual grasses, especially if local native populations cannot tolerate severe drought. Intraspecific variation may result in populations that differ in their responses to drought or competitors. We set up a common garden greenhouse experiment focusing on *Juncus bufonius* (toad rush) populations that were subjected to drought and competition treatments. We collected seed from a Santa Barbara population and two San Diego populations, the latter which have evolved under longer seasonal droughts. We exposed these genotypes to different drought regimes and competition with a dominant invasive species, *Festuca perennis* (Italian ryegrass). We found intraspecific differences in drought and competition responses in aboveground growth, aboveground biomass, mortality, and reproduction among populations. The Santa Barbara

population generally performed the worst under drought conditions, but there was not one

population that consistently outperformed the others in all plant response

variables. Intraspecific variation in responses to drought and competition may affect a

population's ability to persist under climate change, which suggests that the establishment

and sustainability of restored populations can be maximized if we can identify specific

source populations with adaptations to future climate conditions. Lacking specific climate

predictions or population adaptations, maximizing genetic diversity by sourcing seed from

multiple populations may also increase a restored population's resilience to climate change.

B. Introduction

Widespread land use change and habitat destruction are major causes of population decline in

native plant species. In California, USA, less than 10% of historical pre-industrial native

grasslands and wetlands still exist, resulting in the endangerment and extinction of many

native plant species locally and throughout the state (Stromberg et al. 2007). As a

consequence, it may be difficult to collect seeds from remnant populations without

overharvesting, and habitat restoration projects that aim to restore native species are often

faced with choosing which plant material to use for restoration projects. Different seed

provenancing strategies can increase the likelihood of establishing and sustaining restored

populations at specific sites (Breed et al. 2013). Local provenancing, or using seed from

proximate source populations, can preserve adaptive advantages evolved by specific

genotypes to past local conditions (Sackville Hamilton 2001). If climate or other

environmental conditions are stable, theory predicts that this strategy should lead to the

greatest success in restoring native species at a site. Yet, although local provenancing can retain local genotypes that have adapted to historical climate conditions, it runs the risk of constraining the adaptive potential of restored populations under future conditions (Jones 2013; Broadhurst et al. 2008). Predictive provenancing, or using seed from a population that has exhibited high fitness under climate conditions similar to those predicted for the restoration site under projected future climate scenarios, focuses on maximizing the adaptive potential for a restored population to persist under predicted climate conditions (Sgró et al. 2011). Admixture provenancing, or using seed from multiple populations to maximize genetic variation, also focuses on increasing the adaptive potential for a restored population to persist under variable climate conditions (Breed et al. 2013). This strategy may be helpful if climate conditions are unpredictable or if there is not adequate information on population characteristics; it provides a large gene pool from which natural selection can select for the most fit genotypes. Each provenancing strategy can be most useful in different scenarios, and careful consideration of specific restoration site characteristics and restoration goals can help practitioners decide which strategy may increase restoration success at their site (Breed et al. 2013).

In the 20th Century, plant restoration has had mixed success, with native plant establishment varying widely across restoration sites and methods (Godefroid et al. 2011). Yet, we can use provenancing strategy theory to critically assess which provenancing strategy may be most suitable under given site characteristics. In particular, restoration of vernal pool plant assemblages in southern California using local provenancing has resulted in variable levels of success, i.e., in native plant establishment and persistence (Tang et al. 2023; Black & Zedler

1998). Vernal pools are temporary wetlands that form when rainwater pools in depressions in the landscape atop an impermeable subsurface soil layer (Keeley & Zedler 1998). In California's Mediterranean climate, vernal pools form during the cool, wet winter months. Water is lost due to evapotranspiration during subsequent warm, dry months, such that the pools dry up completely every summer. Over 40% of the species found in California's vernal pools are endemic, with special adaptations that allow them to withstand this seasonal wetting and drying (Stone 1990). However, only 5% of historical pre-industrial vernal pool habitat still exists (Holland 1978). Along the south coast of California, rapid land use change has destroyed 97% of historical vernal pool habitat (Bauder & McMillan 1998). Applying provenancing strategy theory to Santa Barbara vernal pool restoration allows us to critically assess which provenancing strategy may be most suitable under given site characteristics and may increase the establishment and persistence of restored populations.

One important factor that determines provenancing strategy suitability is local population quantity and quality. Urbanization has destroyed and degraded the majority of vernal pools in Santa Barbara County. Such intense habitat fragmentation can cause a population bottleneck, wherein genetic diversity is constrained by the alleles preserved in the few remaining individuals (Wall et al. 2014). The resulting small gene pool can limit a population's ability to adapt to changing environmental conditions, and collecting from remnant populations can result in overharvesting (Broadhurst et al. 2008). Yet, populations fragmented by urbanization can experience novel and changing environmental conditions, and this often results in isolated populations developing local adaptation or phenotypic plasticity to persist under changing conditions (de Barros Ruas et al. 2022; Liao et al. 2016).

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Another important factor that determines provenancing strategy suitability is climate change. Theory predicts that local provenancing is most successful under stable climate conditions (Breed et al. 2013). Yet, along the south coast of California, downscaled climate models have predicted a shortening of the wet winter season but an increase in total annual rainfall, owing to an increase in large storm events, within the 21st Century (Feng et al. 2019). This is predicted to result in a lengthening of the summer/fall drought season, as well as more episodic large storm events punctuated by periods of dryness within the winter rainy season. These changing precipitation patterns may pose novel conditions for plants that have evolved under the south coast's historical climate regime (Feng et al. 2019). Plant assemblages in vernal pools vary with inundation duration, with species adapted to longer inundation residing in the center of the pools and species adapted to shorter inundation residing in the edges of the pools. The extent and duration of inundation depends on annual precipitation, and California's notoriously variable interannual precipitation has resulted in interannual variation in the spatial distribution of species, with species adapted to longer inundation spreading out from the center of the pool during wetter years and species adapted to shorter inundation spreading from the edges of the pools (from the surrounding invaded grassland landscape) toward the pool center during drier years (Torres-Martínez et al. 2019). Many vernal pool plants produce seeds that can remain dormant but viable in the seed bank for decades, only germinating under favorable conditions (Faist et al. 2013). This results in low germination and biomass of vernal pool species during below-average rainfall years, although these populations bounce back in above-average rainfall years.

As the duration of the wet season contracts due to climate change, vernal pool plant populations can become threatened by inhospitable abiotic conditions and correlated increases in invasive species (Gosejohan et al. 2017). When vernal pools occur in depressions within a grassland landscape in California, invasive annual grasses such as *Festuca perennis* (Italian ryegrass), *Bromus diandrus* (ripgut brome), and *Hordeum marinum* (seaside barley) can invade from the surrounding grassland into pools during dry years. After these invasive grasses establish populations in pools, they appear to interfere with the germination and growth of vernal pool endemics (Gerhardt & Collinge 2003). Thus, vernal pool species established by past restoration projects have not always persisted due to ongoing threats from increased drought and invasive species (Tang et al. 2023; Black & Zedler 1998).

Although some vernal pool plant populations can bounce back during above-average rainfall years, these populations may decline gradually because they are not able to replenish their seed banks every year (Pykälä et al. 2005). Field surveys have reported that lower precipitation correlated with a greater abundance of exotic grasses and a decreased abundance of native endemics (Javornik & Collinge 2016). Gerhardt & Collinge (2007) artificially decreased the inundation period in a vernal pool greenhouse mesocosm experiment and found an increase in exotic species growth, survival, and reproduction. Increased drought and exotic species, then, pose ongoing and future challenges for the persistence of native plant species.

Emery & La Rosa (2019) reported that specialist vernal pool plants adapted to consistent inundation (same duration every year) had limited genetic variation, which reduced their

ability to grow and reproduce under drier conditions. However, they also showed that, when grown under varying moisture treatments, species that historically experienced high variation in soil moisture exhibited higher phenotypic plasticity and maintained stable relative fitness (i.e., reproductive biomass production) compared to species that historically experienced lower variation in soil moisture. Intraspecific variation may result in some populations exhibiting higher drought tolerance and competitive ability than others, especially if one population evolved under more severe drought or competitive conditions than other populations. When considering what source populations to use for restoration projects, practitioners may be able to choose specific populations with characteristics that will result in persistent restored vernal pool plant populations.

This study evaluates the performance (i.e., growth, biomass production, mortality, reproduction) of different local and non-local populations of the native wetland plant, *Juncus bufonius* (toad rush), under imposed drought regimes and in competition with a common invasive plant species, *Festuca perennis*. *J. bufonius* is a facultative vernal pool species that is widespread across California and exhibits inter- and intra-population variation in plant traits (Jepson Flora Project 2024; Cuba-Díaz et al. 1965). Thus, we hypothesized that different populations of *J. bufonius* would exhibit phenotypic variability, which may lead to differences in responses to drought and competition. We also hypothesized that local adaptation to historical climate regimes may influence a local population's response to imposed drought regimes and competition. To test these hypotheses, we grew populations of *J. bufonius* from Santa Barbara and San Diego in a common garden and measured plant responses to different drought regimes and the presence of an exotic competitor, *Festuca*

perennis. San Diego historically experiences a shorter rainy season than Santa Barbara (Isla & Lee 2006; Ryan 1994). Moreover, studies have reported that *F. perennis* can increase biomass production under drought conditions, suggesting an association with drought conditions and increased competition between *F. perennis* and *J. bufonius* (Buttler et al. 2019). Thus, if local adaptation has occurred, we predicted that San Diego populations would be able to better tolerate more severe drought conditions than Santa Barbara populations. If populations exhibit variation in their performance when grown under different drought and competitive regimes, then predictive provenancing (using seeds from populations exhibiting higher performance under predicted future climate conditions at a given site) or admixture provenancing (using source material from several populations that may perform well in a variety of environments) may increase the long-term success of restoration efforts.

