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RESEARCH ARTICLE

Vernal pool wetlands respond to livestock grazing, exclusion and reintroduction

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Handling Editor: Joseph Bennett**Abstract**

1. In disturbance-adapted ecosystems, the removal of disturbance can lead to losses of diversity and sometimes irreversible changes in community composition. It is important to identify the thresholds at which these changes can occur, and to understand the reversibility of these shifts. We examined this question in a vernal pool ecosystem that evolved with low to moderate levels of grazing disturbance. In this system, it is not clear whether the negative effects of long-term grazing exclusion are reversible through grazing reintroduction.
2. We compared adjacent vernal pool wetlands in annual Mediterranean grasslands under three grazing management strategies: continuously grazed (100+ years), long-term excluded (40+ years) and 2 years of reintroduced grazing. We also asked whether grazing treatments altered pool characteristics that are likely to influence plant community composition, and how these relationships changed with environmental conditions.
3. Reintroducing grazing to vernal pools led to both increased diversity and native cover, but the effects on native cover were more immediate than on diversity. We identified several biotic and abiotic mechanisms related to this pattern, including changes to competitive dynamics that favour small statured native annuals and increases in hoofprint microdepressions that make soil moisture more available to plants.
4. *Synthesis and applications.* Our results show that reintroduced grazing at moderate stocking rates can have significant effects on plant communities after just 2 years and can increase native cover more quickly than overall diversity. Our findings suggest that the negative effects of long-term grazing exclusion in vernal pools may be reversible, but that land managers interested in restoring diversity should plan to monitor beyond the first two years of grazing reintroduction.

KEYWORDS

biodiversity, disturbance, grazing, native cover, reintroduction, threshold, vernal pools, wetland restoration

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1 | INTRODUCTION

Grazing by livestock is the most extensive anthropogenic land use worldwide (Ellis & Ramankutty, 2008). Livestock grazing is of particular interest to conservation managers, as grazing disturbance can have strong influences on ecosystems that can be either beneficial or detrimental to biodiversity. While overgrazing by livestock has led to large declines in biodiversity across the globe, grazing at low to moderate stocking rates can promote plant diversity and native cover in several systems including Mediterranean and semi-arid grasslands, subtropical wetlands and wet heath wetlands (Adler et al., 2001; Milchunas et al., 1988; Osem et al., 2002; Stahlheber & D'Antonio, 2013). This is particularly true in systems where biodiversity is limited by invasive cover and where grazing can reduce the dominance of these species (e.g. Koerner et al., 2018; Roche et al., 2015; Van den Broeck, 2019). Likewise, the complete removal of grazing disturbance from ecosystems that were previously grazed can result in biodiversity losses in a variety of ecosystems, from sagebrush steppe to subtropical wetlands (Barry, 1995; Boughton et al., 2016; Groome & Shaw, 2015; Marty, 2015; Porensky et al., 2020). This has led to increased interest in using livestock for conservation purposes, including the reintroduction of livestock to areas that have been under prolonged grazing rest (Gornish et al., 2018; Groome & Shaw, 2015).

Disturbance-adapted ecosystems, including those that evolved under fire, flood or grazing by native ungulates, are especially vulnerable to long-term removal of disturbance regimes (Holl, 2020). As practitioners consider returning disturbance to these landscapes for restoration purposes, they increasingly draw upon models of ecosystem dynamics to guide their actions (Holl, 2020; Ma et al., 2021). These models predict that changes in environmental conditions can follow several different trajectories as they transition to and from degraded states (Bestelmeyer et al., 2013; Scheffer et al., 2009). Some transitions appear to be reversible, in which restoring disturbance to its original level can reverse biodiversity losses. Others can cross a threshold into an alternate stable state, at which point restoring the disturbance to its original level will not lead to recovery (Bestelmeyer et al., 2013) because of strong environmental feedbacks (Ma et al., 2021). Understanding the reversibility of these dynamics can be critical to designing effective conservation and restoration management plans (Palmer et al., 2016).

Threshold dynamics have been well studied in grassland systems in which heavy grazing has led to biodiversity declines and woody encroachment (Bestelmeyer et al., 2013; Lipoma et al., 2021). There is increasing evidence that these dynamics are reversible in semi-arid grassland ecosystems (Kleinhesselink, 2020). However, there is less understanding of threshold dynamics in ecosystems which are adapted to low levels of grazing, and in which the degradation is caused by the complete removal of grazing. This is because the body of literature documenting the outcomes of grazing reintroduction at conservation stocking rates is relatively small (Boughton et al., 2016; Gornish et al., 2018; Stahlheber & D'Antonio, 2013). The reintroduction of grazing to lands that were previously excluded from grazing

provides an excellent opportunity to study the thresholds at which these alternate states occur, and to understand the reversibility of these shifts.

In California grasslands, grazing is currently a widespread management practice for livestock cultivation, wildfire reduction and exotic species control. Relatively, little is known about the natural history of this ecosystem prior to the arrival of the Spanish in the 1700s, but it has been suggested that these grasslands were widely grazed by ungulates such as Tule elk and small granivores. Eurasian exotic annual grasses now dominate the uplands, leaving only small patches of native plants (Stromberg et al., 2007). There is growing interest in the use of livestock grazing to promote diversity in these ecosystems, where low to moderate stocking rates generally select against perennials, taller plants and graminoids, and promotes small-statured forbs (Stahlheber & D'Antonio, 2013).

