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Spring-fed wetland and riparian plant communities respond differently to altered grazing intensity

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Summary

1. Spring-fed wetlands are nested within California's oak savanna–annual grassland, which is considered a non-equilibrium-type system because it shows little community-level response to changes in grazing intensity. This insensitivity to disturbance is thought to result from transient resource limitation and the annual life cycle tending to swamp the effects of defoliation. Because spring-fed wetlands receive relatively consistent and high inputs of water and nutrients, and they are dominated by perennial herbaceous vegetation, we hypothesized that these systems would respond to a grazing intensity gradient in a predictable manner, i.e. equilibrium dynamics would prevail.

2. We experimentally tested plant community responses of spring-fed wetlands to two levels of grazing intensity (light and moderate) and no grazing over 10 years. Wetland vegetation was tracked at two distinct geomorphological parts of the wetland system: spring heads, where emergent water formed marshy zones, and their resultant channelized creeks.

3. We used linear mixed effects models to estimate grazing intensity effects over time. A general result at both springs and creeks was that slope estimates of annual total herbaceous cover over time were negative under moderate grazing but positive under light grazing and grazing removal.

4. Diversity metrics were not affected by grazing treatments at springs. At creeks, Simpson's diversity index increased over time under moderate grazing. When averaged over 10 years, species evenness and Shannon's diversity index were greater under moderate grazing at creeks.

5. Species composition was highly variable from year to year at springs, with no separation of the first ordination axis (detrended correspondence analysis) amongst grazing treatments. In contrast, three relatively stable and distinct equilibria were evident for creeks. These results indicate that springs exhibited non-equilibrium dynamics while their creek counterparts, separated by several metres, behaved in a more equilibrium fashion, in relative terms.

6. Grazing removal significantly increased interannual variability in species composition at both geomorphological types, demonstrating that plant–animal interactions serve as the main control on community composition in these systems by reducing cover and promoting diversity and stability.

7. *Synthesis and applications.* Grazing managers in California's oak savanna–annual grassland have little control of species composition because the annual community is entrained by the weather. Our results show that first-order wetland–riparian communities nested within this annual grassland matrix can be manipulated via grazing intensity adjustments. However, marshy spring-fed wetland areas are less sensitive than channelized creeks to these manipulations and grazing removal will increase variability in species composition for both geomorphological types. Grazing management decisions are usually made at the landscape level based on the matrix vegetation, but nested ecosystems may respond differentially, requiring a more nuanced approach that includes site-specific information.

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Introduction

A major shift in plant community ecology occurred in the last quarter of the 20th century, away from an equilibrium model of community dynamics towards non-equilibrium explanations (DeAngelis & Waterhouse 1987; Ellis & Swift 1988; Oba, Stenseth & Lusigi 2000; Sullivan & Rohde 2002). Non-equilibrium is frequently invoked in rangeland ecology when community changes do not match predictions based on Clementsian successional theory (Westoby, Walker & Noy-Meir 1989; George, Brown & Clawson 1992; Allen-Diaz & Bartolome 1998; Fernandez-Gimenez & Allen-Diaz 1999; Jackson & Bartolome 2002), which posits that communities will respond in a sequential and predictable manner to the environment and disturbances. More importantly, an assumption of these models is that the environment and disturbance additively perturb a system from its equilibrium state, which is the product of competitive plant–plant and plant–animal interactions. The mechanism implicit in these models is the reduction or loss of inferior competitors via Gause's competitive exclusion principle (Grime 1973).

Non-equilibrium explanations of vegetation dynamics tend to be concentrated on arid and semi-arid ecosystems (rangelands) because they possess notoriously erratic weather at time scales that are relevant to their management (Bestelmeyer *et al.* 2003; but see Knapp *et al.* 2002; Seastedt & Knapp 1993). Such models allow for interactive effects between the environment and disturbances, resulting in the possibility of multiple vegetation states that are more or less stable in time (Stringham, Krueger & Thomas 2001). Moreover, non-equilibrium models allow for a decoupling of plant–animal interactions, offering a mechanistic explanation for the often observed lack of grazing effects on vegetation composition (Westoby, Walker & Noy-Meir 1989). Some have argued that non-equilibrium explanations are incorrectly applied to rangeland management and policy, spreading the notion that grazing has no effect on rangeland vegetation (Illius & O'Connor 1999; Cowling 2000; but see Sullivan & Rohde 2002).

Briske, Fuhlendorf & Smeins (2003) sought to integrate the rather polarized equilibrium vs. non-equilibrium debate by relying on Wiens's (1984) description of this framework as a continuum along which all communities can be placed. Subsequent empirical work has shown that not only can ecosystems exhibit more or less equilibrium-type behaviour, but also that within communities and across spatiotemporal scales some areas or components can be better explained with equilibrium and others with non-equilibrium dynamics (Fernandez-Gimenez & Allen-Diaz 1999; Oba *et al.* 2003). For instance, Buttolph & Coppock (2004) showed that riparian areas followed the equilibrium paradigm within an Andean pastoral system that could otherwise be characterized as non-equilibrium. On the other hand, Walker & Wilson (2002) subjected a long-term New Zealand vegetation data set to both formal (mathematical) and informal equilibrium criteria, but were unable to demonstrate formal equilibrium. Indeed, Roxburgh & Wilson (2000) showed that equilibrium was difficult to demonstrate even in a well-manicured university lawn.

NON-EQUILIBRIUM MECHANISMS

Conceptual models notwithstanding, relatively high species richness is maintained in many plant communities, especially grasslands. Much of the plant ecology community seeks mechanisms that allow for the co-existence of multiple species (Levine & Rees 2002; Coomes & Grubb 2003; Palmer, Stanton & Young 2003). The fundamental question arising from these efforts is: what phenomena subvert competitive exclusion in plant communities? Rees *et al.* (2001) summarized current understanding of plant diversity maintenance by stating that co-existence arises from two phenomena: a competition–colonization trade-off and niche differentiation. Under the former, succession towards an equilibrium state is the dominant process as species with small, high-density seed and high growth rates colonize gaps (where resources are abundant) but are ultimately outcompeted by species possessing bigger seed or other life-history characteristics that provide greater resource reserves as environmental resources are diminished. The non-equilibrium aspect of this explanation is the creation of gaps via disturbances that derail the march towards an equilibrium community.

Niche differentiation facilitates species' co-existence by spatial and/or temporal separation of resource supply and demand. An example of spatial separation has been demonstrated in California grasslands where perennial grasses, once established, access deeper belowground resources than annual grasses (Brown & Rice 2000). Here it seems that the competition–colonization trade-off is in effect initially, where the annual grasses proliferate and dominate, but if the better competitor (the perennial grass) can gain a foothold eventually the competition between these grasses with different life histories is reduced by spatial, and to some degree temporal, separation (Rice 1985; Dyer & Rice 1997).

