Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Loss of biodiversity and hydrologic function in seasonal wetlands persists over 10 years of livestock grazing removal

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Ecological restoration provides a means to increase biodiversity in ecosystems degraded by natural and human-induced changes. In some systems, disturbances such as grazing can be key factors in the successful restoration of biodiversity and ecological function, but few studies have addressed this experimentally, especially over long time periods and at landscape scales. In this study, we excluded livestock grazing from plots within a grassland landscape containing vernal pools in the Central Valley of California for 10 years and compared vernal pool hydrology and plant community composition with areas grazed under an historic regime. In all 10 years, the relative cover of native plant species remained between 5 and 20% higher in the grazed versus ungrazed plots. This effect was particularly prominent on the pool edges, though evidence of invasion into the pool basins was evident later in the study. Native species richness was lower in the ungrazed plots with 10–20% fewer native species found in ungrazed versus grazed plots in all years except the first year of treatment. Ungrazed pools held water for a shorter period of time than pools grazed under an historic regime. By the ninth year of the study, ungrazed pools took up to 2 weeks longer to fill and dried down 1–2 weeks sooner at the end of the rainy season compared to grazed pools. The results of this study confirm that livestock grazing plays a key role in maintaining biodiversity and ecosystem function in vernal pools.

Key words: invasive species, land management, vernal pools, wetland restoration

Implications for Practice

- Management changes aimed at restoring diversity and function to a site should be applied at a small scale in an experimental context to allow practitioners to quickly identify negative and positive impacts of the change.
- Monitoring that occurs over longer periods of time is more likely to capture unique effects of climatic variation and better inform restoration and management decisions.
- Grazing management is an effective tool for restoring native biodiversity in invaded grasslands where phytomass management is an important consideration.

Introduction

The role of disturbance in maintaining biodiversity and ecosystem function is one of the most critical elements in the success of ecological restoration yet very few studies measure—let alone experimentally manipulate—disturbance regimes and track the impact on success of the restoration project (Fuhlendorf & Engle 2001; Suding 2011; Mavromihalis et al. 2013). In fact, Brudvig (2011) found that out of 190 articles on ecosystem restoration, only 17% measured the effects of disturbance on restoration outcomes. Also, while restoration is typically implemented as a long-term objective, outcomes are rarely followed up for a timeframe relevant to adequately measuring the success of the stated objectives (Holl & Aide 2011; Driscoll et al. 2012).

One of the greatest challenges facing ecosystem restoration is invasive species management, which is strongly influenced by disturbance (Zavaleta et al. 2001; Kettenring & Adams 2011). While disturbance can promote invasion (D'Antonio & Meyerson 2002) it also plays a critical role in invasive species management. Livestock grazing is the most pervasive management tool utilized in grasslands in Western North America and has been implicated in the degradation of many natural habitats (Fleischner 1994). It is also one of the few management treatments available to restoration practitioners that can be manipulated to treat problematic vegetation and applied at a landscape scale (Watkinson & Ormerod 2001; Hillhouse et al. 2010). While inappropriate grazing can lead to habitat degradation, removal of livestock grazing is generally insufficient to restore biodiversity, particularly at sites with a large invasive species component (Barry 1998; Marty 2005; Dahwa et al. 2014).

Vernal pools are seasonal wetlands that occur throughout California annual grasslands (Barbour et al. 1993). They exist in grasslands with soils that are poorly drained due to a restrictive

Author contributions: JM conceived and conducted the study and wrote the manuscript.

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doi: 10.1111/rec.12226

layer at or beneath the soil surface (Holland & Dains 1990). These unique ecosystems harbor a large number of rare species and have been a focus for both habitat restoration and conservation (Holland 1998; Barbour et al. 2003). In contrast to the high proportion of native grass and forb species within the vernal pools of California's Central Valley, the surrounding grasslands are heavily invaded with exotic grass and forb species (Barry 1998; Pollak & Kan 1998). This presents a challenge for landscape-scale management if the aim is to reduce exotic species cover while not negatively impacting the native species within the vernal pools as the pools cannot be effectively managed differently than the surrounding grasslands.

