



Livestock exclusion alters plant species composition in fen meadows

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Keywords

Fen meadows; Grazing cessation; Litter accumulation; Livestock exclusion; Peat formation; Species functional traits

Abbreviations

NMDS = Non-metric multidimensional scaling; US = United States.

Nomenclature

Baldwin et al. (2012) for vascular plants, Norris & Shevock (2004) for bryophytes

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Abstract

Questions: Our study evaluated how species composition and plant traits that indicate functioning condition in fens responded to grazing cessation over time in an arid ecosystem of the western US. The specific questions addressed were: (1) how does livestock exclusion influence species composition in fens; (2) is grazing cessation associated with shifts in species functional traits that indicate fen condition; and (3) what is the pattern of response to livestock exclusion over time?

Location: Plumas National Forest, CA, US.

Methods: We studied paired fenced and unfenced study sites in two fens to examine the effects of livestock exclusion. Parallel transects were established at each site, and plant species and ground cover were repeatedly surveyed, once prior to and multiple times following treatment, using 0.01 m² frequency frames. We used NMDS to analyse species composition, RLQ and fourth-corner analysis to evaluate species functional traits and environmental variables, and linear mixed effects models to examine differences in responses between fenced and unfenced study sites over time.

Results: After fencing, we observed unexpected shifts in species composition and plant functional traits. Grazed sites were associated with peat-forming obligate wetland, moss and sedge species, while fenced sites were characterized by non-peat-forming facultative upland, and upland forb, grass and early seral species. Species composition also varied between sites and sample years.

Conclusions: We found that livestock exclusion strongly affects plant species composition in fens, including promoting species with functional traits that indicate a loss of functioning condition, such as ruderal and upland species. Possible explanations for these observed shifts include: (1) biomass accumulation in the absence of herbivory, (2) competitive exclusion in fenced sites, (3) succession, (4) the abiotic conditions of our study sites, particularly hydrology and nutrient status, and (5) interactions among these factors. We conclude that degradation of fen wetlands caused by livestock grazing in the arid western US may not be reversed by excluding livestock alone.

Introduction

Livestock grazing has been associated with a number of negative impacts in arid western ecosystems of the US (Belsky et al. 1999; Jones 2000). Although livestock can have positive ecological effects in areas with a long evolutionary history of grazing (Milchunas & Lauenroth 1993), plant communities in much of the western US did not evolve with analogues to modern domesticated cattle, such as bison (*Bison bison*; Mack & Thompson 1982). Instead,

these systems were grazed over the past 10 000 yr at low to moderate intensity by small native herbivores, including mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*) and antelope (*Antilocapra americana*; Ratliff 1985; Dull 1999). Given that domestic cattle can weigh up to 20 times more than these native herbivores, it is not surprising that many of the negative impacts associated with livestock grazing are the physical effects of trampling and hoof action, such as soil compaction and erosion (Belsky et al. 1999; Jones 2000).

One of the most often identified causes of fen degradation in the Sierra Nevada, CA, US, is livestock use (Ratliff 1985; Cooper & Wolf 2006). Fens can be disproportionately targeted by livestock in seasonally dry climates such as the mediterranean regions of the western US, where grazing often becomes concentrated in fens in the late summer when most surrounding areas are dry (Ratliff 1985; Cooper & Wolf 2006). Fens are groundwater-fed wetlands that accumulate organic matter as peat, requiring persistent anaerobic conditions and cold temperatures to limit organic matter decomposition (Bridgham et al. 1995). Fens may be especially prone to damage from livestock because of their saturated soils. Livestock trampling and hoof action in fens can result in soil compaction, exposure and drying of the peat body, causing it to quickly decompose (Ratliff 1985; Whittington & Price 2006; Weixelman & Cooper 2009). Hydrologic alteration caused by livestock can also damage fens, which are sensitive to small fluctuations in the depth of the water table, affecting not only the rate of peat formation, but also the species composition of the fen (Holden et al. 2004; Diggelen et al. 2006). Livestock can alter the nutrient status of fens through manure deposition, causing changes in species composition, declines in biodiversity and loss of rare species (Bedford et al. 1999).