C. Methods

Location

We set up a common garden experiment at the University of California, Santa Barbara, using seed from a single species of vernal pool plant populations from south coast California vernal pool complexes. The species, *Juncus bufonius* L. (Juncaceae), was chosen as the focal native species because it is found throughout south coast vernal pools, and although its abundance in pools varies, it is generally an important component of the transition zone between the very wet pool bottom and the drier upland areas surrounding the pools. Because it generally grows around the edges of the vernal pools, it often faces competition with the invasive

grass, *Festuca perennis* (L.) Columbus & J.P. Sm (Poaceae), which commonly dominates grassland areas surrounding vernal pools. In addition, even though *J. bufonius* has a long-lived seed bank, its seeds only germinate under favorable conditions (e.g., adequate water, soil disturbance; Kotanen 1996). The pool-upland transition zone of vernal pools has the highest intra- and inter-annual moisture variability. During wet years, this transition zone becomes flooded only during large storms and then dries up quicker than the central zone of the pool, but during dry years, it may not be inundated at all (Emery & La Rosa 2019). Transition zone species such as *J. bufonius* will thus be most affected by projected climate change that predicts more variable storms and longer droughts. Hence, restoration involving careful seed provenancing of native species that occur within this zone may allow populations to be more resilient to challenges such as drought and invasive species. *J. bufonius* is an excellent candidate species for examining the patterns and impacts of intraspecific variation because it exhibits ecotypic variation resulting in the evolution of several subspecies (Jepson Flora Project 2024).

Seed of *J. bufonius* was collected in 2019 from the Isla Vista vernal pool complex (Santa Barbara County), the Miramar vernal pool complex (central San Diego County), and the Otay Mesa vernal pool complex (southern San Diego County). Seeds were collected from 3-20 pools and several individual plants per pool. All seeds were stored at room temperature until sown. In December 2023, seeds were tested for viability using tetrazolium staining and then sown in germination flats containing PRO-MIX® BX All Purpose Growing Mix (Verma & Majee 2013). Germination flats were kept covered in the greenhouse at ambient daily temperatures of 10-21ºC until seeds germinated.

Because seed weight can often correlate with seedling performance, we measured average seed weight of our collected populations (Jakobsson & Eriksson 2000). We did this by counting the number of seeds in five 0.02 g samples (weighing individual seeds is quite challenging because each seed of this species weighs <0.04 mg).

Drought Regimes

In January 2024, within three weeks of germination, a random subset of seedlings from each population were transplanted individually into 5.715 cm x 5.715 cm x 8.255 cm plastic pots with drainage holes (one plant per pot) filled with homogenized Kellogg Garden Organics™ Gromulch, pumice, and coconut fiber in a 4:2:1 ratio. Transplanted seedlings were kept in the greenhouse and watered daily for a week to decrease the risk of transplant shock. After transplant mortality stopped, pots were moved to an outdoor space so that seedlings would be exposed to natural winter growing temperatures. After pots were moved outside, seedlings were subjected to one of three drought regimes by placing the pots in plastic trays filled with 3.175 cm water. Each tray containing three pots (one pot per population) was assigned to one of three treatments: 1) End-Season Drought, 2) Mid-Season Drought, 3) Control (no drought; Figure 1). The End-Season Drought pots were placed in trays containing water for 19 days, after which the trays were emptied of water and the pots were allowed to dry naturally, simulating a cessation of the wet season (see Table S1 for full description of treatments). The Mid-Season Drought pots were placed in trays containing water for 38 days, then removed from trays and allowed to dry naturally for 40 days to simulate mid-season drying, after which they were placed back into trays with water for 19 days to

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simulate a late-season storm event. After these 19 days, they were removed and allowed to dry naturally again (see Table S1 for full description of treatments). These drought regimes were determined by calculating the minimum number of days the transition zone of vernal pools in Santa Barbara and San Diego remained inundated by rainwater during severe drought years (Palmer Drought Severity Index <-3; Palmer 1965), according to field site reports from 2019 to 2024 (Table S1). The Control pots were placed in trays containing water for the entire duration of the experiment that lasted through June 2024, i.e., they were not subjected to drought. A translucent plastic roof was constructed over all the pots and trays to prevent additional water from natural rainfall falling into the experimental system while allowing for natural sunlight, temperature, and air flow conditions. We subjected 28 seedlings of each provenance to each inundation treatment. Seedlings were monitored weekly for mortality, fruiting, and maximum height, and pot position was randomized weekly. Upon senescence, the number of fruits per plant was counted (as a measure of fitness) and the total aboveground biomass of each plant was harvested from each pot. Biomass was dried in an oven at 60ºC for two days and then weighed on a Mettler Toledo balance.

Competition x Drought Treatments

In addition to the drought treatments, we subjected a separate set of replicates to Competition x Drought treatments. *Festuca perennis* is the dominant exotic annual grass in vernal pool complexes in southern coastal California, including Santa Barbara and San Diego (Tang et al. 2023). Seed from *F. perennis* individuals was harvested from the Isla Vista vernal pool complex in 2019 and kept at room temperature until sown. In January 2024, seeds were

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sown into germination flats containing PRO-MIX® BX All Purpose Growing Mix. Germination flats were kept covered in the greenhouse at ambient daily temperatures of 10-21ºC until seeds germinated. In February 2024, within two weeks of germination, they were transplanted with *J. bufonius* seedlings that germinated in January into 5.715 cm x 5.715 cm x 8.255 cm plastic pots with drainage holes (four plants per pot) filled with homogenized Kellogg Garden Organics^{TM} Gromulch, pumice, and coconut fiber in a 4:2:1 ratio and moved outside. Individuals from each of the three *J. bufonius* populations were transplanted into a Polyculture with *F. perennis* seedlings (two individuals of each species per pot; Figure 2(a)) and also planted into a Monoculture (four individuals of *J. bufonius* per pot; Figure 2(b)). This allowed us to evaluate the relative effect of being planted within a Polyculture vs. a Monoculture on *J. bufonius* within each drought treatment. We did not test the effect of competition alone, i.e., we did not set up Polyculture or Monoculture pots in a well-watered treatment. Monocultures of four *F. perennis* individuals were also created to examine the effect of each *J. bufonius* population on *F. perennis* performance. We set up 20 replicates of each of the Polyculture and Monoculture pots, 10 of which were subjected to the Mid-Season Drought Regime, with the remaining 10 being subjected to the End-Season Drought Regime (see Table S1 for full description of treatments). Pots were placed in trays filled with water, and then pots were removed from trays according to their assigned drought regime, with each tray representing a replicate block consisting of seven pots (three *J. bufonius* Monoculture pots, one *F. perennis* Monoculture pot, and three Polyculture pots per tray). In each pot, one individual of each species was randomly selected to be measured weekly. This individual was monitored weekly for mortality, fruiting, and maximum height, and pot position was randomized weekly. Upon senescence of every individual of both species, the number of

fruits per plant was counted (as a measure of fitness) and the total aboveground biomass of each plant was harvested for each individual. Biomass was dried in an oven at 60ºC for two days and then weighed on a Mettler Toledo balance.

Data Analysis

All analyses and visualizations were performed in RStudio version 1.4.1106 (R Core Team 2023). The **aov** and **anova** functions from the "stats" package were used to perform analyses of variance. We generated linear models using the **glm** function of the "stats" package. 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). The **emmeans** function from the "emmeans" package was used to perform post-hoc Tukey's least-squares mean tests to examine the effects of treatments on plant response variables (Lenth 2023). All graphs were generated using the package "ggplot2".

We compared the total aboveground growth per plant (with initial height at transplantation subtracted from the final height to account for variation in seedling size), total aboveground biomass per plant, weekly mortality, and number of fruits per plant across populations and treatments. Most of the datasets were not normally distributed based on diagnostic residual tests, thus requiring models tailored to the particular distribution that best fit each dataset. We constructed a generalized linear model (GLM) with a gamma distribution for total aboveground growth and aboveground biomass, with population, treatment, and their interaction as fixed effects. We constructed a Cox hazard model to evaluate population and treatment effects on weekly mortality, using population, treatment, and their interaction as

fixed effects (Therneau 2024; Therneau & Grambsh 2000). We constructed a zero-inflated

hurdle GLM with a Poisson distribution to examine fruit population and treatment effects on

fruit production per individual, with population, treatment, and their interaction as fixed

effects. Post-hoc Tukey's Honestly Significant Difference tests were performed on linear

model outputs to delineate significant interaction effects between populations and treatments

on dependent variables. To test the effects of interspecific vs. intraspecific competition, we

compared total aboveground growth, aboveground biomass, weekly mortality, and number of

fruits from individuals planted in a Polyculture to that from individuals planted in a

Monoculture within each drought treatment. Because we counted fruits and harvested

biomass from multiple individuals from the same pot, we constructed a generalized linear

mixed effects model (GLMM) for aboveground biomass and fruit production, with pot added

as a random effect. We also added the date of senescence as a random effect in the biomass

GLMM because of high variation in the date each individual senesced. In addition, we

constructed a hurdle GLMM for fruit production because that dataset was zero-inflated.