Grazing is also a key management tool for the seasonally flooded depressions within grasslands known as vernal pools, which are among the Californian bioregion's most important and critically threatened reservoirs of endemic plant diversity. In these pools, inundation prevents the encroachment of invasive upland grasses and forbs and selects for native species that are adapted to longer hydroperiods (Bartolome et al., 2014). Many of the remaining vernal pools are located on commercial ranches which have a long history (>200 years) of grazing by domestic livestock during the winter and spring growing season (Stalheber & D'Antonio, 2013). In the past, grazing was assumed to negatively impact these pools and the endemic species they support, and livestock were removed from some protected areas as a result (Joyce, 1989). However, grazing exclusion can result in loss of plant diversity and native plant cover in these systems (Marty, 2005, 2015)—a finding congruent with research in other wetlands demonstrating that plant community response to grazing is context dependent (e.g. Boughton et al., 2016; Jones et al., 2011; Sonnier et al., 2018; Van den Broeck et al., 2019). In California, these findings have encouraged the reintroduction of grazing to lands that were excluded from grazing several decades ago with the goal to conserve vernal pool ecosystems.

It is possible that grazing reintroduction may have novel effects on plant communities when contrasted to the effects long-term grazing. In addition to direct defoliation, livestock interact with several abiotic pool characteristics (Gerhardt & Collinge, 2003). For example, reintroducing grazing may influence the availability and duration of standing water in a different way than the influence of long-term grazing (Marty, 2015). Livestock enter the pools to drink and graze, potentially increasing standing water (a) in local (<1 m²) patches as hoofprint trampling create pockets of lower, wet habitat (Barry, 1995), and (b) at the scale of the whole pool, as trampling can lead to changes to soil compaction and/or water-holding capacity (Marty, 2005, 2015). Hoofprint microdepressions may be most pronounced in uncompacted soil when grazing is first reintroduced, while soil compaction may steadily increase over time with grazing, leading to a gradual reduction in hoofprint microdepressions (Robins & Vollmar, 2002). These differences in

soil surface texture and compaction may contribute to differences in plant community composition and diversity (Díaz et al., 2007; Hayes & Holl, 2003).

In this study, we took advantage of a unique opportunity to examine differences in vernal pools subject to long-term livestock exclusion, long-term continuous livestock access and recent reintroduction of livestock on a mitigation property designated for vernal pool conservation. We addressed the following questions:

1. How do plant diversity and native plant cover differ in response to: continuous livestock grazing (100+ years), long-term (40+ years) grazing exclusion and 2 years of reintroduced continuous grazing after long-term grazing exclusion?
2. To what extent are pool characteristics correlated with plant diversity and cover, and does grazing treatment interact with these pool characteristics?

We hypothesized that the vernal pools would exhibit reversible dynamics in response to grazing reintroduction, rather than threshold dynamics or alternative stable states. Under this model, the pools in which grazing was reintroduced would have higher diversity and native species abundance compared to pools that had been continuously excluded from grazing. The pools with grazing reintroduction would have lower diversity and native species abundance than the long-term continuously grazed pools, as the community composition moves along a trajectory towards one increasingly similar to the continuously grazed pools.

We further hypothesized that the abiotic characteristics would differ between long-term and reintroduced grazing treatments. For example, we expected pools with recently reintroduced grazing to have the most hoofprint microdepressions, which could provide more heterogeneous habitat including refugia for native plants. Long-term grazed pools, on the other hand, may likely have more compacted soil, and therefore hold standing water for a longer duration than short-term grazing or grazing exclusion treatments. Because inundation is one of the dominant factors driving plant communities in vernal pools (Bartolome et al., 2014), we also predicted that the long-term grazed pools would exhibit the highest levels of diversity out of the three treatments, in part because they should have the greatest hydroperiod (Marty, 2015).

2 | MATERIALS AND METHODS

2.1 | Site characteristics

Rancho Seco (38.34°N, -121.11°W) is a 458.10-ha site in Northern California that consists of Mediterranean grassland with vernal pools. Rancho Seco hosts Northern Hardpan vernal pools which span a range of characteristics, including soil type (Redding Gravelly Loam and Corning Complex) and pool size (9.16–336.94 m²), which influence plant composition at this site (Michaels et al., 2021), and across vernal pools, in general (Kneitel, 2015). The climate is Mediterranean

with an average annual precipitation of 526.2 mm per water year (CIMIS Weather Station, 21-year avg. 1997–2018, Fair Oaks, CA). Annual plants germinate with the first significant fall rains (generally October–November), flower as the rainy season ends (April–May) and seeds are dormant through the dry summers.

Most of the site has been grazed continuously with commercial beef cattle for over 100 years. Over the past 20 years, mean annual stocking rate has been 0.31 Animal Unit Year (AUY) per hectare with a 9-month grazing season from October through June, which is considered low to moderate for commercial cattle operations in the region. Livestock were excluded from a portion of this site in the 1970s after a fence was built to restrict access to a nearby reservoir. In January 2016, this fence was removed under the instruction of conservation agencies to control exotic species in the uplands and to increase diversity benefits to the excluded pools (Marty, 2015). Temporary electric fencing was used to prevent grazing on some pools in the area where cattle were being reintroduced, creating three different grazing management areas across the landscape: (a) grazing exclusion, (b) short-term grazed and (c) long-term grazed. All grazed pools had the same stocking rate (0.31 Animal Unit Year [AUY] per hectare, October–June) and cattle were free to move across all pools except for the pools inside the electric fences (Figure 1).