Concerns about the potentially negative effects of livestock use in the arid western US have led land managers to fence degraded riparian wetland, meadow and fen ecosystems (Sarr 2002). However, the effects of livestock exclusion on fens, in particular, are not well known in the US. In European fens, many studies have shown that species diversity decreases without livestock grazing or mowing (Hald & Vinther 2000; Diemer et al. 2001). However, most European fens have been at least partially drained and have an evolutionary history of grazing by large, heavy herbivores that are analogous to modern domesticated livestock. We know of only two studies that have evaluated livestock exclusion from fens in the US. Tesauro & Ehrenfeld (2007) found that grazing cessation from fens in the eastern US increased the cover of invasive species. Middleton (2002) found that after excluding cattle from fens in the mid-western US, shrubs invaded a formerly grazed fen but not a nearby ungrazed reference site. Both authors concluded that the effect of removing livestock from fens is unpredictable, and may depend on the condition of the fen prior to enclosure, including nutrient status and the presence of invasive species.

Fens support a disproportionate number of rare, threatened and endangered bryophytes and vascular wetland plant species, making them a priority for research and conservation around the world (Bedford & Godwin 2003; Diggelen et al. 2006). Assessments of fen condition are often used to identify and prioritize sites for restoration. In

addition to directly evaluating soils and hydrology, fen condition can be determined by the presence of key indicator plant species (Bedford & Godwin 2003; Weixelman & Cooper 2009). Many plant species are sensitive and reliable indicators of soil moisture (Lichvar et al. 2016). Plants that indicate a healthy fen are obligate wetland species, demonstrating that the water table is near the soil surface. The presence of peat-forming species, whose underground biomass contributes most of the organic matter to the peat body, is also critical for the persistence of fen wetland ecosystems (Timmermann et al. 2006; Schrautzer et al. 2013). A degraded fen, on the other hand, is dominated by upland, non-peat-forming plant species that indicate a lowered water table, eutrophication and soil drying (Weixelman & Cooper 2009). Seral stage can also reflect the condition of fens and meadows, with late seral species indicating stable plant communities and proper functioning condition (USDA 1997; Weixelman & Zamudio 2001).

Objectives and hypothesis

Our study evaluated how species that indicate functioning condition in fens respond to grazing cessation. The research questions we addressed were: (1) how does livestock exclusion influence species composition; (2) is livestock exclusion associated with shifts in species functional traits that indicate functioning condition in fens; and (3) what is the pattern of response to livestock exclusion over time? We hypothesized that excluding livestock would alter species composition and result in an increase in peat-forming obligate wetland and other species with traits that indicate functioning condition in fens. We expected this trend to be linear, and to increase over time.

Methods

Site description

Sampling was conducted in two fens in the northern Sierra Nevada range of California, US. The two fens, referred to as Old House (39°56'3.12" N, 120°34'58.28" W) and Woodsy (39°54'2.52" N, 120°33'25.2" W), are located approximately 4 km apart at 1780 m a.s.l. (Appendix S1). Found within broad montane meadows, our study sites remain wet well into the summer months due to a network of springs that discharge groundwater that is slightly acidic to neutral pH (5.5–6.9), classifying them as moderate-rich fens (Weixelman & Cooper 2009). The study area experiences a montane mediterranean climate, with warm dry summers and cold wet winters. Average annual precipitation over the course of our study was approximately 32 cm (<http://wrcc.dri.edu>, 2/1/17). Our study fens resemble grasslands in structure, and are dominated by peat-forming obligate wetland sedges that do not form tussocks.

Peat-forming mosses such as *Drepanocladus aduncus* and *Philonotis fontana* are dominant; *Sphagnum* moss species are absent. Trees and shrubs are very rare. Prior to our study, these fens were considered at-risk due to physical degradation (i.e. exposed peat and excessive erosion) resulting from livestock use, and fencing was proposed to protect them. Upland, non-peat-forming and disturbance indicator species (Weixelman & Cooper 2009) were also present in both fens.

Our study sites are both located within the 5146-ha Grizzly Valley Grazing Allotment in the Plumas National Forest. This allotment was grazed exclusively with sheep until 1945, when cattle were introduced. We fenced a portion of the two fens, using temporary electric fencing, while the remainder of the fens and the surrounding meadow landscape was left open to livestock grazing. These fenced–unfenced paired sites were located 262 m apart at Woodsy Fen and 550 m apart at Old House Fen. Over the course of this study, 505 cow–calf pairs were permitted annually within the unfenced portions of the fens between 16 Jun and 15 Sept.

Old House Fen was fenced in 2007 and Woodsy Fen was fenced in 2009. Old House was sampled in 2007 and 2008. Both fens were sampled simultaneously in 2009, 2010, 2012 and 2015, however due to different fencing dates, our time since fencing variable varied between fens. We included multiple sampling dates in order to capture pre-fencing condition, to account for inter-annual variability in climatic and environmental conditions, and to evaluate the pattern and rate of vegetation change in response to fencing over time.