D. Results

Population Characteristics

All seeds of *J. bufonius* were less than 0.04 mg/seed in weight, but the Isla Vista population

had the highest individual seed weight (Table S2). All populations had a viability rate of

over 0.06, but the Isla Vista population had the highest viability (Table S2). The Miramar

population exhibited the fruiting pattern of *J. bufonius* var. *bufonius* (one inflorescence per

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node), while the Isla Vista and Otay Mesa populations exhibited the fruiting pattern of *J. bufonius* var. *congestus* (clustered inflorescences).

Effects of Drought Regimes

The two drought regimes reduced per-capita total aboveground plant growth, aboveground plant biomass, mortality, and fruit production of all populations in comparison to the continually-watered Control treatment. In the Control treatment, plants from the Miramar population had more aboveground growth than plants from the other two populations ($p <$ 0.03; Table S3; Figure 3). However, under the Mid-Season Drought Regime, the plants from the Miramar population had less aboveground growth than plants from the Otay Mesa population ($p = 0.0136$; Table S3; Figure 3). Populations did not differ in per-capita aboveground growth under the End-Season Drought Regime (Table S3).

The Isla Vista population was the most negatively affected by the drought regimes in terms of biomass and mortality. Plants from the Isla Vista population produced less biomass than plants from the Otay Mesa population under the Mid-Season Drought Regime ($p < 0.01$; Table S4; Figure 4), and plants from the Isla Vista population produced less biomass than plants from both the Miramar and Otay Mesa populations under the End-Season Drought Regime ($p < 0.01$; Table S4; Figure 4). Moreover, under the End-Season Drought Regime, the Isla Vista population had higher mortality than both the Miramar and Otay Mesa populations ($p < 0.01$; Table S5; Figure 5).

All plants from the Isla Vista and Otay Mesa populations failed to reproduce under both drought regimes. Only one plant from Miramar set seed under the Mid-Season Drought Regime, and none set seed under the End-Season Drought Regime. Yet, in the Control treatment, plants from the Otay Mesa population produced significantly more fruits than plants from the Miramar population ($p = 0.0054$; Table S6; Figure 6).

Effects of Competition x Drought Regimes

Similar to the treatments with individual *J. bufonius* and drought regimes, the per-capita total aboveground plant growth, aboveground plant biomass, and fruit production of *J. bufonius* plants subjected to the End-Season Drought Regime was lower than plants subjected to the Mid-Season Drought Regime, regardless of population. Mortality was not significantly affected by drought or Polyculture treatments (Table S7; Figure 7). Surprisingly, although being grown in a Polyculture with *F. perennis* vs. a Monoculture did not affect aboveground growth of *J. bufonius* plants, it caused an increase in per-capita *J. bufonius* biomass production ($p < 0.01$; Tables S8-S9; Figures 8-9). Plants from the Otay Mesa population produced the most biomass, followed by plants from the Miramar population ($p < 0.01$; Table S9; Figure 9). Plants from the Isla Vista population produced the lowest biomass of the three populations, except when grown in a Monoculture under the Mid-Season Drought Regime, wherein plants from the Miramar population produced the lowest biomass (Table S9; Figure 9).

Unlike the drought-only treatments in the previous experiment, some *J. bufonius* in the Competition x Drought treatments survived to reproduction, likely because the *J. bufonius* in

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the Competition x Drought treatments were transplanted when they were two months old (compared to the *J. bufonius* in the drought-only treatments, which were one month old at transplantation). All three populations produced fewer fruits per individual under the End-Season Drought Regime than under the Mid-Season Drought Regime ($p < 0.01$; Tables S10-S11; Figure 10). Under the End-Season Drought Regime, the Isla Vista population produced more fruits when planted in a Monoculture than when planted in a Polyculture ($p = 0.0421$) and produced more fruits than the other two populations ($p < 0.01$; Table S11; Figure 10).

The populations did not differ in their effect on *F. perennis* per-capita total aboveground growth, but they did differ in their effect on *F. perennis* mortality, per-capita fruit production, and per-capita aboveground biomass (Tables S12-S16). *F. perennis* planted in a Polyculture with *J. bufonius* from Miramar had higher mortality than *F. perennis* individuals planted in a Monoculture ($p < 0.05$; Table S13). *F. perennis* individuals planted in a Polyculture with *J. bufonius* from Otay Mesa (when subjected to Mid-Season Drought) produced fewer fruits than *F. perennis* individuals planted in a Polyculture with *J. bufonius* from Isla Vista ($p = 0.0146$; Tables S14-S15). Additionally, *F. perennis* individuals planted in Polyculture with *J. bufonius* from Otay Mesa produced lower biomass than the *F. perennis* individuals planted in a Monoculture ($p < 0.05$; Table S16).

E. Discussion

Our common garden experiment revealed intraspecific variation in the performance of *J. bufonius* from different vernal pool complexes along the south coast of California. In

particular, we found variation in different populations' responses to drought and competition treatments in an experimental greenhouse setting. Drought and competition from exotic annual grasses such as *F. perennis* pose threats to restored and natural *J. bufonius* populations existing in grassland vernal pools. In our greenhouse experiment, both end-season and mid-season drought regimes affected all three *J. bufonius* populations; however, the strength of these drought effects differed among populations. The population sourced from Isla Vista (Santa Barbara County) exhibited the highest mortality and lowest biomass production when grown under both mid- and end-season drought. The Isla Vista population also produced lower biomass than the other two populations when grown in competition with *F. perennis*, although this population did produce more fruits than the other two populations. Yet, overall, the poor performance of *J. bufonius* from Isla Vista under drought and competition suggests that *J. bufonius* from Isla Vista is not as tolerant to these stressors as other populations. In a restoration context, this suggests that provenancing seed from Isla Vista may restore populations that are intolerant of drought and invasive species and thus decrease the persistence of such populations. Because of the prevalence of *F. perennis* in Santa Barbara County and because Santa Barbara County is predicted to experience mid- and end-season drought, local provenancing from Isla Vista may jeopardize long-term restoration success of drought-intolerant populations. Indeed, local provenancing may have hindered past restoration efforts that used local provenancing, which are now exhibiting an increase in *F. perennis* and a decrease in native species over time (Tang et al. 2023).

Although local provenancing minimizes risks associated with genetic dilution and outbreeding depression, it results in a higher risk of restored populations experiencing

inbreeding depression, genetic drift, and loss of adaptive potential, especially if source

populations are small (Breed et al. 2013). Where climate is predicted to change, theory

predicts that admixture or predictive provenancing may be able to increase restoration

success if the goal is to ensure species persistence, regardless of intraspecific genetic makeup

(Havens et al. 2015). Predictive provenancing can match future climate conditions of a

restoration site with genotypes that exhibit specific adaptations to those conditions (Hancock

& Hughes 2014). Because Santa Barbara is predicted to experience mid- and end-season

drought similar to current conditions in San Diego, we hypothesized that *J. bufonius*

populations from San Diego might perform better under drought regimes. One *J. bufonius*

population sourced from Otay Mesa in San Diego County did produce the most biomass

under both drought regimes, suggesting that it is the least affected by drought. It also

produced the greatest biomass under non-drought conditions, suggesting that it is adapted to

producing more biomass regardless of climatic conditions. The Otay Mesa population also

had a much smaller average seed size than the Isla Vista population, so its greater growth

cannot be explained by seed size at planting, as has been reported for other species

(Jakobsson & Eriksson 2000). Moreover, the Otay Mesa population had the most negative

effect on *F. perennis* fruit and biomass production when grown in competition. This

suggests that this population from San Diego County has the highest drought and competition

tolerance. However, the other population from San Diego County, from Miramar, was the

population whose aboveground growth was most negatively affected by mid-season drought.

On the other hand, the Miramar population was the only population that increased the

mortality of *F. perennis* when grown in competition together. Thus, some San Diego

populations did exhibit greater drought and competition tolerance in some plant traits,

although one population did not consistently outperform the others in all plant traits and under all treatments. Because several different populations exhibited variation in their response to drought and competition, admixture provenancing may improve restoration success. Admixture provenancing can maximize genetic variation by sourcing seed from a variety of different populations, thereby increasing the capacity of the population to adapt to changing conditions (Carvalho et al. 2021; Fedriani et al. 2019). Yet, long-term studies are needed to evaluate the long-term responses of mixing genotypes, which can also be modulated by site conditions and the type of genetic variation exhibited by populations (Breed et al. 2013).