SPRING-FED WETLANDS NESTED WITHIN CALIFORNIA ANNUAL GRASSLANDS

Non-equilibrium is invoked with niche differentiation especially where niche space is partitioned in the temporal realm (Blair 1997; Seastedt & Knapp 1993). A good example of this is manifested in Californian annual grasslands where species composition is notoriously variable from year to year (Pitt & Heady 1978; Bartolome 1989; Evans & Young 1989). Jackson & Bartolome (2002) showed that most of this variability is linked to the vagaries of the Mediterranean climate. Indeed, non-equilibrium vegetation dynamics are most often cited in areas with a highly variable climate (Huntsinger & Bartolome 1992; Sharp & Whittaker 2003; Stringham, Krueger & Shaver 2003). Nested within this non-equilibrium matrix of annual grasslands are spring-fed wetlands (Allen-Diaz & Jackson 2000; Allen-Diaz, Jackson & Phillips 2001), which are dominated by perennial herbaceous species. The nested nature of spring-fed wetlands makes them interesting systems for studying plant community dynamics because resources are abundant and their availability is synchronized to the growing season, compared with the surrounding annual grasslands where water, energy and sometimes mineral nitrogen availability are limiting and out of phase (Jackson *et al*. 1988, 1990; Chiariello 1989; Dahlgren, Singer & Huang 1997; Reynolds *et al*. 1997; Herman, Halverson & Firestone 2003). It is likely that plants of spring-fed wetlands undergo little abiotically driven resource limitation during their growing season as their forward-shifted phenology (spring–summer growth) allows consumption of ample supplies of exogenous water, light and nutrients during summer months (Jackson *et al*. 2006). This convergence of resource availability should favour equilibrium dynamics (Seastedt & Knapp 1993), where responses to disturbance regime alteration are sensitive and predictable. This follows from equilibrium theory, which holds that competitive exclusion is the primary structuring force of communities and that plant–plant and plant–animal interactions should be the most important modulators of competitive balance (Wiens 1984).

We tested hypotheses borne from equilibrium-type community dynamics by measuring vegetation responses to grazing intensity manipulations for over a decade in spring-fed wetlands and their associated creeks (Fig. 1). Our three equilibrium-based hypotheses were as follows.

1. Plant cover and grazing intensity will negatively co-vary because increasing defoliation intensity exposes an increasing amount of bare soil. An alternative and more general hypothesis that would also conform to equilibrium dynamics is that plant cover would be some function of grazing intensity, linear or otherwise. For instance, plant cover might respond to grazing intensity in a unimodal way, constituting evidence for the grazing optimization hypothesis (McNaughton 1979). The important part of our prediction is that plant cover would be related to grazing intensity in any way. If it was not, we would either determine that our grazing treatments did not have the desired effect or that factors other than plant–herbivore interactions were driving plant cover.

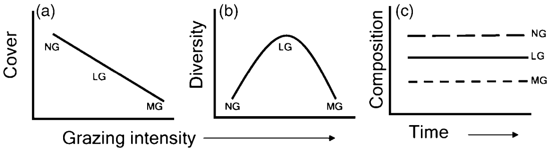

Fig. 1. Equilibrium-based hypotheses that (a) herbaceous cover would decline with increased grazing intensity, (b) diversity would have a unimodal response (i.e. the intermediate disturbance hypothesis) to increased grazing intensity, and (c) composition would be different across grazing intensity treatments over time. Under non-equilibrium dynamics, these parameters would not respond in a predictable manner to changes in grazing intensity because the vegetation state is not a function of plant–animal interactions but rather shaped by stochastic processes such as weather.

2. If a herbaceous plant community is in equilibrium with its environment and the organisms living within it, then plant diversity will show a unimodal response to a grazing intensity gradient, i.e. the intermediate disturbance hypothesis (Connell 1978). Low levels of defoliation result in a few fast-growing tall species, shading out others and resulting in low diversity. On the other hand, grazing-intolerant species would be outcompeted by grazing-tolerant species under high grazing intensities, so we would predict low diversity at either end of the grazing intensity gradient. In a non-equilibrium situation, environmental variability would swamp such diversity shifts, resulting in diversity measurements that are not related to grazing intensity.

3. Plant species composition will track grazing intensity changes because the realization of the plant community will be species whose competitive abilities are maximized under a particular level of defoliation. Hence this variable can be thought of as an integrator of plant cover and diversity responses.

We propose that a failure to reject any or all of these hypotheses would constitute more or less support for equilibrium dynamics prevailing in these systems, with the understanding that ecosystems need not be classified exclusively as either equilibrium or non-equilibrium (Fernandez-Gimenez & Allen-Diaz 1999; Jackson & Bartolome 2002; Briske, Fuhlendorf & Smeins 2003) but acknowledging the utility of such a classification for management (Allen-Diaz & Bartolome 1998; Wiens 1984; Westoby, Walker & Noy-Meir 1989; Behnke & Scoones 1993; Illius & O'Connor 1999)

Materials and methods

STUDY SYSTEM

A significant problem for managing riparian systems is the variability among systems themselves (Rosgen 1985). The diversity among riparian system characteristics has made them difficult to classify (Brown, Lowe & Pase

1984; Nelson & Nelson 1984). For example, first-order riverine systems may maintain vegetation similar to a fourth-order stream, yet their response to grazing may differ based on substrate or slope differences. Spring-fed wetlands are first-order riparian systems where subsurface water emerges in an often diffuse way. However, these waters usually come together to form more channelized creek systems within 1–20 m of the emergent source and maintain distinctive vegetation (forbs and grasses) compared with the up-slope wetlands (sedges and rushes).

In the blue oak woodlands of the Sierra Nevada foothills, spring-fed wetlands form small patches and corridors within a matrix of annual grassland that may or may not contain an oak *Quercus douglasii* Nee and/or foothill pine *Pinus sabiniana* Douglas overstorey. These first-order riparian areas are perennially moist and seasonally flooded; they usually occur at slope-breaks where underlying bedrock or relatively impervious clay layers intercept the soil surface. The resulting emergent water creates favourable conditions for highly productive cattails *Typha angustifolia* L., sedges (*Cyperus* spp., *Carex* spp., *Eleocharis* spp.) and warm-season grasses *Paspalum dilatatum* Poiret and *Echinochloa crus-galli* L. (P. Beauv.). Annual net primary production has been estimated at 400–1000 g m^{-2} dry biomass (Jackson 2002), making these some of the most productive herbaceous ecosystems in California. Cattails occur in saturated soils where water actually pools on relatively flat slopes. Sedges dominate where undulating microtopography creates a mosaic of vegetated tussocks and standing pools of water, which serve to baffle the flow of water on intermediate slopes. Finally, grass-dominated wetlands are characterized by perennial grass species that occur where soils are wet, but not necessarily saturated, most of the year.