In 2000, the Natural Resources Conservation Service (NRCS) purchased a Wetland Reserve Program (WRP) easement on a 5,000-ha ranch in Eastern Sacramento County, California, U.S.A. to protect the vernal pool habitat. In addition to protecting the wetlands from future development, the easement required restoration of the vernal pools. The vernal pools had not been physically altered except for any impacts sustained from grazing cattle for 150–200 years. The WRP easement removed all grazing rights from the property; however, the NRCS could make an allowance for a modified grazing regime to be applied as a restoration strategy. This grazing management modification would have removed grazing from the easement area during at least part if not all of the historic grazing season.

We designed an experiment to determine whether adjusting the cattle-grazing regime could restore biodiversity or function in these vernal pools. We initially implemented four different grazing treatments (wet-season grazed, dry-season grazed, continuous grazed, and ungrazed) to test a range of grazing management options. The initial results (2001–2003) of the study showed that altering the cattle-grazing regime from the historic season of use (October through June) had a negative impact on plant and aquatic animal biodiversity and on the hydrology of the vernal pools (Marty 2005). While the initial results were compelling, we were interested in the longer-term outcomes on plant diversity and vernal pool hydrology in two of the grazing treatments (continuous grazed and ungrazed). We continued monitoring these treatments for an additional 7 years to determine the longer-term outcome of grazing removal.

Methods

Study Site

This study was conducted on a 5,000-ha parcel located in eastern Sacramento County, CA, U.S.A. (38°38′N, 121°02′W; elevation, 75 m). The climate of this region is Mediterranean with average annual rainfall of 56 cm occurring between the months of October and May. Less than 2 cm of rain falls during the summer months.

The ranch is relatively flat with elevations from 50 to 160 m above mean sea level. Vernal pools are found on the flatter areas of the site and are abundant on approximately one-third of the property. Approximately 3,500 ha of the site are covered under an NRCS WRP easement. Cattle have grazed the site for the past 150 or more years. In the recent past, cattle have grazed the entire site each year from approximately October through June at a stocking rate of 1 animal unit (cow-calf pair) per 2.4 ha. This grazing season and stocking rate are typical for grasslands in this part of the Central Valley of California.

Experimental Design

In 2000, we established six blocks (replicates) of four grazing treatment plots across two major geologic formations on the site (3 blocks each on the Laguna and Valley Springs formations). Within each treatment plot, we monitored three pools (6 replicates × 4 grazing treatments × 3 pools = 72 vernal pools total) of varying sizes (range: 70–1,130 m^2, mean: 252 m^2) and shapes based on soil maps, aerial photographs, and available geographic information system (GIS) layers. We randomly assigned treatments to the four plots within each block (Marty 2005).

This study initially tested four different grazing treatments from 2000 to 2003 (ungrazed, continuous grazed, wet-season grazed, and dry-season grazed). The wet-season and dry-season grazed treatments utilized temporary electrical fencing to exclude cattle. The wet-season grazed treatments allowed cattle continuous access to the pools from roughly January through April, or when the pools held water. The dry-season grazed treatments allowed cattle access from October through roughly January and then again from April through June. These treatments were discontinued due to the difficulty of implementation and lack of compelling differences in treatment effects from the ungrazed treatment. From 2003 to 2010, we implemented only the continuous (CG) and ungrazed treatments (UG); (2 treatments × 6 replicates × 3 pools = 36 pools). Cattle were excluded from all pools within the ungrazed plots throughout the grazing season and had continuous access to pools in the continuous grazing treatment during the grazing season (October–June). Cattle exclosures ranged in size from 0.33 to 0.80 ha. Mean pool area and depth did not differ significantly among treatments at the beginning of the experiment.

Once the pools filled with water, weekly depth measurements were taken at a permanent marker located in the deepest part of each pool. The weekly presence or absence of water was used to calculate both total and maximum inundation period for each pool as well as the number of dry down periods during the grazing season. In 2001, we did not start collecting pool depth data until February, so period of inundation data are not available for the first season of the study.