As California's winter storms become more episodic due to climate change, vernal pools can experience periodic drying and rewetting within the wet season (Pyke 2004). Our findings corroborate other studies that show that the timing and magnitude of rain and storm events affect the growth, biomass, production, survival, and reproduction of native plant populations (Liu et al. 2020). Across populations, end-season drought negatively affected biomass growth and reproduction compared to continuously inundated plants, but even mid-season drought significantly reduced biomass growth and reproduction. This suggests that severe drought conditions may cause declines of *J. bufonius* populations in Santa Barbara and San Diego vernal pools, although drought regimes imposed in greenhouse settings often exaggerate drought effects on plants because plants, water, and nutrients are constrained in pots and because potting soils differ in texture and structure from natural soils (Cerrillo et al. 2013). As such, this experiment did not allow us to evaluate intraspecific variation in fitness or adaptation because the imposed drought regimes were too severe, preventing most plants

from setting seed, and we only evaluated individual plant responses to drought within a single generation.

Given the prevalence of drought and competition at restoration sites, and the projected increase in such pressures, our results can help inform provenancing strategies for local restoration projects. For example, even though we did not find a single population with clear adaptations to drought and competition, the local Isla Vista population generally performed the worst under our imposed treatments. In contrast, the population from Otay Mesa, which is on the southern border of San Diego County with more severe drought conditions, produced the greatest biomass under all our drought and competition treatments imposed in the greenhouse, and the other San Diego County population from Miramar also caused the highest mortality of *F. perennis* when grown in competition. This suggests that admixture provenancing in Santa Barbara may capture genetic variation that may allow for the greater persistence or performance of restored populations under predicted future conditions of drought and competition. As climate models predict widespread and localized changes in temperature precipitation patterns in the future, some restoration projects choose to focus on restoring native populations that will be able to survive and reproduce under future climate conditions of restoration sites, even if this results in the loss of local genotypes. Our findings show how investigating the consequences of intraspecific variation on plant performance can inform restoration decisions.

F. Figures

Figure 1. Control replicates consisting of one plant from each of the three populations of *J. bufonius* placed in a tray of water. Drought treatments were taken out of water trays after a designated number of days.
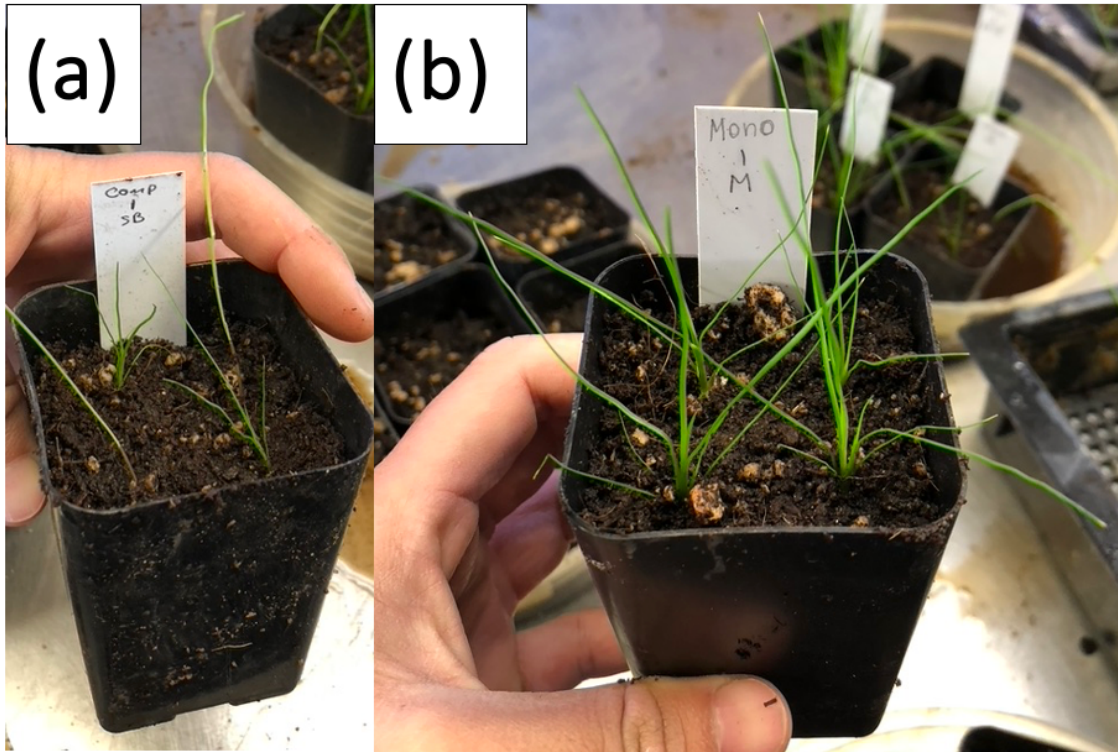
Figure 2. Polyculture (a) of *J. bufonius* planted with *F. perennis* and Monoculture (b) of *J. bufonius*. Polycultures and Monocultures with each *J. bufonius* population were placed in water trays and then taken out of water trays after a designated number of days to simulate drought regimes.
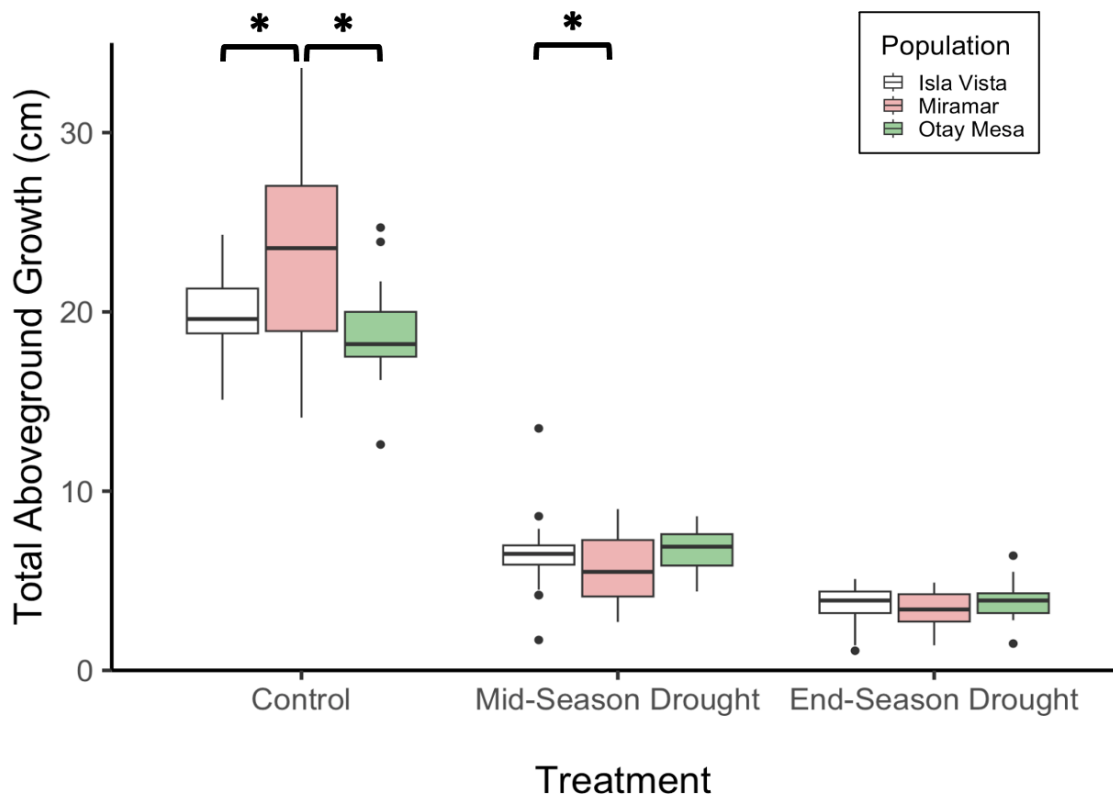
Figure 3. Drought Regime effects on aboveground growth of *J. bufonius*. Boxplots show medians and interquartile ranges of growth, with whiskers extending 1.5*IQR and outliers shown as solid points. Asterisks represent significant post-hoc Tukey comparisons ($p < 0.05$).
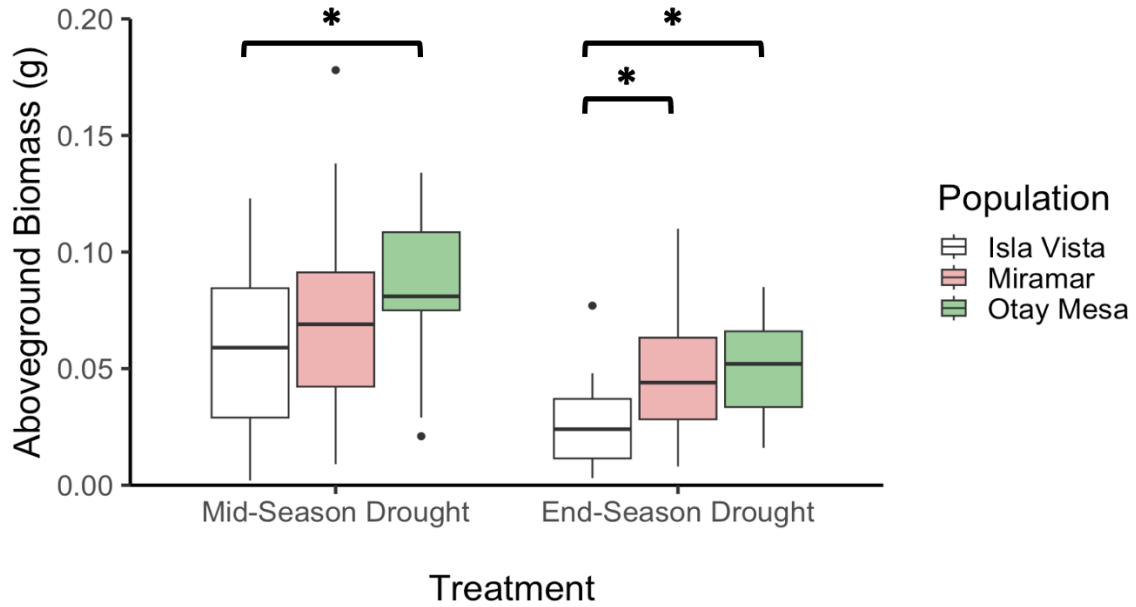
Figure 4. Drought Regime effects on aboveground biomass per plant of *J. bufonius*. Boxplots show medians and interquartile ranges of biomass, with whiskers extending 1.5*IQR and outliers shown as solid points. Asterisks represent significant post-hoc Tukey comparisons ($p < 0.05$).
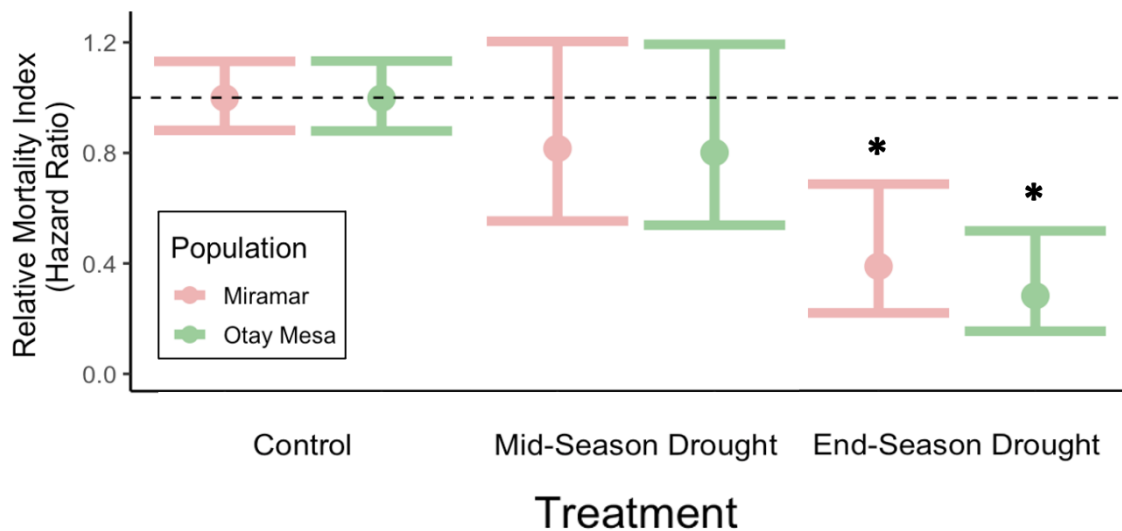