2.2 | Pool selection

Prior to the removal of the fence, we characterized 51 grazed and 37 ungrazed pools (by size, depth, catchment area size and underlying soil type). Of the pools that we characterized, we selected 36 total pools to compare: 12 long-term grazed, 12 short-term grazed (newly exposed to grazing) and 12 grazing exclusion (achieved by constructing temporary electric fencing around those pools between 10 and 30 m from the pool edge; Figure 1). We matched each long-term grazed pool with a short-term grazed and grazing exclusion pool with the same soil type and similar in size. Collectively, the 12 replicate pools for each treatment represented a range of pool characteristics present at the site (see Appendix S1). Due to the fence design, the short-term grazed pools were located in the same Eastern portion of the pasture. However, vegetation surveys at this site conducted in the same pools in the 2 years prior showed no spatial autocorrelation at the site (Michaels, 2020).

2.3 | Pool basin depth and catchment size

After the pools were selected, we also characterized each pool by basin depth (cm) and catchment area (m²) to account for these additional factors that may affect vegetation characteristics at the pool scale. We calculated basin depth using a Real Time Kinematic (RTK) geographic positioning system (GPS), subtracting the height of the lowest point in the pool from points taken at the highest edge of the basin perimeter. Basin depth remains constant in vernal pools

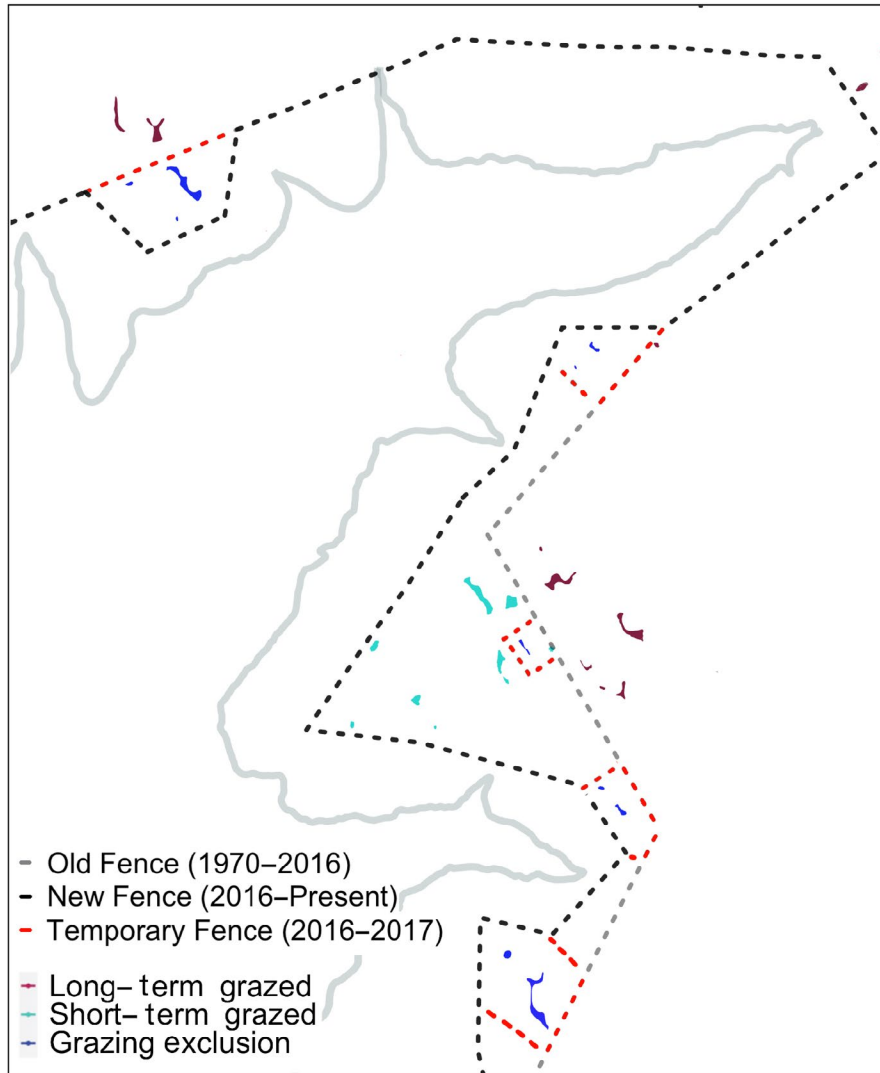


FIGURE 1 Site map. Grey solid line indicates the perimeter of the reservoir. The grey dotted line represents the perimeter of the old fence (removed in fall 2016), and the black dotted line represents the new fence (constructed in fall 2016). The red dotted lines represent the temporary electric fencing constructed to prevent grazing reintroduction

while surface water level fluctuates. In some pools, large mounds on the perimeter lead to particularly 'deep' basins, with depth ranging from 53.95 to 516.64 cm. We also calculated catchment as the area of upland from which each individual pool collects surface and groundwater using RTK GPS points collected at 3–10 m intervals while walking transects across the landscape. A single upland point could be designated to multiple pool catchments, and if a pool was deeper than a neighbouring one, we included catchment area of both. These points were processed using Surfer software (version 16; Golden Software, Golden CO). Pool catchment area ranged from 39 to 5,029 m² (Appendix S1).