Field sampling

Within each site, four or five parallel 25-m long transects were established using a systematic sampling approach. Twenty-five 0.01 m² frequency frames were placed along each transect at 1 m intervals, for a total of 100–125 frames per site. All plant species rooted within the frequency frames were identified following the nomenclature of Baldwin et al. (2012) for vascular species and Norris & Shevock (2004) for bryophytes. Frequency was calculated for each species by dividing the number of occupied frames by the total number of frames ($n = 25$) along each transect. Species richness was calculated as the total number of species per transect. Species turnover (β -diversity) between sampling years was calculated as $\beta = [Y_1 - C] + [Y_2 - C]$; where Y_1 is the total species richness of the first year, Y_2 is the total species richness of the following year, and C is the number of species they have in common. Percentage cover of ground cover variables (exposed peat, water, litter, moss, hoof prints, cow dung and basal cover of vegetation) was calculated from point intercept measures collected at

the four corners of each frequency frame for a total of 100 points per transect. Basal cover of vegetation refers to the amount of ground occupied by plant stems where they emerge from the soil (Stocking 1994). Transect was the unit of analysis for all variables.

We included annual precipitation in our analyses to serve as a proxy for hydrologic variables, such as water table depth; we did not measure directly. Inclusion of this variable in our models allowed us to separate the response of the plant community to our fencing treatment from the effect of inter-annual variation in climatic and other environmental conditions. Precipitation data were obtained from a National Weather Service station located 18 km from our study sites (<http://wrcc.dri.edu>, 10/1/16).

Species functional traits

We classified both vascular and non-vascular species according to functional traits commonly used to assess fen condition. Wetland indicator status was defined according to the National Wetland Plant List (Lichvar et al. 2016). Peat-forming species and disturbance indicator species, which include both early seral and species that indicate lowered water tables and drying soil conditions, were identified according to Weixelman & Cooper (2009). We classified species as early, mid- or late seral following the definitions in U.S. Department of Agriculture (1997) and Weixelman & Zamudio (2001). Functional trait classification of the most common species in our study is provided in Appendix S1.

Statistical analysis

How does livestock exclusion influence species composition?

To examine species composition, we evaluated species frequency data using NMDS analysis. Data from all sampling years were utilized, with the exception of species that occurred in <5% of transects, leaving a total of 37 species and 88 transects for the analysis. A second matrix of environmental variables included percentage cover values for exposed peat, basal vegetation, litter, water, cow dung, moss, hoof prints; as well as annual precipitation (cm); time since fencing (years); fen (Woodsy or Old House), treatment (fenced or unfenced) and sample year. A Multi-Response Permutation Procedure (MRPP; Mielke 1984) with a rank-transformed Sørensen (Bray-Curtis) distance measure was used to test whether site, treatment or time since fencing affected species composition. We employed indicator species analysis to identify species with both high specificity and fidelity for fenced and unfenced treatments (Dufrêne & Legendre 1997). All analyses were conducted in PC Ord (v 6; MjM Software Design, Gleneden Beach, OR, US).

Is livestock exclusion associated with shifts in species functional traits?

The relationships between species functional traits and environmental variables were tested by combining RLQ and fourth-corner analyses as recommended by Dray et al. (2014). In the RLQ analysis we used correspondence analysis (CA) for the L (species frequency) table, Hill-Smith principal components analysis (PCA) for the R (environmental variables) table (Hill & Smith 1976) and multiple correspondence analysis (MCA) for the Q (functional traits) table. We then applied fourth-corner tests to the output of the RLQ ordinations, allowing us to statistically test and quantify the relationships between environmental variables and species traits. Significance was assessed based on 49 999 permutations, and *P*-values were adjusted using the false discovery rate method (Dray et al. 2014). Analyses were performed with the *ade4* package (Dray & Dufour 2007) in R (v 3.3.2; R Foundation for Statistical Computing, Vienna, AT).

Does the response to livestock exclusion change over time?

To evaluate how individual species, species richness and turnover, environmental variables and functional traits responded to fencing over time, we fitted linear mixed effects models (LMEM) in the R *lme4* package (Bates et al. 2015). All models specified time since fencing (years) and treatment (fenced or unfenced) as fixed effects, with transect specified as a random effect. The frequency of tree and shrub species, and of upland and facultative upland species, were combined to create sufficient sample sizes for analysis.