Figure 5. Drought Regime effects on weekly mortality of *J. bufonius* individuals, with 95% confidence intervals represented as error bars. A higher Hazard Ratio corresponds to

mortality higher than the Isla Vista population, which is calibrated at 1 (dashed line).

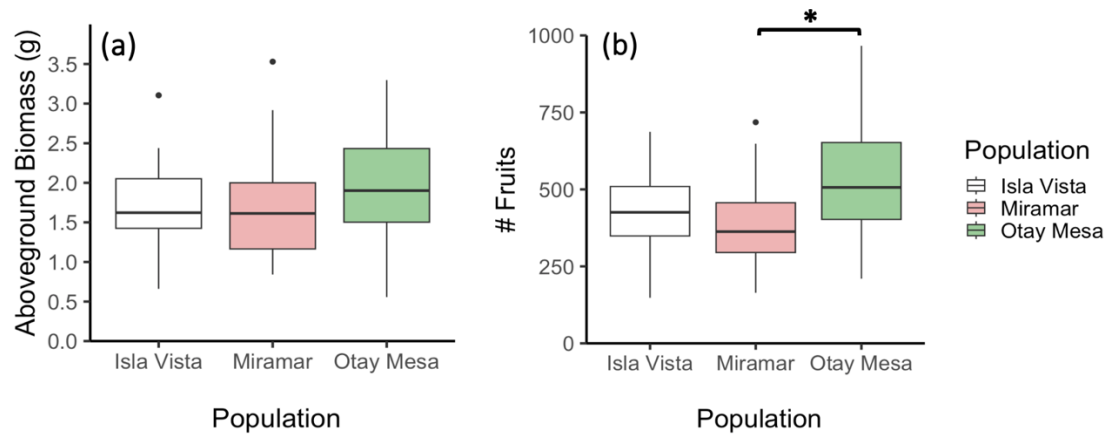Asterisks represent significant post-hoc Tukey comparisons ($p < 0.05$).

Figure 6. Aboveground biomass (a) and fruit production (b) per plant of *J. bufonius* populations under well-watered Control treatment.   Boxplots show medians and interquartile ranges, with whiskers extending 1.5*IQR and outliers shown as solid points. Asterisks represent significant post-hoc Tukey comparisons ($p < 0.05$).

Figure 7. Competition x Drought effects on weekly mortality of *J. bufonius* individuals, with 95% confidence intervals represented as error bars. A higher Hazard Ratio corresponds to mortality higher than the Isla Vista population, which is calibrated at 1 (dashed line). Asterisks represent significant post-hoc Tukey comparisons ($p < 0.05$).

Figure 8. Competition x Drought effects on total aboveground growth per plant of *J. bufonius*. Boxplots show medians and interquartile ranges of growth, with whiskers extending 1.5*IQR and outliers shown as solid points.