2.4 | Vegetation monitoring

We focused our sampling efforts in the transition zone ecotones within the pools where the pool bottom meets the non-inundated uplands surrounding the pool (Marty, 2015; Michaels et al., 2021; Robins & Vollmar, 2002). The transition zones are small in area compared to the area of the uplands and pool bottoms, but are

areas of conservation concern because of their high diversity and sensitivity to grazing (Marty, 2015; Michaels et al., 2021). We delineated these transition zones in early spring 2016, after the pools dried down and before plant taxa were identifiable, by recording water marks across the slope that indicated differences in flooding duration. In May 2018, during peak flowering season, we sampled species using 50 × 50 cm PVC quadrat frames divided into one hundred 5 × 5 cm squares. For each species, we recorded the number of cells in which the canopy of the species occurred. The abundance of each species is therefore the number of cells (of 100) in which it occurred. This sampling method is beneficial for detecting less-common species as well as tiny forbs that are common in vernal pools (Gerhardt & Collinge, 2003). Since the smallest individual forb in our pools covered more than 50% of the 5 × 5 cm square in which it occurred, this measure of abundance is similar to a measure of cover. We herein use the term 'cover' to refer to the abundance measurements derived from this method. We repeated this procedure three times in each pool (3 quadrats/pool × 12 pools per management type × 3 management types = 118 quadrats total).

2.4.1 | Water level

We measured standing water depth in each pool in winter 2017–2018 by installing a permanent staff gauge and recording the height of standing water above the lowest point of the pool basin. These depths, checked weekly from November 2017 to June 2018, were used to calculate the total number of days of standing water for each pool per season. We assumed that hydrology remained stable in the time between consecutive measurement dates (i.e. if a pool held water at three points taken 7 days apart from each other, we recorded this as 2 weeks of inundation; Shaffer et al., 2000). This measure is the most robust way to assess the hydrology of a vernal pool, since inundation of the transition zone itself can be highly variable, depending on elevational profile and greater short-term temporal variability in inundation in the transition zone.

2.4.2 | Hoofprint cover

We measured hoofprints in the transition zones during the May 2018 vegetation quadrat surveys. In each quadrat, the number of 5 × 5 cm cells in which a hoofprint that depressed and exposed the soil was counted and recorded. We only counted depressions deeper than 13 mm, which is the threshold considered to be biologically relevant in rangeland management technical guidelines (Burton et al., 2011).

2.4.3 | Residual dry matter

To measure upland biomass that could potentially reduce standing water in the pools, we collected Residual dry matter (RDM) in the upland zones immediately adjacent to the transition zones, following removal of livestock for the 2017–2018 grazing season (July 2018). Residual dry matter is the mass (kg/ha) of dry, senescent annual herbaceous vegetation remaining following the growing-grazing season (October through June), and provides a relative estimate of vegetation biomass. Quadrats (15 × 15 cm) were placed in the upland zones within 5 feet of the pool edges and all biomass per quadrat was clipped and air-dried at 60°C to a constant weight.

2.5 | Data analysis

2.5.1 | Relating pool characteristics to grazing

To test the prediction that (a) continuously grazed pools would have the longest inundation, and that (b) the pools recently reintroduced to grazing would exhibit highest hoofprint microtopography, we used two linear mixed models (LMM), one with total days of inundation and one with hoofprint cover as the dependent variable, with Pool ID as a random effect. Pairwise comparisons were made

using Tukey's honestly significant difference (HSD) test (Rohlf & Sokal, 1995).

We used Pearson's correlation analysis to examine potential cross-correlations among the following variables: pool size, soil type, basin depth, RDM, hoofprint count and total days of standing water. We also included grazing treatment as a continuous variable (1 = grazing exclusion, 2 = short-term grazed and 3 = long-term grazed).

2.5.2 | Relating pool characteristics and grazing to plant diversity and cover

We used a conditional inference tree (CIT) and linear mixed models (LMM) to test the level to which grazing interacts with pool characteristics to affect plant diversity and native cover.

The CIT recursive partitioning algorithm looks for a predictor and a threshold at each stage that divides between low and high responses for the dependent covariable. Unlike other methods such as structural equation modelling, CITs are useful because the number of explanatory variables that can be included is not limited by replicates. This method is also robust to multicollinearity of explanatory variables, and explanatory variables do not need to be normally distributed. We included the following variables in our CIT analysis: pool size, soil type, basin depth, RDM, hoofprint count, total days of standing water and grazing treatment (to represent grazing-related mechanisms that we were unable to account for in our study, such as direct defoliation, soil compaction, nutrients, etc.). Conditional inference trees (CITs) can be useful for selecting the key subset of covariates and informing model fitting (Hothorn et al., 2006; Schweinberger, 2021). We used CIT to select a separate subset of covariables for each of three diversity metrics: species richness, abundance-weighted diversity (Shannon–Weiner Index) and the relative cover of natives (Appendix S2). Next, we used three LMMs to look at the response of each of these diversity metrics to the selected set of covariables. In all three LMMs, pool identity was specified as a random intercept. We specified a normal distribution in the analysis, after confirming residual normality via standard diagnostic plots. We determined the best LMM model using AIC model selection, testing each predictor separately and combined and in interaction, if an interaction was indicated by the CIT analysis. Pairwise comparisons were made using Tukey's HSD test (Rohlf & Sokal, 1995).

To identify the specific species driving grazing effects on the plant community, we visualized compositional differences in two dimensions using Bray–Curtis (abundance-weighted) similarity. We projected species onto the NMDS plots to visualize their contributions to grazing effects. For visual clarity, we only projected species that had an abundance above 1% in at least one of the three grazing treatments. We also compared the mean relative abundance of each species for each grazing treatment using two-sample *t* tests and the Benjamini–Hochberg correction for multiple comparisons (Benjamini & Hochberg, 1995; Waite & Campbell, 2006).