Plant species composition data were collected each year in permanently marked 35 × 70 cm quadrats after the pools had dried and the majority of the plant species were flowering (April–May). Permanent quadrat locations were established during the first year of the experiment in three different pool zones and then located each year using a metal detector (3 quadrats × 3 zones = 9 quadrats per pool). The three zones were (1) the deepest part of the pool, (2) the edge of the pool (selected in the first year based on the high water mark of the pool), and (3) the upland area (5 m from the adjacent edge quadrat). Each plant species occurring in the quadrat was recorded and given a modified Daubenmire cover class value

(Barbour et al. 1987). Cover class values were converted to midpoint cover values to calculate absolute percent cover. For vegetation analyses, we used the pool zone as the sampling unit and pooled data across the three vernal pools monitored within each replicate grazing treatment ($n = 3$ pool zones $\times$ 2 grazing treatments $\times$ 6 replicates = 36).

Residual dry matter (RDM) levels were measured in each treatment plot each year in early fall (September to October) before the first rains of the season. Five, 0.1 m^2 hoops were randomly placed in the upland area of each treatment plot, and all herbaceous material located within the hoop was clipped down to bare soil. The dry herbaceous material was then weighed (grams) in a paper bag with a field scale (Pesola™, Baar, Switzerland). The weight of the bag was subtracted from the total sample weight to get the weight of the dry matter. All RDM data are reported in kilograms per hectare (kg/ha).

For the hydrologic data, we used the pool as the sampling unit ($n = 36$). Soil compaction was measured at each of the vegetation sampling points ($n = 9$ per pool) in October 2003 and 2010, prior to the first rainfall of the season using a soil penetrometer (Geotest Instrument Corporation, Evanston, IL, U.S.A.).

Statistical Analyses

We used repeated-measures multivariate analysis of variance (MANOVA) to test for significant treatment effects across years ($F_{\text{df-time, df-error}} = F$-value, p-value). In cases where the data violated the sphericity assumption, the degrees of freedom were adjusted for the effect and the Greenhouse-Geiser corrected values are reported. We used a two-way analysis of variance (ANOVA) with experimental block and grazing treatment as main effects for each variable measured in each year ($F_{\text{df-model, df-error}} = F$-value, p-value). For the hydrologic data, we tested for treatment effects by year with pool as the sampling unit. For the vegetation data, we tested for treatment effects by year and within each pool zone separately. Pairwise comparisons were made using Tukey's Honestly Significant Difference (HSD) test (Sokal & Rohlf 1995). Diversity is reported as species richness (s). All analyses were conducted using JMP statistical software v.9 (SAS Institute, Cary, NC, U.S.A.).

Results

After 10 years of grazing removal, the relative cover of native species remained higher in the continuous grazed versus ungrazed plots across all pool zones, and this effect was detectable in all 10 years of the study ($F_{[9,20]} = 5.96$; $p < 0.001$; Fig. 1a). The greatest difference between grazing treatments was measured on the pool edge where CG plots had higher relative native species cover in 4 of the 10 years of the study (Fig. 1c). Grazing removal also decreased relative native species cover in the pool zone in 2 years (Fig. 1b). The upland zones in the study plots had the lowest native cover of any of the pool zones, and removing grazing significantly reduced relative native cover in 2 years of the study (Fig. 1d).

The composition in the plots tended to change in favor of grasses with the removal of grazing, but this was dependent on year ($F_{[9,182]} = 3.65$; $p = 0.03$; Fig. 2a). The ratio of grass cover to forb cover was higher in ungrazed plots in 2002, 2003, 2004, 2008, and the final year of the study in 2010. RDM levels also varied by grazing treatment and year ($F_{[9,90]} = 2.62$; $p = 0.05$; Fig. 2b). RDM in the ungrazed plots was significantly higher than in the continuous grazed plots in all years except 2005, 2006, and 2010.