Figure 9. Competition x Drought Regime effects on aboveground biomass per plant of *J. bufonius*. Boxplots show medians and interquartile ranges of biomass, with whiskers extending 1.5*IQR and outliers shown as solid points. Asterisks represent significant post-hoc Tukey comparisons (*p* < 0.05).
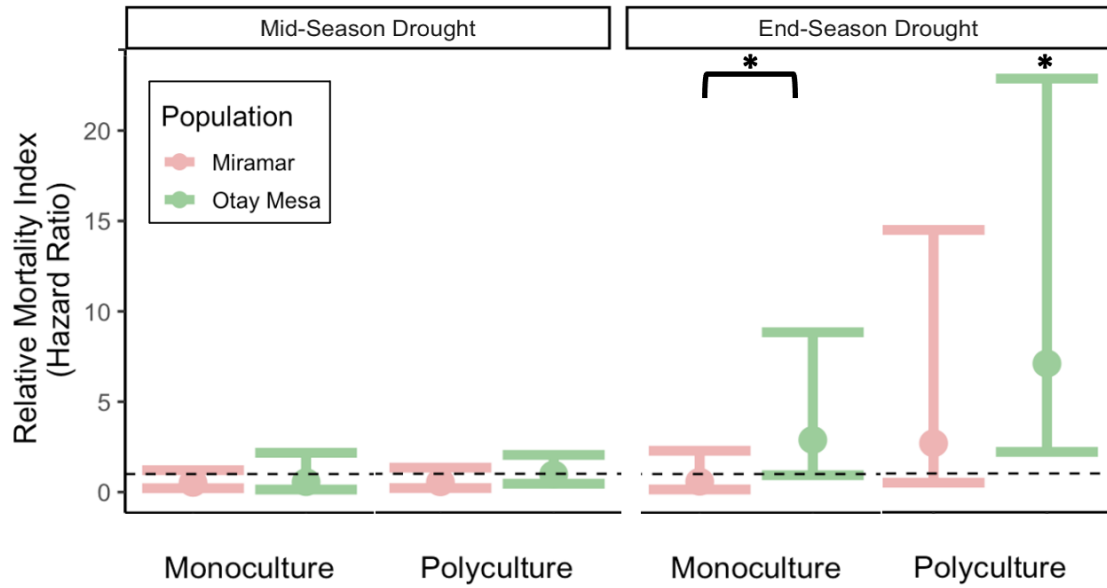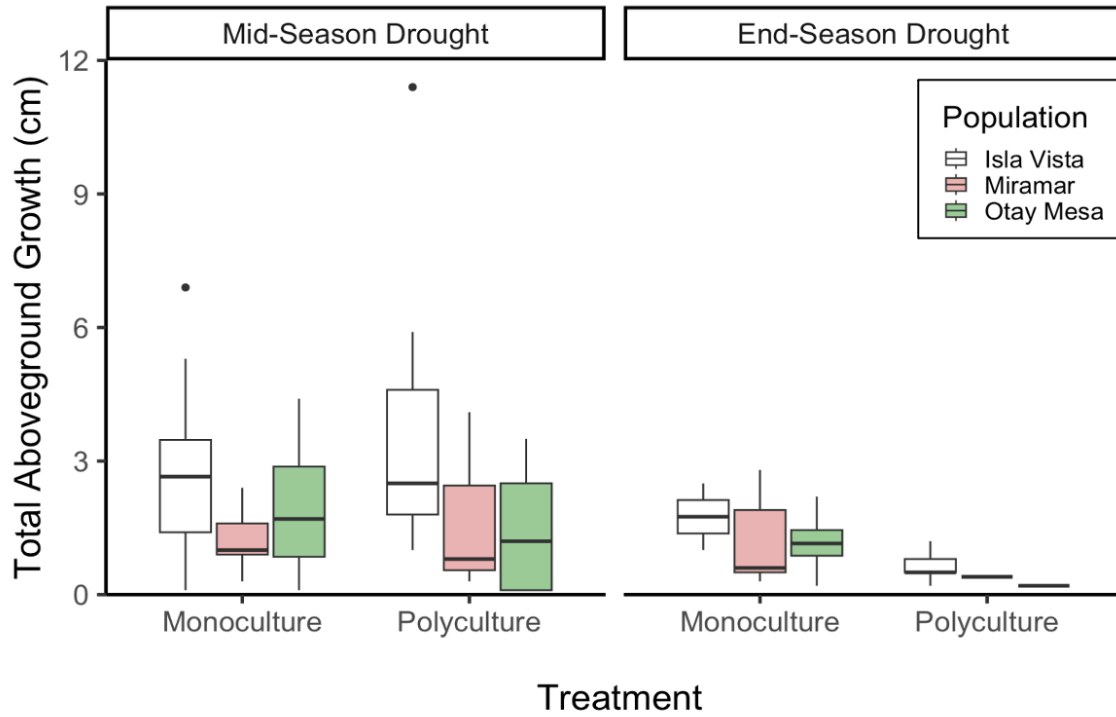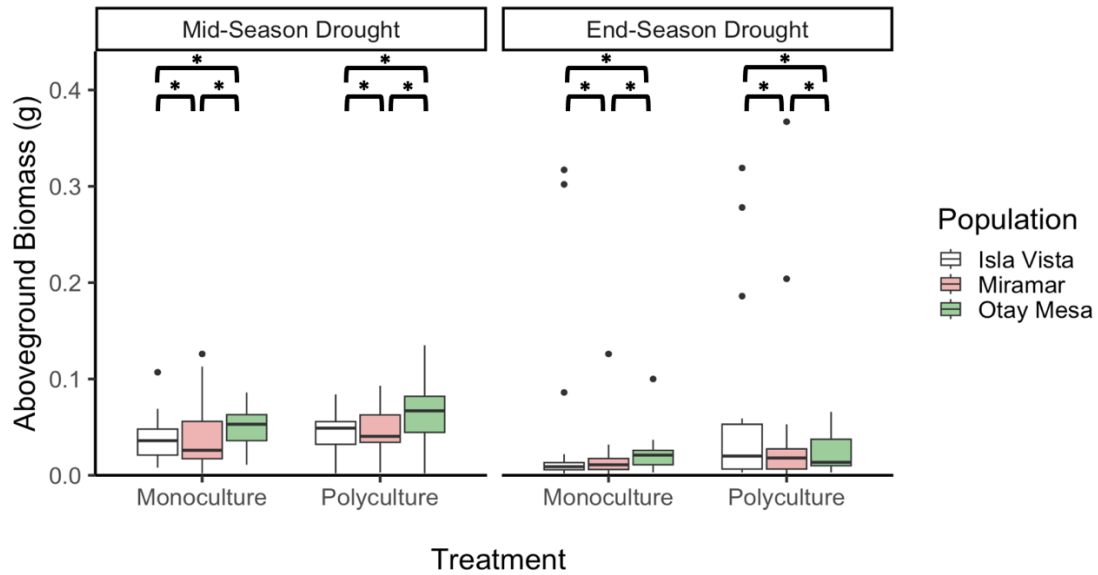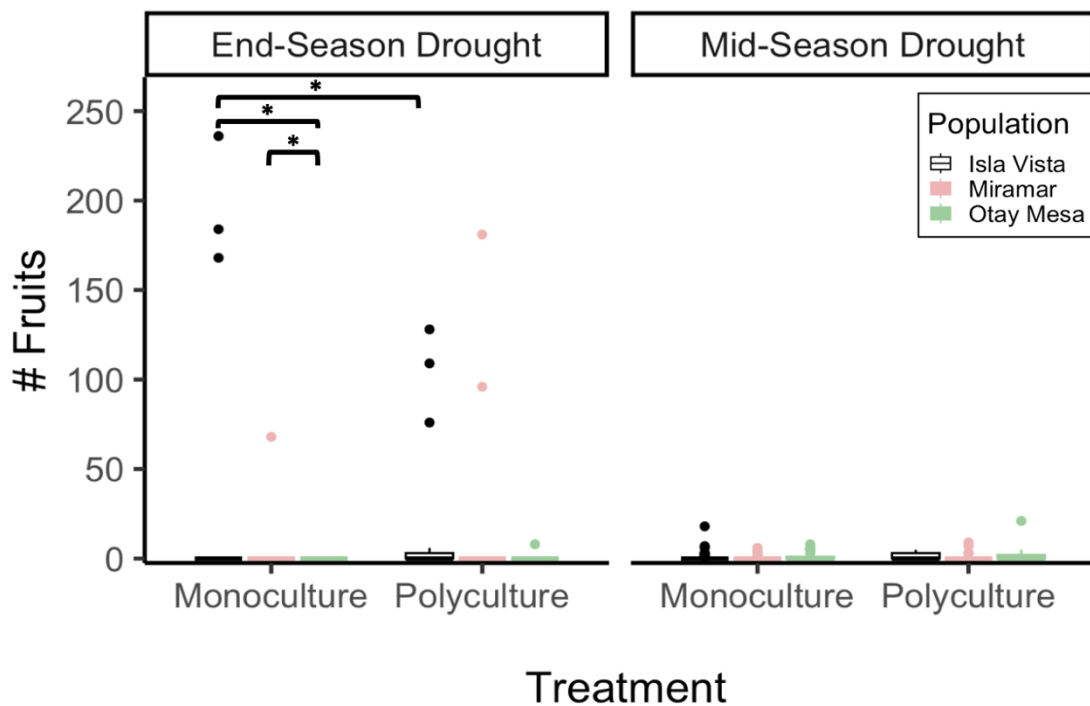
Figure 10. Competition x Drought Regime effects on fruit production per plant of *J. bufonius*. Boxplots show medians and interquartile ranges of fruits, with whiskers extending 1.5*IQR and outliers shown as solid points. Asterisks represent significant post-hoc Tukey comparisons ($p < 0.05$).

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H. Appendix C

Supplemental Information

Table S1. Calendar of treatments. From the 2019-2020 site report of Otay Mesa (San Diego County, California), which was a drought year, the center of the vernal pools remained inundated for 39 days. *Juncus bufonius* establishes populations in the transition zone, which typically remains inundated for half the number of days as the center of the pool. Thus, End-Season Drought Regime treatments were watered for 19 days. Mid-Season Drought Regime treatments followed the inundation that natural pools in Santa Barbara, California, experienced during the 2023-2024 water year, which experienced historic episodic storms punctuated. This resulted in pools being inundated for ~1 month after an early-November 2023 storm, and then drying out before being re-inundated by a late-January 2024 storm.

Date	Drought Treatments	Competition x Drought Treatments
December 14, 2023	*Juncus bufonius* seed sown in germination flats	*Juncus bufonius* seed sown in germination flats
January 18-22, 2024	Drought treatment *Juncus bufonius* transplanted from germination flats into pots; all pots placed into watering trays	
January 29, 2024		*Festuca perennis* seeds sown in germination flats
February 6, 2024	End-Season Drought pots removed from watering trays	
February 13, 2024		Competition treatment *Juncus bufonius* and *Festuca perennis* transplanted from germination flats into pots; pots placed into watering trays
February 25, 2024	Mid-Season Drought pots removed from watering trays	
March 3, 2024		End-Season Drought x Competition pots removed from watering trays

March 22, 2024		Mid-Season Drought x Competition pots removed from watering trays
April 5, 2024	Mid-Season Drought pots placed back into watering trays	
April 24, 2024		Mid-Season Drought x Competition pots placed back into watering trays
June 13, 2024	All individuals senesced	
July 19, 2024		All individuals senesced

Table S2. Differences in seed size and viability of different populations of *Juncus bufonius*.

Population	Seed size (#seeds/g, mean±SD)	Viability (mean±SD)
Isla Vista	33,785 ± 8,670	0.10 ± 0.020
Miramar	63,945 ± 2,677	0.067 ± 0.031
Otay Mesa	50.314 ± 8,560	0.073 ± 0.012

Table S3. ANOVA table of GLM of population and drought treatments on total aboveground growth per plant of *Juncus bufonius*, compared to the Isla Vista population under well-watered Control treatment. Bold values are significant at $p < 0.05$.