Statistics were conducted using the *VEGAN* and *LME4* packages in R v. 3.5.2 (Bates et al., 2015; Oksanen, 2001).

3 | RESULTS

3.1 | Relating pool characteristics to grazing

Contrary to our hypotheses, we did not observe significant differences in the total days of standing water between the three grazing treatments (ANOVA; Grazing: $F(2, 64) = 1.227, p = 0.272$). However, we did observe higher deeper standing water in the long-term grazed pools than the other two treatments on several dates (Figure 2). We also found that hoofprint cover did not significantly differ between long-term and short-term grazing reintroduction (ANOVA; Grazing: $F(2, 64) = 1.227, p = 0.272$).

Pearson's correlation analysis revealed additional relationships between covariables, although these relationships were generally weak (Table 1). Hoofprint cover was weakly positively correlated with days of inundation ($R = 0.43$), and pool size (m^2) showed a moderate positive relationship with days of inundation ($R = 0.61$; Table 1).

3.1.1 | Relating pool characteristics and grazing to plant diversity and cover

As we predicted, both grazing treatments had significantly higher diversity than the exclusion treatment, measured both as

species richness and abundance-weighted (Shannon–Weiner) diversity (Species richness ANOVA: Grazing (2, 31) = 21.31, $p < 0.001$, Shannon–Weiner diversity ANOVA: Grazing (2, 31) = 18.8, $p < 0.001$; Figure 3). While all three treatments were significantly different from one another, we found the strongest difference to be between the exclusion and the long-term grazed treatments. The pools with short-term reintroduced grazing exhibited an intermediate level of diversity. The relative cover of natives was also higher in both grazing treatments compared to the exclusion treatment; however, the two grazing treatments did not differ from one another (Relative Cover of Natives ANOVA: Grazing (2, 31) = 9.37, $p < 0.001$; Figure 3).

Our compositional analyses (NMDS) suggest that invasive grasses and forbs were more closely associated with pools under grazing exclusion while native forbs and rushes were more closely associated with the grazed pools. Long-term and short-term grazed pools were similar in species composition, as evidenced by the high level of overlap in 95% confidence ellipses in the NMDS visualization (Figure 4). The exotic forb *Leontodon saxatalis* was more closely associated with exotic grasses (*Elymus caput-medusae*, *Festuca bromoides* and *Festuca perennis*) while native forbs such as *Gratiola ebracteata*, *Lasthenia fremontii* and *Ranunculus bonariensis* were more closely associated with native rushes (*Eleocharis acicularis* and *Eleocharis macrostachya*; Figure 4).

Our analysis of individual species abundance identified some significant grazing-driven differences in both exotic and native forbs and grasses. The exotic forb *Leontodon saxatalis* was reduced from 27.47% in the grazing exclusion treatment to 7.51% in the short-term and 13.10% in the long-term grazed treatments ($p < 0.001$; Appendix

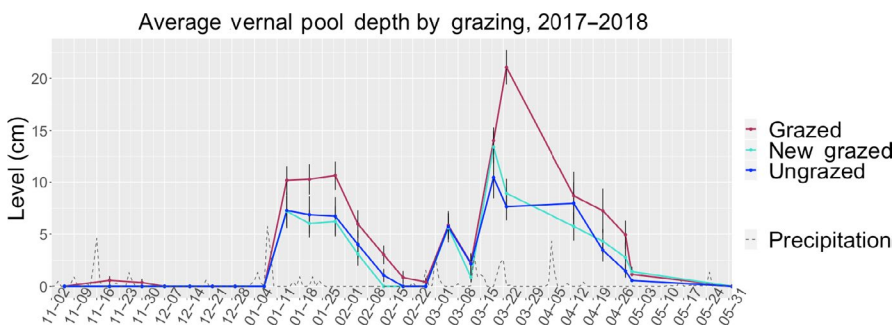


FIGURE 2 Weekly average vernal pool depth by grazing treatment

TABLE 1 Matrix of Pearson-type correlation values between variables. Stars indicate significance level (* < 0.05; ** < 0.001)

	Total days of standing water	Hoofprint count	RDM	Catchment area	Pool size	Basin depth
Total days of standing water	1.00					
Hoofprint count	0.43**	1.00				
RDM	-0.11	-0.15	1.00			
Catchment area	0.14	0.10	-0.22	1.00		
Pool size	0.61**	0.28	-0.31	0.24	1.00	
Basin depth	0.21	0.03	0.30	0.34*	0.20	1.00
Grazing treatment	0.36*	0.53**	-0.26	0.19	0.01	-0.15

FIGURE 3 Diversity and native cover by grazing treatment. Letters indicate significant differences. Relative cover of natives ANOVA: Grazing (2, 31) = 9.37, $p < 0.001$. Shannon–Weiner diversity ANOVA: Grazing (2, 31) = 18.8, $p < 0.001$. Species richness ANOVA: Grazing (2, 31) = 21.31, $p < 0.001$