Native plant species richness was significantly lower in the ungrazed plots than in the grazed plots for all years except 2001 ($F_{[3.57,104]} = 3.42$; $p = 0.01$; Fig. 3). The ungrazed plots tended to have between 1.0 and 2.5 fewer native species than the continuous grazed plots. This effect was most pronounced in 2003 and 2004 where CG plots had two more species on average per quadrat than UG plots.

The total number of days that the pools were inundated was strongly affected by grazing removal in all years where inundation measures were taken (2002–2010). Mean number of days inundated was significantly less in the ungrazed pools than the continuous grazed pools in all years ($F_{[4.5,130]} = 4.48$; $p < 0.0001$; Fig.4a). This effect was particularly pronounced in the driest years like 2007, where only 27 cm of rain fell during the entire season. The continuous grazed pools averaged 41 days of inundation while the ungrazed pools were full for an average of only 15 days ($F_{[1,29]} = 24.80$; $p < 0.0001$). This difference between grazing treatments manifested as both later filling and earlier drying in the ungrazed pools. Figure 4b illustrates this effect for the 2008/2009 rainfall year where the first significant rainfall event filled most of the pools, but nearly all of the ungrazed pools dried completely within 10 days while the continuous grazed pools were inundated for the rest of the season. The ungrazed pools did not fill again for another 20 days and they dried on average 2 weeks earlier than the continuous grazed pools.

The maximum depth achieved by the pools differed significantly only in one year, 2007, the driest year in the study where CG pools achieved a depth of 11.5 ± 0.96 cm while the UG pools were on average 8.1 ± 0.96 cm deep ($F_{[1,29]} = 3.37$; $p = 0.01$). Soil compaction differed significantly between grazing treatments in 2003 with compaction in the CG pools at 4.47 ± 0.07 kg/cm^2 versus the UG pools at 3.88 ± 0.07 kg/cm^2 ($F_{[1,29]} = 38.30$; $p < 0.0001$), In 2011 compaction was 4.37 ± 0.08 kg/cm^2 in the CG pools and 3.98 ± 0.08 kg/cm^2 in UG pools ($F_{[1,29]} = 11.02$; $p = 0.002$). Soil compaction measurements taken in 2011 did not differ significantly from those measurements taken in 2003.

Discussion

Consistent with the initial results from Marty (2005), removal of cattle from historically grazed vernal pool grasslands decreased native plant cover and richness and increased the cover of exotic species for up to a decade. The consistency of these results over the additional 7 years was remarkable given the fact that species composition in California annual grasslands is