Results

We identified 53 plant species in our fen study sites. An additional ten taxa could only be identified to family or genus due to immaturity or lack of sufficient plant material (Appendix S1). Obligate wetland peat-forming sedges, such as *Eleocharis quinqueflora* and *Carex simulata*, were among the most frequently occurring species across all sites and years (Appendix S1). However, species from every functional trait category were represented, including a large number (39 species) of forbs (Appendix S1). There was very little exposed peat at either of our study sites, with a mean cover of only 3%. Mosses, basal vegetation and litter were the most common ground cover variables, averaging 27%, 22% and 18% cover, respectively. Total species richness, obligate wetland, and peat-forming species frequency were the same at both fens prior to fencing. However, Woodsy Fen had more early seral and forb species than Old House Fen, and also supported the only shrub species, *Salix eastwoodiae*. Annual precipitation over

the 9 yr of our study ranged from 21 cm in 2007 to 57 cm in 2010, averaging 32 cm. This represented drought conditions relative to the average annual rainfall of 52 cm recorded over the past 100 yr (<http://wrcc.dri.edu>, 10/1/16; Diffenbaugh et al. 2015).

Effect of livestock exclusion on species composition patterns

The final NMDS ordination solution had three dimensions and a stress of 13.08, an instability of <0.001, and a cumulative R^2 of 0.892 (R^2 axis 1 = 0.505, axis 2 = 0.192, axis 3 = 0.196). Litter cover was strongly correlated with axis 1 ($R^2 = 0.31$), while variables associated with livestock utilization (hoof print and cow dung cover) were correlated with axis 2 ($R^2 = 0.112$ and 0.109, respectively; Fig. 1). Annual precipitation and other ground cover variables were not significantly related to the ordination axes. Species composition significantly differed between fens ($T = -14.14$, $A = 0.05$, $P < 0.001$), between fenced and unfenced treatments, ($T = 10.88$, $A = 0.200$, $P < 0.001$) and as a result of the number of years since fencing ($T = -11.36$, $A = 0.095$, $P < 0.001$).

Three species were identified as significant indicators of unfenced sites. These were perennial, obligate wetland, peat-forming sedge species *Carex nebrascensis* (indicator value (*IV*) = 59.1, $P < 0.001$) and *Eleocharis quinqueflora* ($IV = 57.6$, $P < 0.001$), and an obligate wetland peat-forming moss, *Drapanocladus aduncus* ($IV = 55.4$, $P < 0.001$). A

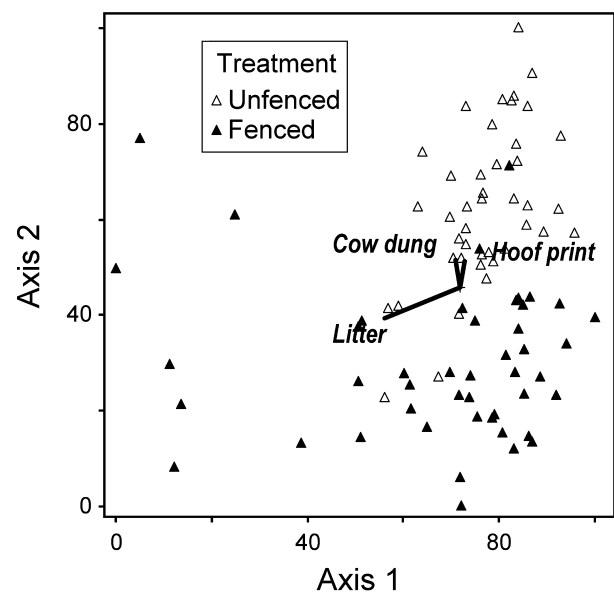


Fig. 1. Scatter plot of NMDS axis scores for fen species ordination. Plots are symbolized to show the distribution of fenced and unfenced treatments and the bi-plot of environmental variables where $R^2 > 0.1$ (litter, hoof print and cow dung cover) along ordination axes 1 and 2.

larger number of species (19 species) were significant indicators of fenced sites (see Appendix S1). Of these, six species are considered indicators of disturbance, 14 are not peat-forming, seven are facultative wetland or upland species, six are early establishers and one is a shrub (*S. eastwoodiae*).

The influence of livestock exclusion on species functional traits and environmental variables

The first axis of the RLQ analysis accounted for 80% of the total co-inertia (i.e. link between the traits and environmental variables) and the second axis for 9%. This represented 38% of the correlation expressed for the first axis in the CA of species composition (table L), 68% of the total variance expressed for the first axis in the Hill-Smith PCA of the environmental variables (table R) and 90% of the total variance expressed for the first axis in the MCA of the traits table (table Q). The global test of the fourth-corner analysis revealed a highly significant relationship between species distribution and environmental variables (model 2; $P < 0.001$) as well as between species composition and functional traits (model 4; $P = 0.032$). Total inertia of the combined models was also significant ($P_{srlq} = 0.03$; Dray & Legendre 2008).