STUDY SITE

We conducted this research at the Sierra Foothill Research and Extension Centre (SFREC), located on the western slope of the Sierra Nevada foothills in Yuba County, California, USA (Fig. 2). Owned and managed by the University of California (UC) for more than 40 years, it covers 2300 ha of steep to rolling landscape, 90–600 m a.s.l. The foothill oak savannas of this region have supported livestock grazing for more than 120 years. Grazing was especially heavy during the Gold Rush period of the late 1800s. When SFREC came under UC ownership and management in the 1960s, a more moderate grazing regime was implemented that persists today.

Weather data were downloaded from SFREC's web site (http://danrrec.ucdavis.edu/sierra_foothill/resources_climate_precipitation.html (accessed 22 Feb 2006).). The 30-year average total annual precipitation at SFREC is 72 cm, which falls as rain from autumn through spring. During the study period total rainfall was higher than normal (81 cm rain year^{-1}, CV = 31%, rain year October–September). Maximum and minimum air temperatures in the region range from 32·0 °C (July) to 2·2 °C (January). Soils in this area are generally shallow clay loams classified as auburn (loamy, oxidic, thermic, ruptic lithic xerochrepts) and argonaut (fine, mixed, thermic mollic haploxeralfs) series (Herbert & Begg 1969).

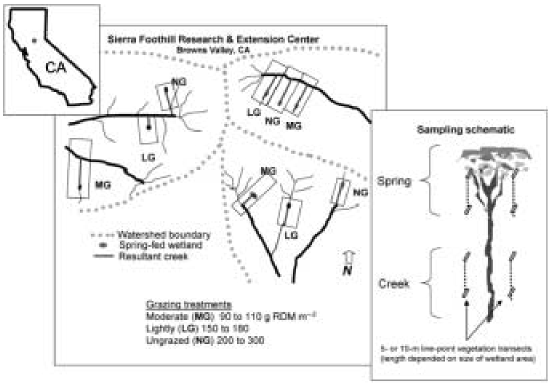

Fig. 2. Study site location, experimental layout and sampling schematic. Grazing treatments were applied to 2–5-ha pastures enclosing spring–creek wetland systems. Intensity of these treatments was applied based on the amount of residual dry matter (RDM) in annual grass uplands surrounding the wetland areas because this is the relevant management scale.

GRAZING TREATMENTS AND VEGETATION DATA COLLECTION

Within each of three watersheds, three spring-fed wetlands and their resultant first-order creeks were randomly assigned a grazing treatment, not grazed (NG), lightly grazed (LG) or moderately grazed (MG), applied annually from 1993 through 2002 (Fig. 2). Cattle were placed within 2–5-ha treatment areas surrounding wetland zones that were enclosed by a three-wire electrical fence for variable periods in November, January–March and May, to approximate customary autumn–winter–spring grazing practices and to achieve the desired residual dry matter (RDM) levels in the annual grass-dominated uplands. Because grazing during the growing season has little effect on the present year's forage composition and productivity in California's annual grasslands (Bartolome & McClaran 1992; Jackson & Bartolome 2002), managers use grazing intensities that leave the desired amount of RDM, thereby protecting soil and optimizing future productivity, which is generally related to RDM in a positive and linear way (Bartolome, Stroud & Heady 1980; Heady *et al*. 1992). Experienced SFREC range managers monitored grazing treatment intensity during each treatment period. Cattle were left on a site until visually estimated RDM target levels were attained for each period, representing moderate grazing (MG, *c*. 150 g RDM m^{-2}) or light grazing (LG, *c*. 250 g RDM m^{-2}). To verify grazing treatment levels, we clipped aboveground herbaceous biomass each June (1993–98) from three randomly located 0·0625-m^2 quadrats per fenced treatment plot, dried clippings for 2 days at 65 °C, and weighed and recorded biomass. These data demonstrated that we were effectively applying a grazing intensity gradient to these plots (NG, 375 ± 46; LG, 233 ± 38; MG, 149 ± 16; mean g RDM m^{-2} ± SE, $n = 18$).

Depending on the size of the wetland area, two permanent 10- or 5-m vegetation sampling transects were randomly established on each side of a spring and each side of a creek running parallel to surface water flow at each site (Fig. 2, inset). From 1992 to 2002, transects were sampled using the line-point method (Heady, Gibbens & Powell 1959) to determine plant species cover 3 weeks after late spring cattle removal from grazing treatments (late May/early June). Grassland vegetation sampling methods were reviewed by Sorrells & Glenn (1991) and point-based methods were preferred because they were correlated with biomass measurements of species abundance (Arny & Schmid 1942). The first interception of a lowered, sharpened metal rod with any part of herbaceous vegetation was recorded for 100 systematically sampled points along each transect (i.e. 200 points per experimental unit), irrespective of transect length. The variable transect lengths were imposed because perennial herbs associated with riparian zones occurred in very small areas at some sites. While the transect length and therefore the interval differed, the number of points recorded did not. We do not believe this introduced any bias into the measurements because the interval in both cases (either 1 or 0·5 dm) was larger than individual plant stems and leaves. Bias towards taller vegetation may be introduced with this method, although observations at other California grassland sites showed no differences between data collected in this fashion and where multiple hits were recorded through the herbaceous layer for each point (J.W. Bartolome, unpublished data). The herbaceous layer of these systems are 10–150 cm tall depending on species composition but they do not exhibit distinctive layers of vegetation, so we do not believe our line-point technique introduced significant bias into the estimation of species cover. This method has been employed by range scientists and grassland ecologists for decades (Heady 1958, 1977; Cook & Stubbendieck 1986; Heady *et al*. 1992; Bartolome *et al*. 2004; Kluse & Allen-Diaz 2005).

DATA ANALYSES

Total herbaceous cover was calculated as total vegetation hits (by species) divided by total possible hits (100). In subsequent statistical analyses, this response variable was arcsin transformed as suggested by Crawley (2002). Plant species identification and nomenclature followed *The Jepson Manual* (Hickman 1993). The site × species matrix was subjected to detrended correspondence analysis (DCA; PC-Ord vs. 4·01; McCune & Mefford 1999) from which the first ordination axis (DCA1) was extracted for use as a synthetic species composition index variable. Species richness and the Shannon and Simpson diversity indices (Mueller-Dombois & Ellenberg 1974) were also calculated for each plot × year combination using PC-Ord software.