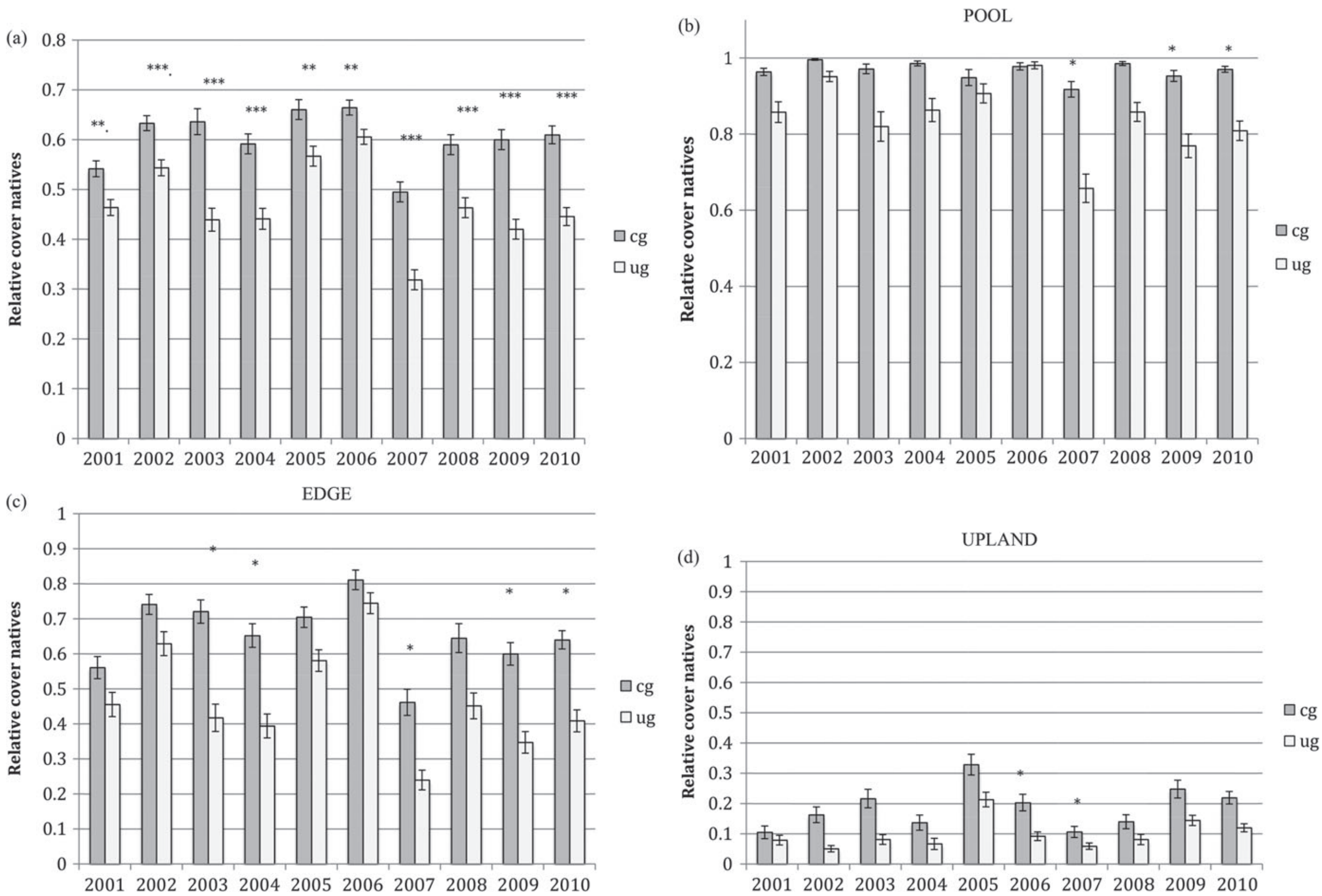

Figure 1. Effect of grazing treatments on mean (± SE) relative cover of native species (cover of native species/total plant cover) in all study years (a) averaged across all zones; (b) in the pool zone; (c) in the edge zone; and (d) in the upland zone. (CG, continuous grazed; UG, ungrazed; no asterisk = not significant; $*p < 0.05$, $**p < 0.01$, $***p < 0.001$).

notoriously variable from year to year due to a highly variable climate (Jackson & Bartolome 2002). We expected the impact of grazing removal on native species cover to be most evident at the edges of the pools where the wetland edge creates an ecotone and thus a mix of wetland and upland plant species (Gerhardt & Collinge 2003). Changes in pool inundation would presumably create new opportunities for invasion of less hydrophytic plants into this zone (Bauder 2000; Collinge et al. 2013). This study clearly demonstrates this effect with an increase in relative cover of exotics (decrease in relative native species cover) in ungrazed pools. We did not expect to see a significant increase in exotic cover in the pool basins yet the final 4 years of the study indicated that the relative cover of non-native species in the pool basins was increasing with grazing removal.

Native species richness declined in the second year of the study and remained lower in the ungrazed plots for the next 8 years. It is possible that the species that were least tolerant of the increased cover of plants and thatch created by the ungrazed treatment were lost fairly rapidly from the species pool and did not germinate in subsequent years. This is a common finding in Mediterranean grasslands released from disturbance where grasses tend to become dominant, adding substantially to residual matter remaining at the end of the season, and the more diminutive forbs tend to disappear (Noy-Meir 1995; Hayes & Holl 2003; Allen-Diaz et al. 2004).