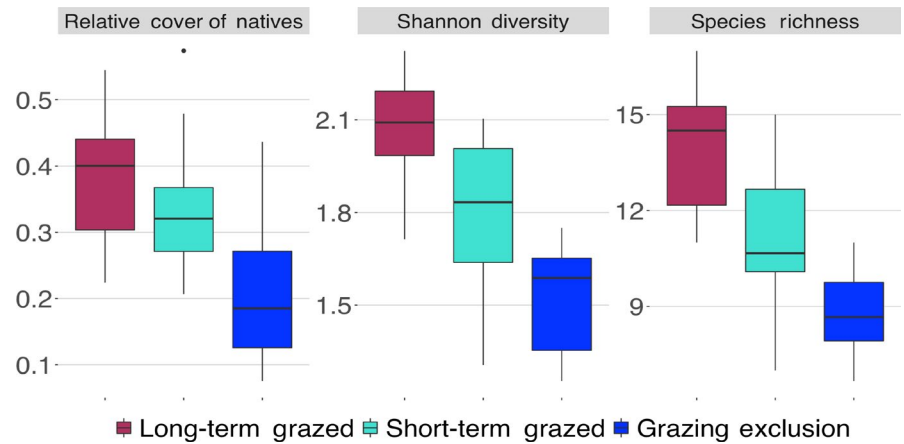
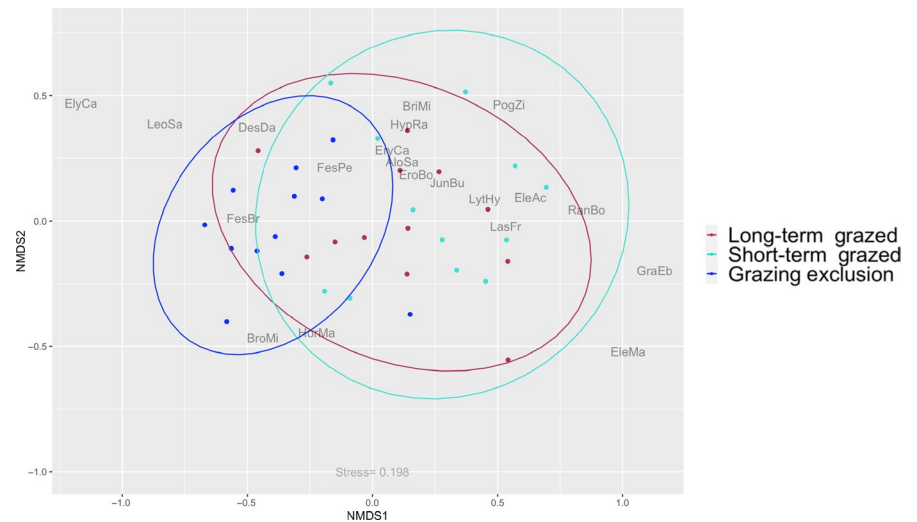


FIGURE 4 Non-metric multidimensional scaling (NMDS) by pool (quadrats averaged) with 95% confidence ellipses displayed, based on Bray–Curtis dissimilarity. Only species with abundances >1% in at least one of the treatments in the study are projected. Species codes available in Appendix S3



S3). The native species *Eryngium castrense* was significantly higher in abundance with long-term grazing ($p < 0.00$) and short-term grazing ($p < 0.03$). Short-term grazing also increased the abundance of two other native forbs, *Gratiola ebracteata* ($p < 0.00$) and *Ranunculus bonariensis* ($p < 0.04$) relative to grazing exclusion. In both grazing treatments, *Downingia bicornuta*, primarily associated with pool basins, was found in low abundance, but was not present in the grazing exclusion treatment. The long-term grazed pools had four exotic forbs that were not present in the short-term grazed or grazing exclusion treatment, although they had very low relative cover (<1.0%; Appendix S3).

3.1.2 | Relating pool characteristics to plant diversity and cover

Conditional inference tree analysis selected the following subset of variables for each of the following diversity metrics: Species Richness (Grazing treatment, Hoofprint cover, Pool basin depth, RDM, Pool Size), Shannon–Weiner diversity (Grazing treatment, Hoofprint cover, Pool Size) and Relative Cover of Natives (Hoofprint cover, RDM, Total Days of Standing Water). For Relative Cover of

Natives, grazing treatment was not selected by CIT analysis but was added back into the model because of its importance when tested as an individual variable. Models without interaction terms were selected by AIC, so no interaction terms were included in the final LMMs (Appendix S2).

We found that species richness, Shannon–Weiner diversity and native cover increased with hoofprint cover (Table 2). Pool size also significantly increased species richness while total days of standing water significantly increased the relative cover of natives. Our model also found the grazing treatment term to be significant for both species richness and abundance-weighted diversity, suggesting that other grazing mechanisms that were not directly measured could also be affecting diversity (Table 2).

4 | DISCUSSION

Our study contributes to a small but growing body of literature that directly compares the effects of grazing reintroduction to systems that have been under prolonged rest from herbivores (Gornish et al., 2018; Groome & Shaw, 2015; Johnson & Cushman, 2007; Pykälä, 2004). These studies, which span arid, mesic and

TABLE 2 Results of three separate linear mixed-effects models (LMM) for species richness, Shannon–Weiner diversity and relative cover or natives. Covariables for the final LMM were selected by conditional inference tree (CIT) analysis