Predictors	Total aboveground growth (cm)		
	Estimates	CI	p
(Intercept)	2.99	2.90 – 3.09	**<0.001**
population [Miramar]	0.17	0.04 – 0.30	**0.010**
population [Otay Mesa]	-0.06	-0.19 – 0.07	0.382
treatment [Mid-Season]	-1.13	-1.26 – -1.00	**<0.001**
treatment [End-Season]	-1.69	-1.83 – -1.56	**<0.001**
population [Miramar] × treatment [Mid-Season]	-0.30	-0.47 – -0.12	**0.001**
population [Otay Mesa] × treatment [Mid-Season]	0.10	-0.07 – 0.28	0.252
population [Miramar] × treatment [End-Season]	-0.25	-0.44 – -0.06	**0.009**
population [Otay Mesa] × treatment [End-Season]	0.13	-0.05 – 0.32	0.157
Observations	258		
R^2 Nagelkerke	0.915		

Table S4. ANOVA table of GLM of population and drought treatments on aboveground biomass per plant of *Juncus bufonius*, compared to the Isla Vista population under well-watered Control treatment. Bold values are significant at $p < 0.05$.

Predictors	Aboveground biomass (g)		
	Estimates	*CI*	*p*
(Intercept)	0.54	0.37 – 0.72	**<0.001**
population [Miramar]	-0.02	-0.27 – 0.22	0.854
population [Otay Mesa]	0.15	-0.10 – 0.39	0.240
treatment [Mid-Season Drought]	-3.37	-3.62 – -3.13	**<0.001**
treatment [End-Season Drought]	-4.20	-4.45 – -3.96	**<0.001**
population [Miramar] × treatment [Mid-Season Drought]	0.20	-0.15 – 0.54	0.263
population [Otay Mesa] × treatment [Mid-Season Drought]	0.21	-0.14 – 0.56	0.233
population [Miramar] × treatment [End-Season Drought]	0.61	0.27 – 0.96	**<0.001**
population [Otay Mesa] × treatment [End-Season Drought]	0.52	0.17 – 0.87	**0.003**
Observations	249		
R^2 Nagelkerke	0.982		

Table S5. Cox proportional hazards model of population and treatment effects on weekly mortality of *Juncus bufonius* individuals, compared to the Isla Vista population under well-watered Control treatment. Higher Hazard Ratio (HR) estimate indicates higher mortality.

Bold values are significant at $p < 0.05$.

Characteristic	HR[1]	95% CI[1]	p-value
treatment			
Control	—	—	
Mid-Season Drought	487	183, 1,297	**<0.001**
End-Season Drought	6,478	1,941, 21,617	**<0.001**
population			
Isla Vista	—	—	
Miramar	1.00	0.88, 1.13	>0.9
Otay Mesa	1.00	0.88, 1.13	>0.9
treatment * population			
Mid-Season * Miramar	0.84	0.58, 1.21	0.3
End-Season * Miramar	0.37	0.20, 0.65	**<0.001**
Mid-Season * Otay Mesa	0.82	0.56, 1.20	0.3
End-Season * Otay Mesa	0.25	0.14, 0.45	**<0.001**

[1] HR = Hazard Ratio, CI = Confidence Interval

Table S6. ANOVA table of Poisson hurdle GLM of population on fruit production per plant of *Juncus bufonius* under well-watered Control treatment, compared to the Isla Vista population. Bold values are significant at $p < 0.05$.

Predictors	Number of fruits		
	Log-Mean	CI	p
(Intercept)	6.09	5.96 – 6.21	**<0.001**
population [Miramar]	-0.07	-0.25 – 0.11	0.428
population [Otay Mesa]	0.21	0.03 – 0.38	**0.021**
treatment [drought]	-3.71	-4.63 – -2.78	**<0.001**
Observations	85		
R^2 Nagelkerke	0.593		

Table S7. Cox proportional hazards model of population and Competition x Drought treatments on weekly mortality of *Juncus bufonius* individuals, compared to the Isla Vista population planted in a Monoculture under End-Season Drought Regime. Higher Hazard Ratio (HR) estimate indicates higher mortality. Bold values are significant at $p < 0.05$.

Characteristic	HR[1]	95% CI[1]	p-value
competition treatment			
Monoculture	—	—	
Polyculture	0.27	0.05, 1.53	0.14
population			
Isla Vista	—	—	
Miramar	0.51	0.09, 2.71	0.4
Otay Mesa	4.52	1.05, 19.5	0.043
drought regime			
End-Season Drought	—	—	
Mid-Season Drought	0.87	0.24, 3.08	0.8
competition * population			
Polyculture * M	5.95	0.42, 84.0	0.2
Polyculture * A	3.93	0.55, 28.2	0.2
competition * drought regime			
Polyculture * Mid-Season Drought	3.78	0.61, 23.4	0.2
population * **drought regime**			
Miramar * Mid-Season	1.13	0.19, 6.77	0.9
Otay Mesa * Mid-Season	0.14	0.02, 0.82	0.029
competition * population * drought regime			
Polyculture * Miramar * Mid-Season	0.19	0.01, 3.13	0.2
Polyculture * Otay Mesa * Mid-Season	0.38	0.04, 3.68	0.4

[1] HR = Hazard Ratio, CI = Confidence Interval

Table S8. ANOVA table of GLM of population and Competition x Drought treatments on

total aboveground growth per plant of *Juncus bufonius*, compared to the Isla Vista population

planted in a Monoculture under Mid-Season Drought Regime. Bold values are significant at

$p < 0.05$.

Predictors	Total aboveground growth (cm)		
	Estimates	*CI*	*p*
(Intercept)	1.01	0.63 – 1.45	**<0.001**
population [Miramar]	-0.79	-1.55 – 0.07	0.051
population [Otay Mesa]	-0.31	-0.94 – 0.34	0.337
drought [End-Season]	-0.45	-1.47 – 0.92	0.447
treatment [Monoculture]	0.25	-0.34 – 0.85	0.398
population [Miramar] × drought [End-Season]	0.43	-1.21 – 1.87	0.574
population [Otay Mesa] × drought [End-Season]	-0.09	-1.69 – 1.34	0.907
population [Miramar] × competition [Monoculture]	0.08	-1.16 – 1.41	0.901
population [Otay Mesa] × competition [Monoculture]	-0.56	-1.57 – 0.50	0.284
inundation [End-Season] × competition [Monoculture]	-1.26	-2.81 – 0.09	0.080
(population [Miramar] × drought [End-Season]) × competition [Monoculture]	-0.19	-2.54 – 2.52	0.880
(population [Otay Mesa] × drought [End-Season]) × competition [Monoculture]	-0.20	-2.46 – 2.44	0.866
Observations	68		
R² Nagelkerke	0.387		

Table S9. ANOVA table of GLMM of population and Competition x Drought treatments on aboveground biomass per plant of *Juncus bufonius*, compared to the Isla Vista population planted in a Monoculture under Mid-Season Drought Regime. Bold values are significant at $p < 0.05$.

Predictors	Aboveground biomass (g)		
	Estimates	*CI*	*p*
(Intercept)	-3.05	-3.05 – -3.05	**<0.001**
treatment [Polyculture]	0.18	0.18 – 0.18	**<0.001**
population [Miramar]	-0.08	-0.08 – -0.08	**<0.001**
population [Otay Mesa]	0.32	0.32 – 0.32	**<0.001**
drought [End-Season]	-1.05	-1.05 – -1.05	**<0.001**
competition [Polyculture] × population [Miramar]	0.17	0.17 – 0.17	**<0.001**
competition [Polyculture] × population [Otay Mesa]	0.05	0.04 – 0.05	**<0.001**
competition [Polyculture] × drought [End-Season]	0.24	0.23 – 0.24	**<0.001**
population [Miramar] × drought [End-Season]	0.16	0.16 – 0.16	**<0.001**
population [Otay Mesa] × drought [End-Season]	0.37	0.37 – 0.37	**<0.001**
(competition [Polyculture] × population [Miramar]) × drought [End-Season]	-0.23	-0.24 – -0.23	**<0.001**
(competition [Polyculture] × population [Otay Mesa]) × drought [End-Season]	-0.41	-0.42 – -0.41	**<0.001**

Random Effects

σ^2	0.46
$\tau_{00\ pot}$	0.02

$\tau_{00 \text{ date\_senesced}}$	0.64		
ICC	0.59		
N $_{pot}$	20		
N $_{date\_senesced}$	19		
Observations	327		
Marginal R^2 / Conditional R^2	0.184 / 0.667		

Table S10. ANOVA table of negative binomial hurdle GLMM of population and Competition x Drought treatments on absence of fruit production of *Juncus bufonius* individuals, compared to the Isla Vista population planted in a Monoculture under End-Season Drought Regime. Bold values are significant at *p* < 0.05.