Total cover, diversity and composition variables were subjected to linear mixed effects (LME) modelling (S-plus V.6) using the restricted maximum likelihood (REML) algorithm in three distinct ways. First, we used an ANCOVA LME approach where the fixed effects of fully parameterized models were slope estimates of the response variable (y) vs. year for each combination of geomorphology (subscripted by j) and grazing treatment (subscripted by k). This approach allowed us to determine how a given vegetation parameter was changing over time (significant slope) and how such a change might be modified by grazing management. Random effects included estimating the variance of intercepts across years for each level of watershed (subscripted by l), each level of grazing nested within watershed, and each level of geomorphology nested within grazing nested within watershed:

$$\begin{aligned}&y_{ijkl} = \beta_0 + \beta_1(year)_{jk} + (b_0)_l + (b_0)_{k,l} + (b_0)_{j,k,l} + \varepsilon_{ijkl}\\&i = (1, \ldots, 90),\ j = (1, 2),\ k = (1, 2, 3),\ l = (1, 2, 3)\\&b_l \sim N(0, \sigma_1^2),\ b_{k,l} \sim N(0, \sigma_2^2),\ b_{j,k,l} \sim N(0, \sigma_3^2),\\&\varepsilon_{ijkl} \sim N(0, \sigma^2) \qquad \text{eqn 1}\end{aligned}$$

Secondly, we used ANOVA LME models for responses variables whose 1993–2002 values had been normalized to the pre-treatment year (1992) by dividing the value for each experimental unit × year combination by its 1992 value. For these analyses the fixed effects were year (as a categorical factor subscripted by j), grazing treatment (subscripted by k) and interactions among these two factors. Random effects of fully parameterized ANOVA LME models were watershed (subscripted by l) and grazing nested within watershed. Geomorphology was excluded as a model term because there were insufficient degrees of freedom to test more general models; data for springs and creeks were analysed separately. ANOVA LME models had the following structure:

$$\begin{aligned}&y_{ijkl} = \beta_0 + year_j + graz_k + year \times graz_{jk} + (b_0)_l\\&\qquad + (b_0)_{k,l} + \varepsilon_{ijkl}\\&i = (1, \ldots, 90),\ j = (1, \ldots, 10),\ k = (1, 2, 3),\ l = (1, 2, 3)\\&b_l \sim N(0, \sigma_1^2),\ b_{k,l} \sim N(0, \sigma_2^2),\ \varepsilon_{ijkl} \sim N(0, \sigma^2) \qquad \text{eqn 2}\end{aligned}$$

Finally, we examined the amount of variation in species composition from year to year by calculating the coefficient of variation (CV = SD/mean) for DCA1 site scores for each plot over the 10-year study period, creating the variable DCA_{CV}. This variable (y) was subjected to ANOVA LME modelling with grazing treatment (subscripted as j) as the categorical fixed effect and random effects for the saturated model specified as (i) watershed (subscripted as k), (ii) grazing treatment nested within watershed and (iii) geomorphology (subscripted as l) nested within grazing treatment nested within watershed:

$$\begin{aligned}&y_{ijkl} = \beta_0 + graz_j + (b_0)_k + (b_0)_{j,k} + (b_0)_{l,j,k} + \varepsilon_{ijkl}\\&i = (1, \ldots, 9),\ j = (1, 2, 3),\ k = (1, 2, 3),\ l = (1, 2)\\&b_k \sim N(0, \sigma_1^2),\ b_{j,k} \sim N(0, \sigma_2^2),\ b_{l,j,k} \sim N(0, \sigma_3^2),\\&\varepsilon_{ijkl} \sim N(0, \sigma^2) \qquad \text{eqn 3}\end{aligned}$$

Serial correlation and heteroscedasticity functions were fitted and tested to these models, which along with random and fixed effects were tested by model comparison using likelihood ratios of competing models as described below.

For both the ANCOVA and ANOVA approaches random effect terms were sequentially dropped and nested models compared with those with more parameters by likelihood ratio tests. If models were significantly different ($P < 0{\cdot}05$), the model with the lower Akaike's information criterion (AIC) was selected, otherwise we selected the model with fewer parameters. We fitted all models with both correlated and heteroscedastic error structures but dropped these parameters if they did not significantly improve the model as determined by likelihood ratio tests ($P > 0{\cdot}05$; Pinheiro & Bates 2000). Specifying correlated variance–covariance matrices allows data collected from the same experimental unit over time to be treated as independent observations (Crawley 2002). To account for serial correlation of observations from the same plot over years (i.e. repeated measures), we used an autoregressive function (AR1) that fits a parameter describing residuals whose correlation declines exponentially with time. Once the random effects and error matrices were in place, residual vs. fitted plots were assessed visually for randomness and quantile–quantile plots were examined for departures from normality for each random factor and residuals, as suggested by Pinheiro & Bates (2000).

The significance of fixed effects was determined by dropping terms sequentially and comparing models with likelihood ratio tests. Treatment levels of significant terms were then sequentially combined and subsequent models compared with likelihood ratio tests to 'separate means'. For these comparisons, the full optimization maximum likelihood (ML) algorithm was used because likelihood ratio tests on models with different fixed effects parameters fitted with REML are not interpretable (Pinheiro & Bates 2000).

Results

COVER

For total vegetation cover, the most likely random effects structure with the highest likelihood included three nested categorical terms (model 1 in Table 1). Serial correlation amongst residuals from year to year was tested by including an autoregressive correlation coefficient in model 4, but the likelihood ratio test showed this model offered no improvement over the simpler model 1. To test for heteroscedasticity we fitted separate error variances for each level of grazing (model 5), which improved the model significantly.

With the random effects and variance–covariance matrix settled, we assessed the importance of fixed effects after refitting model 5 using the full optimization ML method (i.e. model 6 in Table 1 comprises the same parameter structure as model 5 but parameter estimates are made with ML rather than REML). We then sequentially dropped the fixed terms geomorphology (model 7) and grazing (model 8) and compared these models with likelihood ratio tests. Dropping the geomorphology term did not significantly alter the likelihood of the model, so the more general model 7 was retained. When the grazing fixed effect was dropped, the resulting model 8 had a significantly different likelihood than model 7, whose AIC was lower, and thus retained.

In model 9 (Table 1) ungrazed (NG) and lightly grazed (LG) treatment levels were combined for comparison with the more complicated model 7, which maintained all three treatment levels. As these models were not different, we concluded that the slope of cover over time was not different between NG and LG plots, and these treatment levels could be combined without significantly altering the predictive ability of the model. However, using this same approach we concluded that NG and LG treatments had slopes that were significantly different from moderately grazed (MG) plots with respect to cover (i.e. models 10 and 11 were significantly less likely than model 7). Model 9's fixed effects coefficients (data not shown) indicated that total vegetation cover was declining under MG and increasing under NG and LG plots.