Applying the fourth-corner method to the RLQ ordination scores revealed a number of significant associations between RLQ axes, species traits and environmental variables (Fig. 2, Appendix S1). The first RLQ axis was positively correlated with grazing (unfenced), water and cow dung cover and non-disturbance indicator, peat-forming, obligate wetland, moss and sedge species functional traits. The first RLQ axis was negatively associated with livestock exclusion (fenced), covers of litter and exposed peat, and species functional traits of non-peat-forming, facultative upland, forb, grass and early seral species functional traits. The second RLQ axis was negatively associated with the ground cover of mosses. No species functional traits emerged as significantly associated with this axis.

Changes over time in response to livestock exclusion

Species richness, including both vascular and non-vascular species, was significantly higher in fenced sites than in unfenced sites, and this did not change over the 9 yr of our study (LMEM: main effect of fencing: $t = -4.1$, $P < 0.001$; of time since fenced: $t = 1.6$, $P = 0.11$). The mean number of species was 18 (± 0.6) in fenced sites and 11 (± 0.5) in unfenced sites. Species turnover (β -diversity) between the

(a) Functional traits				(b) Environmental variables		
Trait	Category	AxR1	AxR2	Variable	AxcQ1	AxcQ2
Disturbance indicator	No			Unfenced		
	Yes			Fenced		
Peat-forming	Yes			Years since fencing		
	No			Sample year		
Wetland status	Facultative			Exposed peat cover		
	Facultative upland			Basal vegetation cover		
	Facultative wetland			Cow dung cover		
	Obligate wetland			Moss cover		
	Upland			Hoof print cover		
Life form	Forb			Litter cover		
	Grass			Water cover		
	Moss			Precipitation		
	Rush					
	Sedge					
	Shrub					
	Tree					
Seral stage	Late					
	Mid					
	Early					

Fig. 2. Combination of fourth-corner and RLQ results. Fourth-corner tests between the first two RLQ axes for significant relationships between: (a) environmental gradients (AxR1/AxR2) and traits, and (b) trait syndromes (AxcQ1/AxcQ2) and environmental variables. Positive significant associations are black cells, negative associations are grey cells, and variables with no significant associations are left blank. Significance was assessed with 49 999 permutations and false discovery rate adjusted P -values.

first sampling period prior to fencing and the first year after fencing was almost two-fold greater in fenced sites compared with unfenced sites ($\beta = 10$ and 5.5 , respectively) and remained significantly greater in fenced sites for the remainder of the study (LMEM: main effect of fencing: $t = -3.4$, $P < 0.01$; of time since fenced: $t = -9.4$, $P = 0.79$).

The frequency of a number of individual species changed over time in response to fencing. *Eleocharis quinqueflora*, an obligate wetland, peat-forming, sedge species, declined significantly over time after fencing relative to unfenced sites (Fig. 3a). On the other hand, the frequency of *Carex utriculata*, also an obligate wetland, peat-forming sedge, increased significantly after sites were fenced, but remained unchanged with continuous grazing (Fig. 3b). *Philonotis fontana*, an obligate wetland, peat-forming moss species, also declined in fenced sites over time relative to

unfenced sites ($t = 2.0$, $P = 0.04$). Several other species increased in fenced sites relative to unfenced sites over time, including *Muhlenbergia filiformis*, an early seral, non-peat-forming, obligate wetland grass species ($t = -2.1$, $P = 0.03$), *Deschampsia cespitosa*, a disturbance indicator, non-peat-forming, facultative wetland grass species ($t = -2.1$, $P = 0.03$), and *Micranthes oregana*, a peat-forming, obligate wetland forb species ($t = -1.95$, $P = 0.05$).