The results also show a consistent trend toward decreased inundation in the pools with cattle grazing removal. This likely explains some of the vegetation changes measured during the study. We hypothesized previously that the primary cause of the dramatic decrease in pool hydroperiod in the ungrazed treatment was increased evapotranspiration (ET) rates from the abundance of vegetation, principally grasses, in and around the pools (Marty 2005). This was based on the first 3 years of the experiment where we saw an increase in cover of water-inefficient grasses but did not see a difference in the onset of inundation in the pools between treatments. In those first years, we only recorded a difference in inundation between grazing treatments at the end of the season with the onset of major vegetation growth. While we believe increased ET rates affect pool hydroperiod, it is now clear that increased plant growth is not the only cause, especially given the fact that the cover of grasses relative to forbs did not remain higher in the latter years of the study. The delayed ponding of the ungrazed pools over the duration of the experiment suggests that another factor must

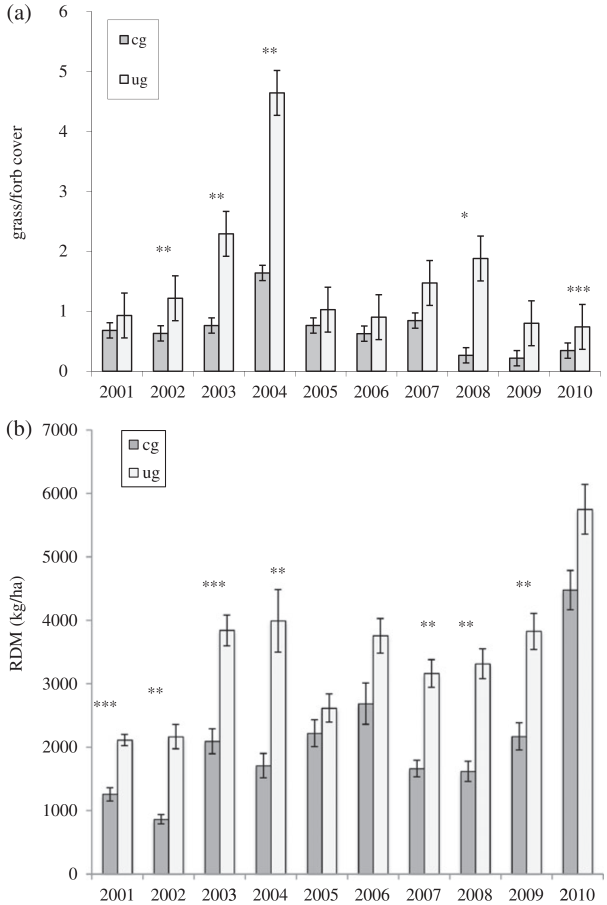

Figure 2. Effect of grazing treatments on (a) the mean (± SE) grass to forb cover ratio over the 10 years of the experiment across all three pool zones; and (b) the mean (± SE) RDM levels measured in the uplands within the treatment plots over the 10 years of the experiment (CG, continuous grazed; UG, ungrazed; no asterisk = not significant; $*p < 0.05$ $**p < 0.01$, $***p < 0.001$).

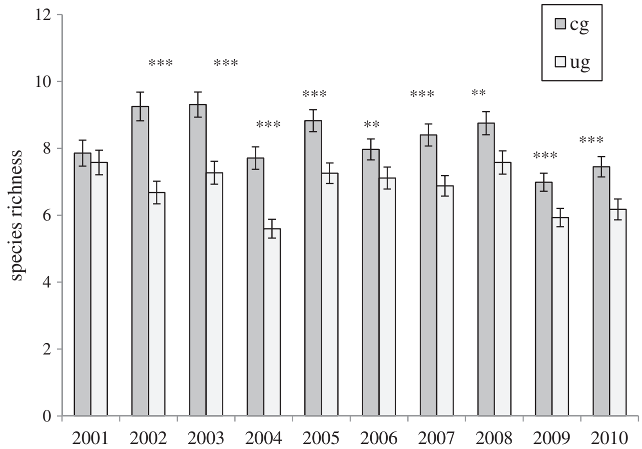

Figure 3. Effect of grazing on mean (± SE) native species richness (s) per quadrat across all study years and pool zones (CG, continuous grazed; UG, ungrazed; no asterisk = not significant; $**p < 0.01$, $***p < 0.001$).