Species richness			
Covariable measured	Selected for LMM?	Coefficient (SE)	p-value
Catchment area (m ²)			
Grazing treatment	X	2.20 (0.36)	<0.001
Hoofprint cover	X	0.15 (0.05)	0.003
Pool basin depth (cm)	X	0.07 (0.09)	0.460
Residual dry matter (g)	X	0.02 (0.02)	0.270
Pool size (m ²)	X	0.01 (0.003)	0.006
Soil type			
Total days of standing water			
Intercept		3.65 (1.57)	0.028
Shannon–Weiner diversity			
Covariable measured	Selected for LMM?	Coefficient (SE)	p-value
Catchment area (m ²)			
Grazing treatment	X	0.21 (0.04)	<0.001
Hoofprint cover	X	0.02 (0.01)	0.005
Pool basin depth (cm)			
Residual dry matter (g)			
Pool size (m ²)	X	<0.01 (<0.01)	0.06
Soil type			
Total days of standing water			
Intercept		1.23 (0.09)	<0.001
Relative cover of natives			
Covariable measured	Selected for LMM?	Coefficient (SE)	p-value
Catchment area (m ²)			
Grazing treatment	(added in post-CIT)	0.04 (0.10)	0.06
Hoofprint cover	X	0.01 (0.003)	0.02
Pool basin depth (cm)			
Residual dry matter (g)	X	−0.00 (0.001)	0.86
Pool size (m ²)			
Soil type			
Total days of standing water	X	0.002 (0.001)	0.01
Intercept		0.992 (0.09)	0.59

Bold indicates the variable were found to be significant by the model ($p < 0.05$).

coastal grasslands, suggest that reintroducing large herbivores at low to moderate grazing levels in certain ecosystems can positively influence plant diversity and native cover. Our findings

parallel previous results that reintroduced grazing can have significant effects on annual species in the first 2–5 years (Johnson & Cushman, 2007) and can affect native cover more strongly than diversity (Gornish et al., 2018).

Threshold dynamics have been well studied in grassland systems in which heavy grazing has led to biodiversity declines and woody encroachment (Bestelmeyer et al., 2013; Lipoma et al., 2021), with evidence that these grazing dynamics may be reversible in some systems (Kleinhesselink, 2020). This is encouraging to managers looking to restore biodiversity in these grasslands. Our study looked at a system in which removal moderate grazing has led to declines in diversity (Michaels, 2020) and similarly found that these dynamics were reversible. Pools with short-term reintroduced grazing reached the same level of native cover as the long-term continuously grazed pools in just 2 years. Diversity also appeared to be on a trajectory towards recovery, although our findings suggest that it may take longer than 2 years of reintroduced grazing to reach the levels of the long-term (40+ years) grazed pools. There are several potential mechanisms by which grazing led to these results in our study system.

Based on our observations and our review of the literature, we suggest that reintroduced grazing led to increased diversity and native cover due in part to the following conditions: (a) diversity in this system is mainly driven by low-statured native annuals that are not targets of defoliation, and limited by invasive grasses and forbs, so that reduced competition from grazing can lead to increased native cover; (b) in this upland/wetland transition system, grazing can make soil moisture more available to plants through microdepressions; (c) this system is dispersal-limited so that grazing can increase diversity through increasing dispersal potential and (d) our grazing pressure is moderate.

4.1 | Grazing favours native plant characteristics in our system

First, the effects of grazing on native diversity and cover depend on the life-history guild of plants that are being affected. In upland systems, livestock have been shown to select against taller plants and graminoids (Díaz et al., 2007), select for plants with prostrate growth forms and tougher stems (Myers et al., 2015; Stahlheber & D'Antonio, 2013), and to generally increase plant diversity (Bartolome et al., 2014). In wetland systems, grazing generally selects against upland species and for wetland-obligate forb, moss and sedge species (Groome & Shaw, 2015; Merriam et al., 2018; Middleton, 2016). Therefore, grazing outcomes will depend on whether the native species tend to be the targets of defoliation, or benefit from reduced competition. For example, Johnson and Cushman (2007) documented the 5-year reintroduction of native tule elk (*Cervus canadensis nannodes*) into mesic coastal grasslands and found that grazing targeted the competitively dominant grass *Holcus lanatus*, allowing native annual species to increase in abundance. On the other hand, Bovee et al. (2017) found that livestock grazing in montane wetlands

benefitted annual native species at the expense of native perennial species, which were reduced by the indirect effects of grazing. This led to both positive and negative outcomes on the overall plant community in terms of diversity and native cover.

In our vernal pool ecosystem, which includes a wetland, upland and a transition zone associated with each pool, we chose to focus our sampling effort in the transition zone, where the native species have been observed to be mainly low-statured annuals that are not targets of defoliation (Barry, 1995; Marty, 2015). We found that grazing reduced the most dominant exotic forb in our system, *Leontodon saxatilis*. Since diversity in this system is limited by invasive grasses and forbs (Gerhardt & Collinge, 2007), we can assume that selective grazing on these dominants reduced competition and opened niche space for native forb species, leading to increased cover of subdominant natives. This pattern has been observed in grassland and savannah ecosystems across gradients of temperature and precipitation on several continents (Koerner et al., 2018).

4.2 | Grazing affects diversity indirectly via abiotic mechanisms

We observed hoofprint microdepressions in the soil in both the long-term and short-term grazing reintroduction treatments (short term: 6.58%, long term: 8.78% hoofprint cover). These microdepressions likely allowed more native forb species to persist in areas where they would otherwise be outcompeted by exotic grasses. Trampling by livestock can increase microtopography (Allen-Diaz et al., 2004; Stammel & Kiehl, 2004) that provides lower, moister refugia for native plants away from competitively dominant grasses, which cannot withstand prolonged soil moisture and/or inundation (Allen-Diaz et al., 2004; Barry, 1995; Gornish et al., 2018; Robins & Vollmar, 2002). Trampling may also aid in the germination of seeds after dispersal by increasing the light and moisture available to seedlings (Faust et al., 2011).