DIVERSITY

No significant fixed effects were determined for ANCOVA LME models predicting species richness, evenness or Shannon's diversity index. However, using model selection criteria as above, model 6 was more likely than models 7 and 8 (Table 2) indicating, a significant year × grazing × geomorphology interaction was observed for Simpson's diversity index, which emphasizes species dominance (Mueller-Dombois & Ellenberg 1974). Rather than interpret the three-way interaction directly, we separated the data set along geomorphology lines, i.e. springs and creeks. Subsequent model selection showed the grazing term could be dropped from spring models without reducing the explanatory value (model S5; Table 2). Creek models for Simpson's diversity index showed that all treatment levels were significantly different from each other in the following sequence: LG < MG < NG (models C6–C8; Table 2).

Using the ANOVA LME approach, no significant differences amongst grazing treatments or years were found at springs for any of the diversity metrics. At creeks however, evenness and the Shannon diversity index were significantly greater on the MG plots than either NG or LG plots (Table 3).

COMPOSITION

For both springs and creeks our index of species composition was the first DCA ordination axis extracted from species × plot matrices (DCA1). In both cases the eigenvalue associated with these axes were quite high ($\lambda_{\text{springs}} = 0{\cdot}79$, $\lambda_{\text{creeks}} = 0{\cdot}84$), indicating strong gradients

Table 1. ANCOVA linear mixed effects model selection procedure for the response variable total vegetation cover

Model	Fixed effects	Random effects	Variance–covariance structure	d.f.*	AIC	Log L	Model test	L ratio	*P*	Interpretation of model comparison and subheader conclusion
Selecting random effects structure										
1	Year:Grazing:Geomorph†	1 | Watershed/Grazing/Geomorph‡	Equal var – Zero cov	11	–163·04	92·52				
2	Year:Grazing:Geomorph	1 | Watershed/Grazing	Equal var – Zero cov	10	–130·21	75·10	1 vs. 2	34·83	< 0·0001	Models are sig. diff.– > choose lower AIC (model 1)
3	Year:Grazing:Geomorph	1 | Watershed	Equal var – Zero cov	9	–113·03	65·51	1 vs. 3	54·08	< 0·0001	Models are sig. diff.– > choose lower AIC (model 1) Three levels of random effects represent best model given the data
Testing var-cov structure										
4	Year:Grazing:Geomorph	1 | Watershed/Grazing/Geomorph	Equal var – corAR1§	12	–162·23	92·50	1 vs. 4	1·22	0·26	Models not sig. diff.– > choose model 1 because simpler
5	Year:Grazing:Geomorph	1 | Watershed/Grazing/Geomorph	varIdent¶ – Zero cov	13	–169·62	97·81	1 vs. 5	10·58	0·005	Models are sig. diff.– > choose lower AIC (model 5) Heteroscedastic variances represent best model
Selecting fixed effects structure										
6**	Year:Grazing:Geomorph	1 | Watershed/Grazing/Geomorph	varIdent – Zero cov	13	–226·44	126·22				
7	Year:Grazing	1 | Watershed/Grazing/Geomorph	varIdent – Zero cov	10	–225·14	122·57	6 vs. 7	7·20	0·06	Models not sig. diff.– > choose model 7 b/c simpler
8	Year	1 | Watershed/Grazing/Geomorph	varIdent – Zero cov	8	–204·46	110·24	7 vs. 8	24·67	< 0·0001	Models are sig. diff.– > choose lower AIC (model 7) Differences in slope estimates for grazing intensity improve model
Separating means										
9	Year:(NG-LG vs. MG)††	1 | Watershed/Grazing/Geomorph	varIdent – Zero cov	9	–226·97	122·49	7 vs. 9	0·16	0·68	Combining NG and LG treatment levels no different than keeping the separate
10	Year:(NG-MG vs. LG)	1 | Watershed/Grazing/Geomorph	varIdent – Zero cov	9	–207·42	112·71	7 vs. 10	19·73	< 0·0001	Combining NG and MG significantly reduces deviance explained
11	Year:(LG-MG vs. NG)	1 | Watershed/Grazing/Geomorph	varIdent – Zero cov	9	–206·48	112·24	7 vs. 11	20·65	< 0·0001	Combining LG and MG significantly reduces deviance explained

*d.f., number of parameters estimated.

†Use of colon (:) indicates specification of interaction terms but no main effects. Multiplication sign (×) indicates main effects + interaction terms.

‡Vertical bar (|) separates continuous from categorical random effects in S-plus syntax. The forward slash (/) specifies nesting with general to specific moving from left to right. The random effects syntax for model 1 specifies random intercepts for each level of watershed, grazing within watershed, and geomorphology within grazing/watershed. A '1' to the left of the vertical bar indicates no random slopes should be fitted, only intercepts for those terms to the right of the vertical bar.

§corAR1 specifies residual correlation that decays exponentially with distance between time periods (i.e. years).

¶varIdent specifies separate error terms for each level of grazing (i.e. heteroscedasticity).

**Model 6 has a parameter structure identical to model 5 but estimates made with full optimization maximum likelihood rather than restricted maximum likelihood so that comparisons of models with different fixed effects terms could be performed.

††Combined treatment levels NG (not grazed) and LG (light grazed) for comparison with MG (moderately grazed).

Table 2. ANCOVA linear mixed effects model selection procedure for the response variable Simpson's diversity index (syntax explained in Table 1 footnotes)