The frequency of early seral species increased after fencing (Fig. 3d), as did the frequency of facultative upland and upland species (time since fenced \times treatment interaction: $t = -2.4$, $P = 0.02$). Conversely, the frequency of mosses declined over time in fenced relative to unfenced sites, (time since fenced \times treatment interaction: $t = 2.3$, $P = 0.02$). We did not observe changes in the frequency of woody species (*Pinus jeffreyi* and *S. eastwoodiae*) or the frequency of forbs over time in response to fencing. Litter

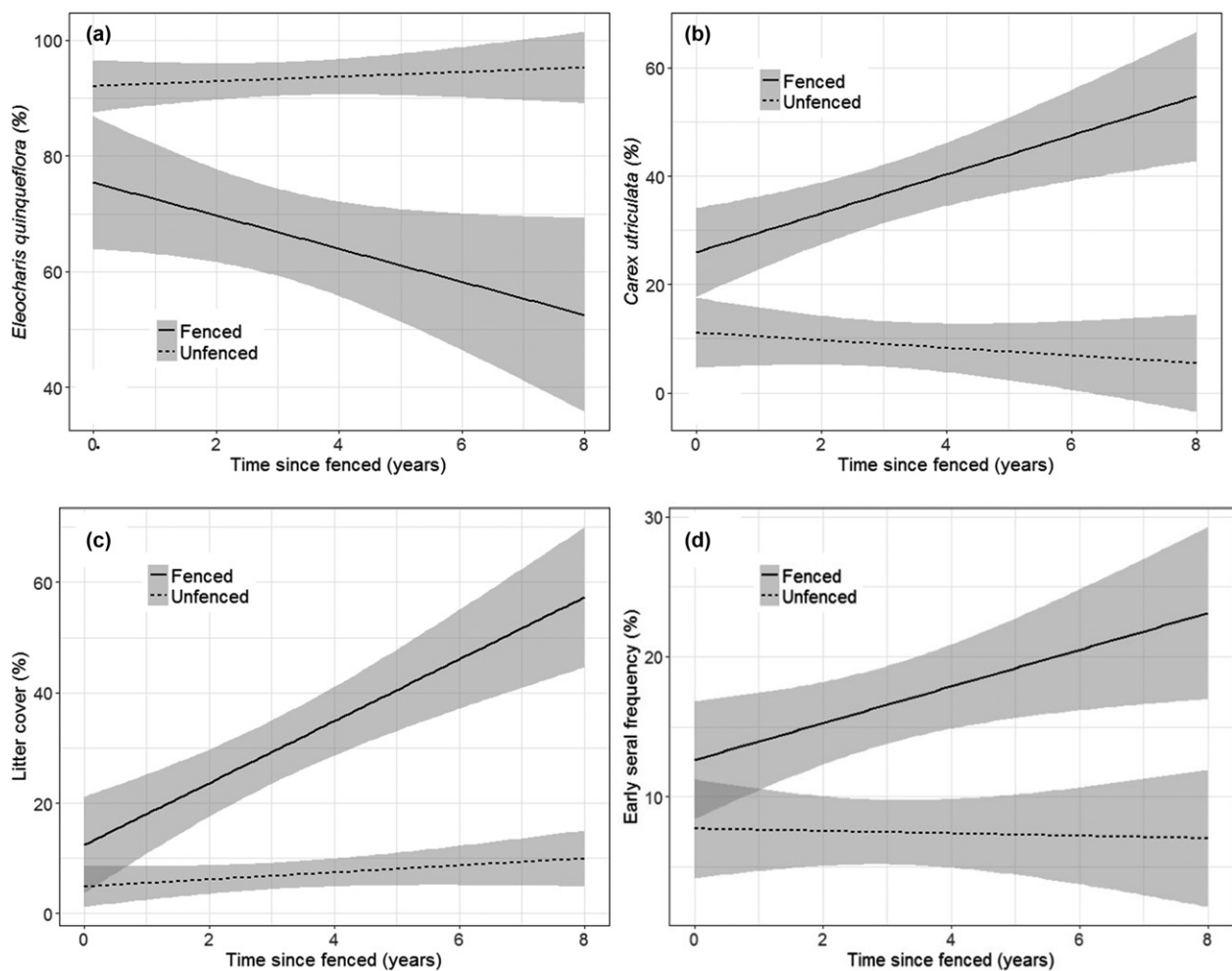


Fig. 3. Linear mixed effects models with transect specified as random effect. Results reported are for time since fenced \times treatment interaction: (a) *Eleocharis quinqueflora* frequency ($t = 3.14$, $P = 0.002$), (b) *Carex utriculata* frequency ($t = -3.81$, $P < 0.001$), (c) Litter cover ($t = -4.7$, $P < 0.001$) and (d) Early seral frequency ($t = -2.0$, $P = 0.04$). Grey bands indicate 95% CI.

cover exhibited a significant linear increase over time after removal of grazing (Fig. 3c), while moss cover declined (time since fenced \times treatment interaction: $t = 3.2$, $P = 0.002$).