be in play. In 2003, we measured higher soil compaction in grazed than in ungrazed treatment plots and hypothesized that this might increase soil water holding capacity in the ungrazed pools (Marty 2005). We discounted this effect because the pattern of water depths showed little difference between grazed and ungrazed pools when first filling at the beginning of the season, but we recorded a sharp decline in depth quickly followed by complete drying in the ungrazed pools once the primary vegetation growth period began in early March (Marty unpublished data 2003). While soil compaction did not change between 2003 and 2011, by 2008, the hydrology in the UG pools differed significantly at the beginning of the rainy season rather than just at the end of the season. This effect is potentially due to an increase in organic matter from the excess vegetation and thatch accumulation in and around the ungrazed vernal pools. Soils with higher organic content have lower bulk density and therefore higher water holding capacity than more mineral soils or soils with less organic material (Hudson 1994), which could result in water being maintained in the soil with a decrease in ponding above the soil surface.

As discussed by Marty (2005), this decrease in inundation period has major negative consequences for species that require longer continuous inundation periods like the federally-threatened California tiger salamander (*Ambystoma californiense*) (Shaffer & Trenham 2004). The long-term results presented here underscore the importance of this finding across multiple years and show how the continued degradation of vernal pool function that leads to unsuitable breeding conditions for such species might lead to its extirpation at a site if grazing is removed. It is also possible that a potential positive feedback loop may be set in motion by grazing removal within the vernal pool plant community wherein shorter inundation periods facilitate encroachment of grass growth and residual matter build-up in the pool basin which then further reduces inundation periods.

Studies in other grassland and wetland ecosystems have found similar results with complete grazing removal. In the Dambo wetlands of Zimbabwe, ungrazed wetlands had much lower species richness than both moderately grazed and year-round grazing regimes (Dahwa et al. 2014). Using various grazing exclusion trials in grasslands in southeastern Australia, Mavromihalis et al. (2013) recorded an overall loss of plant species richness coupled with an increase in herbage mass with complete exclusion of sheep but found little consistent changes in native species composition with other seasonal grazing exclusion treatments. A study of depressional wetlands in British Columbia, Canada, found differential responses of the plant community to grazing intensity depending on the type of wetland with a general increase in annual forbs and decrease in perennial herbaceous species with increasing intensity (Jones et al. 2011).

Despite their noted importance, field studies lasting longer than a few years are rare in ecology (Strayer et al. 1986; Franklin 1989). Long-term field studies collecting data over a number of variable climate years offer a way to understand how a community or population will respond to climate change or extremes (Smith 2011). The changes in inundation patterns observed