Model	Fixed effects	Random effects	Variance–covariance	d.f.*	AIC	Log L	Model test	L ratio	*P*	Interpretation of model comparison and subheader conclusion
Selecting random effects structure										
1	Year:Grazing:Geomorph	1 | Watershed/Grazing/ Geomorph	Equal var – Zero cov	11	−96·37	59·18				
2	Year:Grazing:Geomorph	1 | Watershed/Grazing	Equal var – Zero cov	10	−87·48	53·74	1 vs. 2	10·88	0·001	Models sig. diff.– > choose lower AIC (model 1)
3	Year:Grazing:Geomorph	1 | Watershed	Equal var – Zero cov	9	−24·18	21·09	1 vs. 3	76·19	< 0·0001	Models sig. diff.– > choose lower AIC (model 1) Three levels of random effects (model 1) represent best model given the data
Testing var-cov structure										
4	Year:Grazing:Geomorph	1 | Watershed/Grazing/ Geomorph	Equal var – corAR1	12	−107·04	65·52	1 vs. 4	12·67	0·0004	Correlation parameter improves model
5	Year:Grazing:Geomorph	1 | Watershed/Grazing/ Geomorph	varIdent – Zero cov	14	−109·06	68·53	1 vs. 5	6·02	0·049	Variance estimates for each grazing level improve model Model 5 the best model given the data up to this point
Selecting fixed effects structure										
6*	Year:Grazing:Geomorph	1 | Watershed/Grazing/ Geomorph	varIdent – Zero cov	14	−160·25	94·13				Fitted with ML (maximum likelihood) instead of REML (restricted ML)
7	Year:Grazing	1 | Watershed/Grazing/ Geomorph	varIdent – Zero cov	11	−153·48	87·74	6 vs. 7	12·77	0·005	Cannot drop geomorph, choose model 6
8	Year:Geomorph	1 | Watershed/Grazing/ Geomorph	varIdent – Zero cov	10	−158·82	89·41	6 vs. 8	9·43	0·05	Cannot drop grazing, choose model 6
Separate model into springs and creeks										
Springs										
Selecting random effects structure										
S1	Year:Grazing	1 | Watershed/Grazing	Equal var – Zero cov	7	−55·68	34·84				
S2	Year:Grazing	1 | Watershed	Equal var – Zero cov	6	−28·35	20·18	S1 vs. S2	29·33	< 0·0001	Models sig. diff.– > choose lower AIC (model S1)
Testing var-cov structure										
S3	Year:Grazing	1 | Watershed/Grazing	varIdent – Zero cov	9	−54·63	36·31	S1 vs. S3	2·95	0·23	Unequal variances do not improve model (choose model S1)
S4	Year:Grazing	1 | Watershed/Grazing	Equal var – corAR1	10	−61·39	40·69	S1 vs. S4	8·76	0·003	Correlation parameter improves model (choose model S4)
Selecting fixed effects structure										
S5	Year	1 | Watershed/Grazing	Equal var – corAR1	8	−64·33	40·17	S4 vs. S5	1·05	0·59	Dropping grazing improves the model
Creeks										
Selecting random effects structure										
C1	Year:Grazing	1 | Watershed/Grazing	Equal var – Zero cov	7	−83·24	48·62				
C2	Year:Grazing	1 | Watershed	Equal var – Zero cov	6	−48·44	30·22	C1 vs. C2	36·80	< 0·0001	Models sig. diff.– > choose lower AIC (model C1)
Testing var-cov structure										
C3	Year:Grazing	1 | Watershed/Grazing	varIdent – Zero cov	9	−79·28	48·64	C1 vs. C3	0·05	0·977	Unequal variances do not improve model (choose model C1)
C4	Year:Grazing	1 | Watershed/Grazing	Equal var – corAR1	8	−84·82	50·41	C1 vs. C4	3·58	0·058	Correlation parameter does not improve model (choose model C1)
Selecting fixed effects structure										
C5	Year	1 | Watershed/Grazing	Equal var – Zero cov	5	−78·69	44·34	C1 vs. C5	8·55	0·014	Cannot drop grazing, choose model C1
Separating means										
C6	Year:(NG-LG vs. MG)	1 | Watershed/Grazing	Equal var – Zero cov	5	−77·63	43·82	C1 vs. C6	9·60	0·008	Combining NG and LG significantly reduces deviance explained
C7	Year:(NG-MG vs. LG)	1 | Watershed/Grazing	Equal var – Zero cov	5	−78·61	44·31	C1 vs. C7	8·62	0·013	Combining NG and MG significantly reduces deviance explained
C8	Year:(LG-MG vs. NG)	1 | Watershed/Grazing	Equal var – Zero cov	5	−78·21	44·10	C1 vs. C8	9·03	0·011	Combining LG and MG significantly reduces deviance explained

Table 3. ANOVA linear mixed effects model selection for the response variables evenness and Shannon diversity index [as a difference from pre-treatment (1992) values] at creeks (syntax explained in Table 1 footnotes)

Model	Fixed effects	Random effects	Variance–Covariance structure	d.f.	AIC	Log L	Model test	L ratio	*P*	Interpretation of model comparison and subheader conclusion
Evenness index										
Selecting random effects structure										
1	Grazing	1 | Year/Watershed/Grazing	Equal var – Zero cov	7	−49·9043	31·95214				
2	Grazing	1 | Year/Watershed	Equal var – Zero cov	6	−51·9043	31·95214	1 vs. 2	0·00001	0·9982	Models NS diff.– > choose simpler model (model 2)
3	Grazing	1 | Year	Equal var – Zero cov	5	−34·9449	22·47245	2 vs. 3	18·95937	< 0·0001	Models sig. diff.- > choose lowest AIC (model 2)
Testing var-cov structure										
4	Grazing	1 | Year/Watershed	Equal var – corAR1	7	−49·9117	31·95585	2 vs. 4	0·007	0·931	Models NS diff.– > choose simpler model (model 2)
5	Grazing	1 | Year/Watershed	varIdent – Zero cov	9	−51·1665	33·58327	2 vs. 5	3·262262	0·1957	Models NS diff.– > choose simpler model (model 2)
Selecting fixed effects structure										
6	NG-LG vs. MG	1 | Year/Watershed	Equal var – Zero cov	5	−73·0024	41·50121	2 vs. 6	0·42	0·52	NG NS diff. than LG
7	NG-MG vs. LG	1 | Year/Watershed	Equal var – Zero cov	5	−8·41708	9·20854	2 vs. 7	65·00	< 0·0001	NG sig. diff. than MG
8	LG-MG vs. NG	1 | Year/Watershed	Equal var – Zero cov	5	−3·71023	6·85512	2 vs. 8	69·71	< 0·0001	LG sig. diff. than MG
Shannon diversity index										
Selecting random effects structure										
1	Grazing	1 | Year/Watershed/Grazing	Equal var – Zero cov	7	161·7401	−73·87006				
2	Grazing	1 | Year/Watershed	Equal var – Zero cov	6	159·7401	−73·87006	1 vs. 2	0·000	1·00	Models NS diff.– > choose simpler model (model 2)
3	Grazing	1 | Year	Equal var – Zero cov	5	171·7329	−80·86645	2 vs. 3	13·99277	0·00	Models sig. diff.– > choose lowest AIC (model 2)
Testing var-cov structure										
4	Grazing	1 | Year/Watershed	Equal var – corAR1	7	156·9192	−71·4596	2 vs. 4	4·82	0·03	Models sig. diff.– > choose lowest AIC (model 4)
5	Grazing	1 | Year/Watershed	varIdent – Zero cov	9	156·7267	−69·36333	4 vs. 5	4·19	0·12	Models NS diff.– > choose simpler model (model 4)
Selecting fixed effects structure										
6	NG-LG vs. MG	1 | Year/Watershed	Equal var – Zero cov	6	146·0676	−67·03382	4 vs. 6	3·53	0·06	NG NS diff. than LG
7	NG-MG vs. LG	1 | Year/Watershed	Equal var – Zero cov	6	180·3466	−84·17328	4 vs. 7	37·81	< 0·0001	NG sig. diff. than MG
8	LG-MG vs. NG	1 | Year/Watershed	Equal var – Zero cov	6	187·8132	−87·90662	4 vs. 8	45·28	< 0·0001	LG sig. diff. than MG