Discussion

Our results contribute to a growing body of literature demonstrating that livestock exclusion can strongly affect plant community composition in wetland ecosystems worldwide. Contrary to our expectations, livestock removal did not increase the frequency of key plant species. Grazed sites were associated with peat-forming obligate wetland, moss and sedge species, while fenced sites supported more non-peat-forming facultative upland and upland, forb, grass and ruderal species. Possible explanations for these unexpected shifts in species composition after grazing cessation include: (1) biomass accumulation in the absence of herbivory, (2) competitive exclusion in fenced sites, (3) succession, (4) the abiotic conditions of our study sites, particularly hydrology and nutrient status, and (5) interactions among these factors.

Without grazing or mowing, biomass accumulation in fens and grasslands has been repeatedly linked to significant changes in plant community composition (Schrautzer et al. 2013). We found that litter cover increased significantly over time in fenced relative to unfenced sites (Fig. 3c). Biomass accumulation can inhibit germination and reduce light availability for small-statured prostrate plants, such as mosses (Diemer et al. 2001; Mälson et al. 2008). A decline of bryophyte species has been frequently reported in fens in the absence of grazing or mowing (Fojt & Harding 1995; Bergamini et al. 2001; Diemer et al. 2001). We found that both the frequency of the moss life form and the percentage ground cover of mosses declined over time in the absence of grazing. This pattern is concerning because moss species are often rare, and can be the most abundant peat-forming species in fens (Stammel et al. 2003; Weixelman & Cooper 2009).

Excluding grazing from fens can promote tall-statured nutrient-demanding graminoids (Stammel et al. 2003; Mälson et al. 2008; Wesche et al. 2012). We found that fencing increased the frequency of grass life forms, such as *D. cespitosa* and *Poa palustris*. *E. quinqueflora*, a short-statured sedge, declined significantly over time in fenced relative to unfenced sites (Fig. 3a). On the other hand, *Carex utriculata*, a tall robust sedge species, increased significantly after sites were fenced, but remained unchanged with continuous grazing (Fig. 3b). These patterns are consistent with the competitive exclusion hypothesis proposed by Grime (1979), that competitive species, such as perennial graminoids, increase without grazing and dominate less competitive groups, such as short-statured and annual

species. In Europe, active management of fens by mowing and/or grazing is considered necessary to maintain less competitive species, which are often rare (Fossati & Pautou 1989; Middleton et al. 2006).

Unlike most studies that have detected a decline in early seral species after removing active management such as mowing or grazing from fens (Hald & Vinther 2000; Klimkowska et al. 2009), we found an increase in colonizer species after fencing (Fig. 3d). We also observed an increase in species turnover, suggesting that the availability of open niches and removal of grazing pressure after exclusion may have permitted the colonization of species adapted to disturbed or nutrient-enriched sites. This change in species composition may be the result of short-term succession, where livestock exclusion initially favours species with adaptations, such as easily dispersed seeds, that allow them to disperse into exposed areas, such as those created by hoof prints (Middleton 2002; Stammel et al. 2003). These patterns may be temporary, and obligate wetland and peat-forming species characteristic of properly functioning fens may become more common over time. However, we found that changes in species composition occurred within a year of fencing and continued in a linear progression throughout the 8 yr of our study (Fig. 3). Other studies have found that shifts in species composition after removing livestock from fens can establish a successional trajectory that may never resemble ungrazed reference sites (Middleton 2002; Diggelen et al. 2006).

Contrary to our expectations, fencing reduced the frequency of peat-forming species, and increased the frequency of upland and facultative upland species. Some authors have found that in the absence of mowing or grazing, species composition can shift to reflect the underlying hydrology (Fojt & Harding 1995) or nutrient status (Navrátilová et al. 2017) of the fen. Although species composition in fens is primarily determined by the depth of the water table, pH and nutrient availability, livestock grazing can modify species composition by influencing species competitive interactions and tolerances to soil moisture and nutrient status (Fossati & Pautou 1989; Schrautzer et al. 2013). Grazing or mowing can also directly reduce nutrient availability through the removal of vegetative biomass. Fojt & Harding (1995) found that after 30 yr without management such as grazing, mowing and burning, hydrologically degraded fens exhibited colonization by early seral upland and non-fen species, while hydrologically intact fens remained dominated by fen specialists. Navrátilová et al. (2017) concluded that eutrophication and lack of management has resulted in near extinction of nutrient-poor, alkaline fens (i.e. rich fens) and their associated species across Central Europe. Eutrophication triggers succession toward non-fen vegetation because nutrient-