	Absence of fruits		
Predictors	*Log-Odds*	*CI*	*p*
Count Model			
(Intercept)	2.69	1.32 – 4.06	**<0.001**
population [Miramar]	0.40	-1.49 – 2.29	0.678
population [Otay Mesa]	26.23	-533876.63 – 533929.10	1.000
competition [Polyculture]	-1.47	-3.19 – 0.25	0.093
drought [Mid-Season]	-1.37	-3.04 – 0.31	0.109
population [Miramar] × competition [Polyculture]	0.73	-1.99 – 3.44	0.599
population [Otay Mesa] × treatment [Polyculture]	-24.27	-533927.14 – 533878.59	1.000
population [Miramar] × drought [Mid-Season]	0.27	-1.98 – 2.52	0.815
population [Otay Mesa] × drought [Mid-Season]	-26.39	-533929.26 – 533876.48	1.000
competition [Polyculture] × drought [Mid-Season]	0.65	-1.49 – 2.78	0.554

Predictors			
(population [Miramar] × competition [Polyculture]) × drought [Mid-Season]	-0.44	-3.79 – 2.91	0.799
(population [Otay Mesa] × competition [Polyculture]) × drought [Mid-Season]	24.55	-533878.32 – 533927.41	1.000
Zero-Inflated Model			
(Intercept)	-21.96	-15937.24 – 15893.33	0.998
Random Effects			
σ^2	3.29		
$\tau_{00\ pot}$	0.80		
ICC	0.20		
N_{pot}	20		
Observations	329		
Marginal R^2 / Conditional R^2	0.946 / 0.957		

Table S11. ANOVA table of Poisson hurdle GLMM of population and Competition x Drought treatments on fruit production per plant of *Juncus bufonius*, compared to the Isla Vista population planted in a Monoculture under End-Season Drought Regime. Bold values are significant at $p < 0.05$.

	Number of fruits		
Predictors	*Log-Mean*	*CI*	*p*
Count Model			
(Intercept)	5.28	4.63 – 5.93	**<0.001**
population [Miramar]	0.41	-0.62 – 1.44	0.436
population [Otay]	-3.03	-4.79 – -1.27	**0.001**
competition [Polyculture]	-0.90	-1.77 – -0.03	**0.042**
drought [Mid-Season]	-3.71	-4.52 – -2.91	**<0.001**

population [Miramar] × competition [Polyculture]	0.14	-1.28 – 1.57	0.844
population [Otay Mesa] × competition [Polyculture]	0.73	-0.28 – 1.75	0.158
population [Miramar] × drought [Mid-Season]	-0.72	-2.02 – 0.58	0.276
population [Otay Mesa] × drought [Mid-Season]	2.90	1.28 – 4.53	**<0.001**
competition [Polyculture] × drought [Mid-Season]	0.47	-0.66 – 1.61	0.413
(population [Miramar] × competition [Polyculture]) × drought [Mid-Season]	0.73	-1.12 – 2.59	0.439
(Intercept)	3.06	1.87 – 5.00	

Zero-Inflated Model

(Intercept)	-22.02	-15888.46 – 15844.42	0.998

Random Effects

σ^2	0.00
$\tau_{00\ pot}$	0.00
ICC	1.00
N_{pot}	15
Observations	56
Marginal R^2 / Conditional R^2	1.000 / 1.000

Table S12. ANOVA table of GLM of population and Competition x Drought treatments on total aboveground growth per plant of *Festuca perennis*, compared to the Monoculture planted under End-Season Drought Regime. Bold values are significant at $p < 0.05$.

Total aboveground growth (cm)		
Predictors	*Estimates*	*CI*	*p*

	Estimates	CI	p
(Intercept)	2.56	1.59 – 3.98	**<0.001**
population [Isla Vista]	0.84	-1.02 – 3.02	0.378
population [Miramar]	-2.19	-3.96 – -0.30	**0.013**
population [Otay Mesa]	-0.19	-2.05 – 1.99	0.841
drought [Mid-Season]	0.42	-1.35 – 2.31	0.629
population [Isla Vista] × drought [Mid-Season]	-1.64	-4.43 – 0.99	0.218
population [Miramar] × drought [Mid-Season]	0.14	-2.66 – 3.31	0.922
population [Otay Mesa] × drought [Mid-Season]	-3.48	-6.71 – 1.17	**0.046**
Observations	26		
R^2 Nagelkerke	0.616		

Table S13. Cox proportional hazards model of population and Competition x Drought treatments on weekly mortality of *Festuca perennis* individuals, compared to the Monoculture planted under End-Season Drought Regime. Higher Hazard Ratio (HR) estimate indicates higher mortality. Bold values are significant at $p < 0.05$.

Characteristic	HR[1]	95% CI[1]	p-value
population			
F. perennis (monoculture)	—	—	
Isla Vista *J. bufonius*	1.20	0.42, 3.43	0.7
Miramar *J. bufonius*	3.58	1.17, 11.0	**0.025**
Otay Mesa *J. bufonius*	2.54	0.97, 6.62	0.057
drought regime			
End–Season Drought	—	—	
Mid–Season Drought	0.82	0.33, 2.01	0.7
population * drought regime			
Isla Vista * Mid–Season	1.46	0.38, 5.65	0.6
Miramar * Mid–Season	0.62	0.13, 2.98	0.6
Otay Mesa * Mid–Season	0.45	0.09, 2.20	0.3

[1] HR = Hazard Ratio, CI = Confidence Interval

Table S14. ANOVA table of negative binomial hurdle GLMM of population and Competition x Drought treatments on absence of fruits of *Festuca perennis* individuals, compared to the Monoculture planted under End-Season Drought Regime. Bold values are significant at *p* < 0.05.

	Absence of fruits		
Predictors	*Log-Odds*	*CI*	*p*
Count Model			
(Intercept)	1.29	-0.62 – 3.20	0.185
population [Isla Vista]	0.92	-0.84 – 2.68	0.307
population [Miramar]	2.34	0.31 – 4.38	**0.024**
population [Otay Mesa]	25.05	-133787.53 – 133837.62	1.000
inundation [Mid-Season]	-0.17	-2.63 – 2.29	0.892
population [Isla Vista] × drought [Mid-Season]	-0.18	-2.64 – 2.28	0.888
population [Miramar] × drought [Mid-Season]	-0.65	-3.45 – 2.15	0.649
population [Otay Mesa] × drought [Mid-Season]	-25.50	-133838.08 – 133787.08	1.000
Zero-Inflated Model			
(Intercept)	-22.48	-19732.37 – 19687.42	0.998
Random Effects			
σ^2	3.29		
$\tau_{00 \ pot}$	4.97		
ICC	0.60		
N $_{pot}$	20		
Observations	164		
Marginal R^2 / Conditional R^2	0.836 / 0.934		

Table S15. ANOVA table of Poisson hurdle GLMM of population and Competition x

Drought treatments on total aboveground growth per plant of *Festuca perennis*, compared to

the Monoculture planted under End-Season Drought Regime. Bold values are significant at *p*

< 0.05.

	number fruits		
Predictors	Log-Mean	CI	p
Count Model			
(Intercept)	4.64	4.17 – 5.11	**<0.001**
population [Isla Vista]	-0.20	-1.17 – 0.76	0.681
population [Miramar]	0.57	-0.71 – 1.85	0.382
population [Otay Mesa]	-0.58	-1.36 – 0.19	0.141
drought [Mid-Season]	-0.35	-0.99 – 0.30	0.291
population [Isla Vista] × drought [Mid-Season]	1.24	-0.12 – 2.59	0.073
population [Miramar] × drought [Mid-Season]	-1.19	-3.00 – 0.62	0.198
(Intercept)	1.37	0.93 – 2.01	
Zero-Inflated Model			
(Intercept)	-21.30	-12085.53 – 12042.93	0.997
Random Effects			
σ^2	0.00		
$\tau_{00\ pot}$	0.00		
ICC	1.00		
N $_{pot}$	11		
Observations	47		
Marginal R^2 / Conditional R^2	1.000 / 1.000		

Table S16. ANOVA table of GLMM of population and Competition x Drought treatments on aboveground biomass per plant of *Festuca perennis*, compared to the Monoculture planted under End-Season Drought Regime. Bold values are significant at *p* < 0.05.

	Aboveground biomass (g)		
Predictors	Estimates	CI	p

(Intercept)	-3.08	-3.72 – -2.44	**<0.001**
population [Isla Vista]	-0.26	-0.65 – 0.14	0.201
population [Miramar]	-0.23	-0.61 – 0.15	0.226
population [Otay Mesa]	-0.49	-0.85 – -0.13	**0.008**
drought [End-Season]	-0.37	-0.80 – 0.06	0.090
population [Isla Vista] × drought [End-Season]	-0.03	-0.57 – 0.50	0.902
population [Miramar] × drought [End-Season]	0.12	-0.40 – 0.63	0.654
population [Otay Mesa] × drought [End-Season]	-0.09	-0.64 – 0.47	0.760

Random Effects

σ^2	0.32
$\tau_{00\ pot}$	0.04
$\tau_{00\ date\_senesced}$	0.54
ICC	0.64
N_{pot}	20
$N_{date\_senesced}$	17
Observations	149
Marginal R^2 / Conditional R^2	0.074 / 0.669