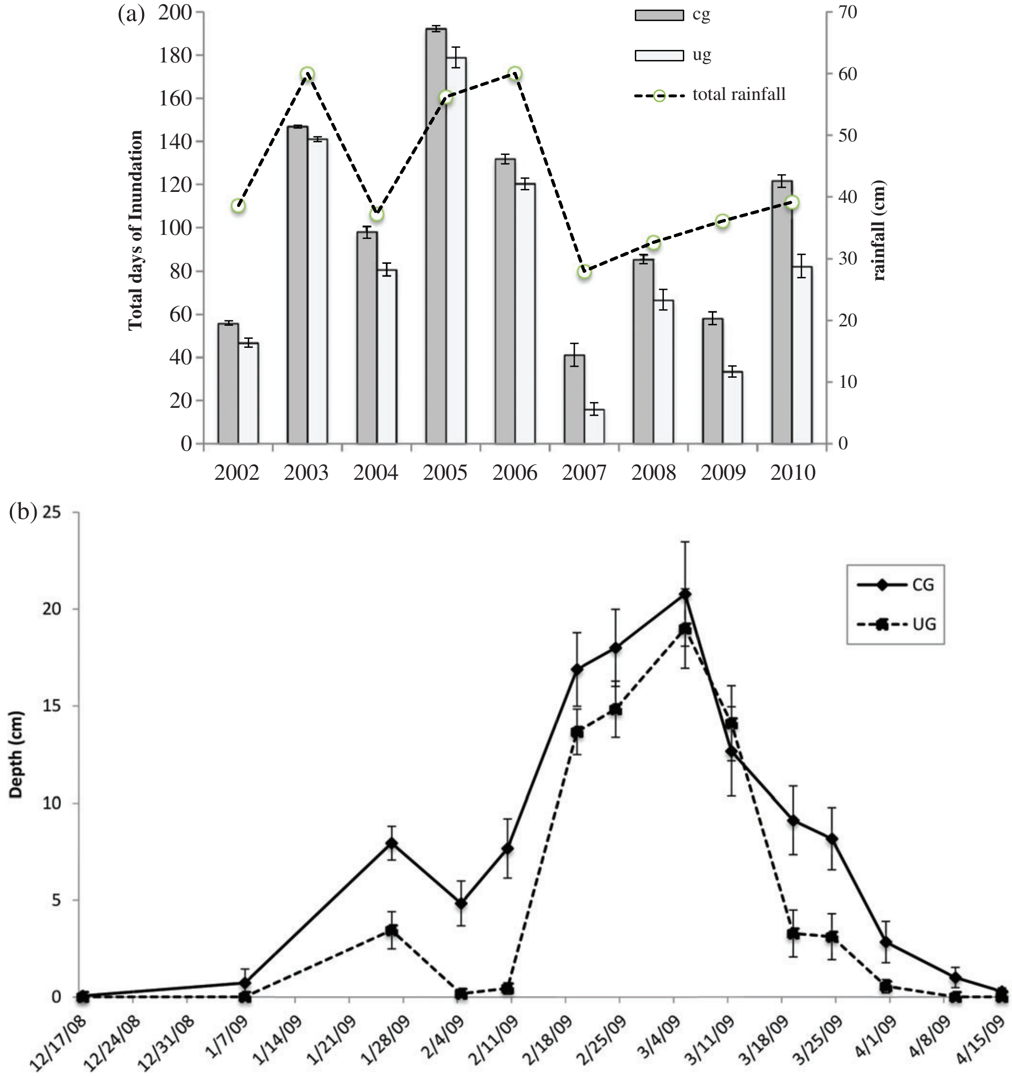

Figure 4. (a) Mean (± SE) number of days of pool inundation for continuous grazed (CG) and ungrazed (UG) pools for 9 years of the study ($p < 0.01$ for all years), including total rainfall (cm) for the area; and (b) mean (± SE) pool depth measured at approximately weekly intervals during the 2008–2009 rainfall season with the average depth of the CG pools shown as a solid line and UG pools as a dashed line.

under drought conditions toward the end of this study period highlight the potential for major interactions of grazing and climate change as presented by Pyke and Marty (2005) as well as the importance of long-term data collection. The remarkable consistency of the results of this study over a number of variable climate years indicates that the effects are quite robust to climatic variation. However, the more important conclusions from this study might be in the record of how the pools responded, especially the inundation patterns, to both very wet and very dry years. This information may be useful for predicting how these pools might function given similar trends in climatic variability in the future.

The results of this study provide a cautionary example of the importance of testing wholesale management changes at smaller scales before implementation across a landscape and tracking those changes over a long period of time. It is clear that this vernal pool landscape would have suffered major, long-term negative effects to overall native biodiversity and vernal pool function had the grazing management been changed as originally planned. The results of this study influenced a change in the NRCS's original WRP Easement policy to allow grazing on easement properties with vernal pool habitats in California (NRCS 2014).

Acknowledgments

I am indebted to all of the TNC technicians who worked on this project as well as J Buck and S Sweet for maintaining the sampling effort from 2005 to 2010. I thank R Kelsey for reviewing the draft manuscript. The Anderson Grasslands Research Fund, Bernard Osher Foundation, and other anonymous donors provided funding support for this research.

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Coordinating Editor: Stuart Allison

Received: 4 August, 2014; First decision: 24 September, 2014; Revised: 17 April, 2015; Accepted: 18 April, 2015; First published online: 20 May, 2015