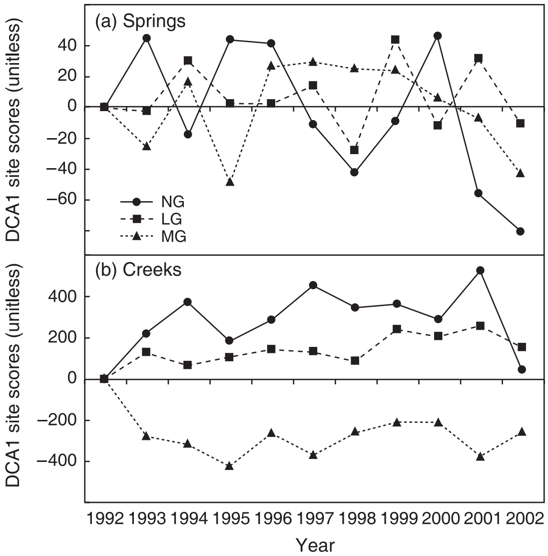

Fig. 3. Means by year of DCA1 site scores normalized to 1992 pre-treatment values for (a) springs and (b) creeks. Raw site scores were subjected to ANCOVA LME with year as the predictor variable, but no significant temporal trends were observed. ANOVA LME showed that normalized site scores were significantly different amongst all three grazing treatments at creeks but not springs, indicating alternative, relatively stable equilibria at the former and non-equilibrium at the latter.

in species space. No trends in DCA1 site scores were determined with the ANCOVA LME approach for either springs or creeks. However, ANOVA LME confirmed the pattern demonstrated in Fig. 3b, that soon after grazing treatment establishment creek vegetation equilibrated at more or less stable compositional states, while spring vegetation did not (Fig. 3a). The creek vegetation was following no directional trajectory, i.e. no significant slopes with the ANCOVA LME, so it was deemed stable. But the vegetation was significantly different amongst the three grazing treatments (models 7–9; Table 4), indicating the existence of distinctive compositional states.

The ANOVA LME for variability in species composition (DCA_{CV}) over years showed that both geomorphology and grazing were significant fixed effects, but no interaction between these factors was observed. Variability in composition was greater at springs than creeks (Fig. 4) but grazing effects were similar in each geomorphological type. Comparison of models comprising all three grazing treatments with those combining two grazing treatments showed that NG could not be dropped without significantly increasing residual deviance. Figure 4 shows that DCA_{CV} in NG plots was greater than LG and MG plots.

Discussion

Equilibrium dynamics were evident in these resource-rich systems, but the strength of the evidence was context dependent (Fig. 5). We did not reject our first hypothesis that herbaceous cover would negatively co-vary with

Table 4. ANOVA linear mixed effects model selection for the response variable DCA1 site scores (normalized to 1992 pre-treatment values) at creeks (syntax explained in Table 1 footnotes)

Model	Fixed effects	Random effects	Variance–Covariacne structure	d.f.	AIC	Log L	Model test	L ratio	P
Selecting random effects structure									
1	Year × Grazing	1 | Watershed/Grazing	Equal var – Zero cov	33	898·98	−416·49			
2	Year × Grazing	1 | Watershed	Equal var – Zero cov	32	899·93	−417·96	1 vs. 2	2·94	0·09
Testing var-cov structure									
3	Year × Grazing	1 | Watershed	Equal var – corAR1§	33	901·09	−417·54	2 vs. 3	0·84	0·36
4	Year × Grazing	1 | Watershed	varIdent – Zero cov	61	908·24	−393·12	2 vs. 4	49·68	0·009
Selecting fixed effects structure									
5*	Year × Grazing	1 | Watershed	Equal var – Zero cov	32	1042·27	−489·13			
6	Grazing	1 | Watershed	Equal var – Zero cov	5	1013·81	−501·14	5 vs. 6	24·81	0·58
Contrasting grazing means									
7	NG-LG vs. MG	1 | Watershed	Equal var – Zero cov	4	1021·087	−506·54	6 vs. 7	10·006	0·0016
8	NG-MG vs. LG	1 | Watershed	Equal var – Zero cov	4	1100·291	−546·15	6 vs. 8	89·2095	< 0·0001
9	LG-MG vs. NG	1 | Watershed	Equal var – Zero cov	4	1070·351	−531·18	6 vs. 9	59·2697	< 0·0001

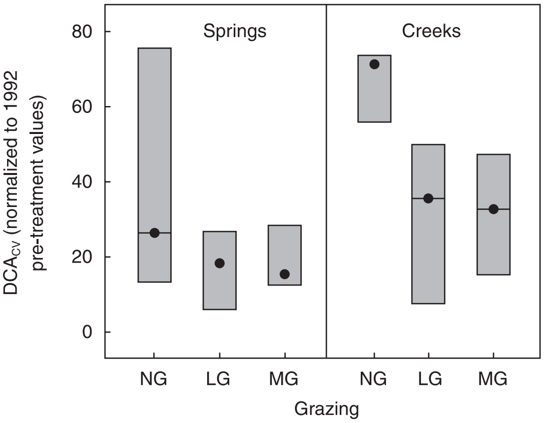

Fig. 4. Boxplots of the coefficient of variation of DCA1 site scores (DCA$_{CV}$) over the 10-year study period. (dot, median, lower and upper edge of boxes; boxes, interquartile range of the data). The species composition of ungrazed plots was more variable than both grazed treatment levels.

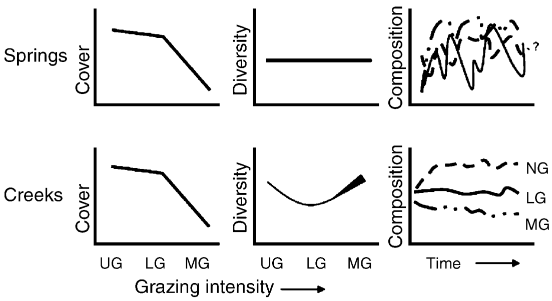

Fig. 5. Patterns we observed at springs and creeks. NG, ungrazed; LG, lightly grazed; MG, moderately grazed. The fatter line for the creek diversity plot indicates that three of four diversity metrics (Shannon's, Simpson's and evenness) were significantly greater under MG.

grazing intensity, lending support to equilibrium theory but also validating the efficacy of our MG treatment. Total covers on LG and NG plots were not significantly different but were both increasing over time. No general diversity patterns were observed. However, our highest grazing intensity level, MG, resulted in greater diversity and evenness at creek systems, which is not surprising given the lower values of plant cover observed in these creeks. Predictions of the intermediate disturbance hypothesis (IDH; Connell 1978; Mackey & Currie 2000), an equilibrium-based response, were not supported, but not because diversity was not related to grazing intensity. Instead, we observed a U-shaped response, where diversity was lowest under our intermediate grazing treatment. Our third hypothesis, that species composition would be controlled by grazing intensity, was strongly supported at creeks but not at all for springs. Composition at springs fluctuated wildly from year to year, while creeks supported alternative, relatively stable vegetation states for each grazing intensity treatment.