In addition to increasing water retention through creating microdepressions, grazing has been suggested to increase overall standing water within vernal pools, due to either soil compaction preventing drainage or reduced soil organic matter, which leads to increases in standing water as soil water-holding capacity decreases (Marty, 2015). This increased water storage is thought to enhance the overall function of vernal pools as refugia from exotic invasive pressure. However, we did not detect a grazing effect on inundation. This difference between our study and the Marty study could be due to many possibilities, including the hydrology of the site, the relatively wet year of this study, the lack of grazing effect on Residual Dry Matter or differences in soils. For example, in our study site, seasonal shrink–swell dynamics are common for the clays found in the San Joaquin soil series, which may annually erase any effects of grazing on soil compaction, and thus inundation periods of the vernal pools.

It is also important to note that our mixed-effects models suggest that other mechanisms that were not measured may have also

contributed to differences in plants diversity across grazing treatments. These mechanisms could include direct effects of defoliation and soil compaction on plant survival (Robins & Vollmar, 2002), or defecation, which could deliver nutrient pulses to vernal pools (Croel & Kneitel, 2011; Olff & Ritchie, 1998; Robins & Vollmar, 2002). Further research is needed to understand how these grazing mechanisms may affect plant communities in vernal pools. It is important to note that our study can assess variations between vernal pools within an individual vernal pool complex, but that variations across pools were restricted to relatively small local-scale variations. Context dependence of grazing effects needs to be assessed across a broader diversity of vernal pools that differ in local climate (i.e. montane), hydrology and edaphic setting (e.g. claypan, hardpan). For example, grazing effects may vary depending on precipitation patterns. Davy et al. (2015) found that reintroduced heavy grazing decreased the invasive *Elymus caput-medusae* only in years when the soil moisture was low in late spring due to low precipitation. When late spring precipitation was high, *E. caput-medusae* was able to recover to pre-grazing levels.

4.3 | Grazing may increase dispersal potential in our system

The differences in diversity that we observed between short-term and long-term grazing treatments may have been related to increases in dispersal over time. Vernal pool ecosystems are characterized by remarkably low dispersal between pools, particularly among native forb species (Solomeshch et al., 2007). The higher species diversity observed in the long-term continuously grazed pools was driven by additional exotic forbs at very low relative cover (<1%). Chuong et al. (2016) found that cattle dung, mud and fur are important vectors of exotic seed dispersal grasslands. Over time, exotic species may colonize grazed pools at low abundances due to their strong dispersal potential. This is evident in our finding that the long-term grazed had four exotic forbs present in low abundances that were not found in the other two treatments. Vernal pool native forbs, on the other hand, have a long-term seedbank and are evolved to respond quickly to reduce competition through increases in abundance within their own localized habitat (Solomeshch et al., 2007). This may explain why short-term grazed pools reached a similar level of relative native abundance to the long-term grazed pools within 3 years, without showing an increase in diversity.

4.4 | Moderate stocking rate is considered typical for conservation-oriented management

Grazing pressure (i.e. stocking rate) is known to be an important factor driving the outcome of livestock on plant communities (Herrero-Jáuregui & Oesterheld, 2018). According to well-established grazing models, the impact of grazing on an ecosystem depends on that system's history of grazing—the longer a system has evolved under

herbivory, the more that grazing can be beneficial to plant communities, but in systems with a short evolutionary history of grazing these benefits decline or are reversed at high stocking rates (Milchunas et al., 1988). In instances where grazing pressure is high, grazing can increase bare ground cover and/or reduce seed germination for species that rely on standing biomass for shelter from arid climates, leading to reductions in diversity and/or native cover (Bovee et al., 2018; Lunt et al., 2007; Stammel & Kiehl, 2004). It is important to note that our study did not assess the effect of stocking rate or rotational grazing, instead it focused on a rate (1 AU/6 acres) typical for conservation-oriented management in California grasslands (Marty, 2015), and moderate for most production-oriented landscapes in the region. More studies are needed that look at appropriate stocking rates to determine how these differences in management affect threshold dynamics.

5 | CONCLUSIONS

Our study provides evidence that, at a moderate stocking rate, grazing disturbance may influence plant communities in a reversible trajectory in our vernal pool ecosystem. However, it is important to acknowledge the context dependence of grazing outcomes, and the interactions between climate, soil conditions, plant community dynamics and grazing management (Adler et al., 2001; Davy et al., 2015; Eldridge et al., 2016; Lunt et al., 2007; Stahlheber & D'Antonio, 2013). Understanding this context dependence is particularly critical when short-term responses to grazing reintroduction cannot necessarily be used as indicators of long-term changes, making adaptive management difficult. Further research that addresses how grazing outcomes vary with both environmental and management characteristics can help identify which sites are most likely to be compatible with changes in grazing management and how quickly different aspects of plant communities (i.e. diversity, native cover) will respond to grazing reintroduction.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to report.

AUTHORS' CONTRIBUTIONS

Study conceived by J.S.M., designed by J.S.M., V.T.E. and K.W.T.; Data acquired by J.S.M.; Analyses conducted and paper written by

J.S.M., V.T.E. and K.W.T. All authors approved and are accountable for the final manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.25338/B8DW6F> (Michaels, 2020).

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SUPPORTING INFORMATION

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