requiring non-fen species can easily out-compete fen specialists when nutrients are abundant (Wesche et al. 2012; Navrátilová et al. 2017). In addition to atmospheric deposition, livestock manure can be a significant source of nutrient addition, and our study sites have likely experienced increased nutrient availability over their long history of livestock use. *Deschampsia cespitosa*, an indicator species for our fenced sites, has been associated with nutrient enrichment and can out-compete fen specialist species after grazing cessation, particularly when nutrients are not limiting (Krahulec et al. 2001). A decline of mosses, in particular, has been linked to increased nutrient availability in fens. Hájek et al. (2015) discovered that mosses adapted to nutrient-poor conditions (i.e., calcicolous brown mosses) declined after nutrient addition, even in otherwise intact undisturbed fens. Both hydrologic degradation and eutrophication can be exacerbated by drought, and our study straddled the onset in 2012 of the most intense drought in recorded history in California (Diffenbaugh et al. 2015; <http://wrcc.dri.edu>, 10/1/16), resulting in lowered water tables throughout the state (<https://waterdata.usgs.gov/nwis/gw>, 15/2/17). However, although we included precipitation in our models, we did not measure site-level variation in water table depth or other hydrologic attributes, and we did not measure nutrient availability. Therefore, we cannot directly assess how species composition or functional trait patterns may have been affected by spatial and temporal hydrologic variability or nutrient status.

Management implications

The legacy of livestock grazing at our study sites may not be ameliorated through excluding livestock. A number of fens and wet meadows in the Sierra Nevada, US, have not been grazed for over a century, and yet the hydrologic alteration associated with livestock utilization during the 19th century is still present in these systems (Dull 1999; Patterson & Cooper 2007). Erosional processes and nutrient addition initiated by livestock can become self-reinforcing and persist indefinitely after livestock are excluded (Ratliff 1985; Belsky et al. 1999). In these cases, specific restoration efforts focused on re-establishing shallow water tables and reversing eutrophication are necessary (Chimner & Cooper 2003; Holden et al. 2004; Lamers et al. 2015).

There may be some role for low-intensity grazing in the maintenance of healthy fen ecosystems, such as to reduce litter accumulation and prevent dominance of certain species, particularly where short-statured species are of management concern (Bergamini et al. 2001; Stammel et al. 2003; Middleton et al. 2006). However, the timing, duration and intensity of grazing must be carefully managed to avoid any potential for livestock to alter fen hydrology,

nutrient status, or to expose peat to desiccation. These permanent and often irreversible negative effects far outweigh any potential benefits of livestock grazing in the arid western US. Depending on the pH, nutrient status and species composition of the fen, mowing or grazing with small animals such as sheep or native herbivores may be an effective management alternative for maintaining biodiversity in fens, without the potential physical damage associated with heavy-bodied livestock such as cattle (Mack & Thompson 1982; Stammel et al. 2003).

Although land managers in the arid western US often use species composition as an indicator of functioning condition in fen ecosystems, our results suggest that species composition at grazed sites may also reflect selective foraging by livestock and differential responses of individual species to herbivory, hydrology and nutrient status (Augustine & McNaughton 1998). Therefore, caution should be used when evaluating fen condition based on species composition alone when the fen is being actively grazed. It may be useful to identify indicator species, or functional traits, with narrow tolerances to hydrologic condition and nutrient status, as well as to grazing pressure. For example, Hájek et al. (2015) suggested that changes in moss species should be closely monitored in order to detect early signs of eutrophication. On the other hand, we found that the amount of exposed peat was not sensitive to grazing cessation and may not be a good indicator of past livestock usage. Alternately, fencing fens, or portions of fens, to establish ungrazed reference areas may allow land managers to more accurately assess fen condition using species composition without the confounding influence of grazing. Ultimately, a direct evaluation of hydrologic indicators or nutrient status may provide more insight into fen condition than species composition alone.

We found that species composition differed between sites and over time, suggesting that fen plant communities are influenced by a number of factors unrelated to management. A large number of environmental and biological variables influence species composition in fens, including site history, water and soil chemistry, hydrologic regime, temperature regime, propagule and seed bank composition, species physiological requirements, competitive interactions, site productivity and disturbance regimes (Timmermann et al. 2006; Schrautzer et al. 2013). Future research that quantifies hydrologic regimes and nutrient status, and that evaluates long-term successional trajectories, is needed to better understand these complex ecosystems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Species list, functional trait classification, indicator species information, study site map and complementary analyses.