Both systems behaved in a more or less equilibrium manner, depending upon the metric used. Perhaps more important than determining whether or not equilibrium dynamics were exhibited, was the observation that in the absence of grazing disturbance these systems tended towards non-equilibrium dynamics, where species composition was much more variable from year to year when grazing was removed and the effects of environmental fluctuations were damped under grazing. This was a general result for both springs and creeks. However, these two separate, but linked, systems also behaved quite differently and would find different niches along Wiens's (1984) equilibrium–non-equilibrium continuum. Very little control of grazing disturbance on plant composition was exhibited at emergent springs, which appeared to be more entrained by year to year variability than creeks (Fig. 3). The creeks very clearly reached alternative equilibrium states that were determined by differences in grazing intensity. This disparity is interesting given these systems are separated by only several metres in all cases. A possible explanation is differences in the geomorphology of these systems. Springs tend to be non-channelized marshy areas with slow subsurface flow, while creeks are by definition channelized with surface flow (Allen-Diaz, Jackson & Fehmi 1998). Along creek channels there is usually a moisture gradient emanating up-slope from the midpoint of the channel that is reflected as a plant composition gradient. Hence a change in water quantity might differentially affect springs and creeks because the entire spring area would be affected by a dry-down, for instance, while the same dry-down conditions at creeks would simply shift the moisture gradient and the corresponding plant community in space. This speculation remains an untested hypothesis.

Many have shown that disturbance promotes diversity (Collins *et al.* 1998; but see Tilman 1983; Pollock, Naiman & Hanley 1998; Mackey & Currie 2000). However, disturbance–diversity relationships have not been consistently demonstrated for wetland systems (Keddy 2000; Moore & Keddy 1989), especially in Mediterranean climates such as California's where interannual weather variability is high. This variability has been noted as key to the development of California's many and varied riparian ecosystems (Gasith & Resh 1999). Disturbance–diversity relationships are often unimodal (Grime 1973; Sousa 1979; Huston 1994) as described by the above-mentioned IDH. A shortcoming of this hypothesis is the conflation on the abscissa of disturbance and productivity (biomass) gradients (Pollock, Naiman & Hanley 1998). As a result, highly disturbed, highly productive ecosystems (such as spring-fed riparian zones) do not fit well into this model. Huston's (1994) dynamic equilibrium model (DEM) allows for the intermediate disturbance level to scale positively with community productivity such that greater disturbance is required to achieve intermediate status along an increasing productivity gradient. Hence our lightly grazed wetlands may have been receiving qualitatively different disturbance treatments than our lightly grazed creeks because of productivity differences, which were not measured but observed, even though grazing intensities on an animal density basis were identical.

Huston's (1994) DEM also allows for temporal or spatial heterogeneity to dampen the effect of disturbance on diversity (Pollock, Naiman & Hanley 1998). Spatial heterogeneity may be greater at creeks compared with wetlands because of the above-mentioned channelization of surface water flow at creek sites. Cross-sectional microsite gradients probably exist from mid-creek to bank edges, adding to the spatial heterogeneity of creeks. Hence moderately grazed creeks maintained greater diversity than either ungrazed or lightly grazed sites. If this is the case, our range of grazing intensity treatments may have encompassed only the ascending part of the unimodal response curve. Although we may not have implemented a full range of disturbances (e.g. we could have implemented a more severe grazing treatment), diversity responses to our disturbance gradient in the long-term study indicated that moderate grazing should promote greatest species co-existence in creek systems but not in springs.

Zedler & Beare (1986) showed that community dominance in estuarine salt marshes of southern California was related to rainfall–drought cycles, where dry periods favoured *Salicornia virginica* and *Spartina virginica* while *Typha domingensis* dominance was contingent upon the length of flooding in high rainfall periods. A similar situation in the Sierra Nevada foothills is plausible, where a disturbance in the form of flushing and scouring of spring-fed wetlands in high-rainfall years creates a more variable environment for alternative plant groups that expand and contract depending on prevailing conditions. Grazing disturbance maintained a more static vegetation state, but release from grazing relinquished more control of the community to the environment, or at least rendered it more sensitive. In a similar vegetation community, the Pampas of South America, Facelli, Leon & Deregibus (1989) found that ungrazed paddocks varied more interannually than grazed paddocks dominated by the bunchgrass *Paspalum dilatatum*, a dominant grass in our ecosystem. Curiously, this is opposite to responses of warm-season grasses of the tallgrass prairie (Collins *et al*. 1998; Knapp *et al*. 1999), but those systems receive high-frequency burning treatments, which tend to decrease plant diversity (Turner, Seastedt & Dyer 1993).

Our findings describe highly dynamic systems, more or less entrained by environmental stochasticity depending on the disturbance regime. They appear to more closely follow environmental phenomena, and therefore exhibit more variability, when grazing disturbance is removed, i.e. non-equilibrial. A more static, equilibrium vegetation state appears to be maintained by grazing disturbance, especially at creeks. We predicted that equilibrium dynamics would prevail at these resource-rich wetlands. We based this prediction on the idea that competitive exclusion is subverted by grazing disturbance, whose removal would instigate a reduction in diversity. A result of the competitive exclusion process is that, via this mechanism, an equilibrium plant community will emerge dominated by competitively superior species. Light to moderate grazing on spring-fed wetlands and their resultant creeks can maintain herbaceous cover and diversity. However, total cover should be frequently monitored in order to assess potentially undesirable trends in the amount of bare ground exposed at higher grazing intensities. Because equilibrium dynamics were evident to some degree, grazing intensities for these systems can be adjusted to manipulate community structure to achieve management goals.

By stratifying geomorphological types, we showed a differential response from proximate systems, demonstrating the need for management decisions based on site-specific criteria. For example, one might adjust grazing intensities specifically for rehabilitation of a marshy spring area differently than for a channelized riparian zone. As a consequence, simultaneous management for multiple types of riparian and matrix vegetation will require persistent monitoring and flexibility. More of the type of information generated from this study, long-term and experimental, is needed for sound adaptive management of highly variable riparian ecosystems of arid and semi-arid regions, but especially those where a Mediterranean climate prevails.

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