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Interactive effects of pasture management intensity, release from grazing and prescribed fire on forty subtropical wetland plant assemblages

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Summary

1. Pasture management intensity, livestock grazing and prescribed fire are three widespread agricultural practices that affect small, isolated wetlands, but few studies have investigated their individual and interactive effects. Pasture management intensity refers to the degree of human alteration of grassland, ranging from intensively managed pastures planted with introduced forage, fertilizer/lime additions and artificial drainage to semi-natural pastures with mixed native and non-native vegetation, no fertilizer/lime additions and little or no artificial drainage.

2. We examined individual and interactive effects of these three agricultural practices on individual, isolated wetlands using a replicated, full-factorial experiment on 40 entire wetlands in south Florida, USA. Wetlands were embedded in two pasture management intensities: intensively managed and semi-natural.

3. After three years of treatment initiation, vegetation of wetlands released from grazing and unburned embedded in semi-natural pastures had significantly lower evenness and coefficient of conservatism scores compared to wetlands released from grazing and burned, grazed unburned wetlands and grazed burned wetlands in the same pasture management intensity. For wetlands embedded in intensively managed pastures, evenness and coefficient of conservatism scores did not differ among treatments.

4. Release from grazing increased abundance of the native, weedy herb, *Eupatorium capillifolium*.

5. Grazing interacted with prescribed fire to affect shrub abundance and non-native richness; relative abundance of shrubs and non-native richness were greater in wetlands released from grazing and burned and did not differ among burn treatments in grazed wetlands. Interactive effects, especially three-way interactions, were uncommon and not as important as differences between the two pasture management intensities.

6. *Synthesis and applications*. Vegetation diversity and floristic quality of wetlands embedded in intensively managed pastures resisted common restoration management techniques such as release from grazing and prescribed fire, at least in the short term. In contrast, removing all top-down disturbances from wetlands embedded in semi-natural grasslands can negatively affect vegetation species diversity and floristic quality. Future studies should examine how intensity and seasonality of grazing and prescribed fire affect wetland vegetation, and track long-term responses to evaluate lag effects.

Key-words: agriculture, biodiversity management, context dependence, disturbance, grazing lands, management intensity, restoration

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Introduction

Understanding how agricultural management affects the structure and function of wetlands is critical for sustaining ecological functions and minimizing adverse effects on water resources and aquatic communities. Wetland functions are especially important in regions where wetlands comprise a significant part of the agricultural landscape and thus are critical interconnections between agricultural production, natural communities and adjacent ecosystems. Grazing lands occupy 25% of the global land surface (Asner *et al.* 2004) and intersect with numerous wetland resources. Wetlands embedded in grazing lands provide several well-known ecosystem services, including water and forage for livestock, high primary productivity, carbon sequestration, nutrient retention, flood amelioration and climate buffering (Zedler 2003; Duffy & Kahara 2011). In addition, wetlands are known for their high biodiversity and provide habitat for organisms critical to food webs and pest suppression (Zedler 2003). A key question is how to manage wetlands embedded in agricultural lands to sustain and enhance these biodiversity and ecosystem services.

Wetlands embedded in grazing lands are often exposed to prescribed fire in addition to grazing (Kantrud 1986; Middleton 2002; Marty 2005; Boughton *et al.* 2010; Jones, Fraser & Curtis 2011). The individual effects of grazing and fire have been studied in wetlands, but very little work has been done on interactions between grazing and fire, which are known to have strong synergistic effects in terrestrial grasslands (Collins *et al.* 1998; Fuhlendorf & Engle 2004). Trampling by livestock selects for annuals, forbs and short species (e.g. Jones, Fraser & Curtis 2011), has negative effects on tall palatable species (Boughton *et al.* 2010; Jones, Fraser & Curtis 2011) and can lead to shrub invasion (Middleton 2002). On the other extreme, grazing exclosures, draining and fire suppression favour recruitment of trees and shrubs (Peroni & Abrahamson 1986; Green & Kauffman 1995, Miller & Halpern 1998, Landman & Menges 1999). The combined effects of grazing and fire are expected to be greater than either disturbance alone (Fuhlendorf & Engle 2004). Release from grazing with prescribed fire increased plant species density and altered competitive relationships resulting in composition changes in one study (Ford & Grace 1998), but relatively few studies examine the interactive effects of fire and grazing on wetlands, let alone the additional effect of pasture management intensity (Kelly, Song & Jenkins 2015). Fewer still used whole wetlands as replicates, which preserve all the functions and interactions of complete ecosystems (Mitsch & Day 2004). Pasture management intensity refers to the continuum of human alteration of grassland; on the high intensity end of the continuum, intensively managed pastures are planted with introduced forage, fertilized, limed and extensively ditched while on the low intensity end, semi-natural pastures contain a mix of non-native and native vegetation, are not fertilized or limed and have low ditch density.

In Florida, the headwaters of the Everglades flow through a 1·062 million ha watershed, which contains 25% wetlands embedded in a mosaic of different land-use types (Swain *et al.* 2013). Approximately one-third (~404 685 ha) of the watershed is occupied by cattle ranches which are typically managed with both intensively managed pastures (planted with non-native forage, fertilized and heavily drained) and semi-natural pastures (native grasses, not fertilized and less drained). In the flat landscape, wetlands are formed by depressions from subsiding limestone bedrock. Wetland vegetation is distinct from pasture vegetation – only a few species of pasture grasses are found in wetland edges – and wetlands represent ‘hotspots’ of diversity for plants, invertebrates and vertebrates within the pasture matrix (Steinman *et al.* 2003; Swain *et al.* 2013). Previous studies showed that wetlands embedded in intensively managed pastures typically had fewer native and more non-native plant species than wetlands within semi-natural pastures (Boughton *et al.* 2010) and differed in composition of functional groups and species composition (Boughton *et al.* 2011).

By virtue of their vast numbers, collective area and intimate association with grazing lands, ranchland wetlands are important as wildlife habitat and for regional hydrology and nutrient runoff (Bohlen *et al.* 2009). State agencies are interested in managing and restoring isolated wetlands to improve downstream water quality and supply and to enhance wildlife habitat. Federal conservation programmes, such as the United States Department of Agriculture’s (USDA) Wetland Reserve Easements (Duffy & Kahara 2011), provide incentives to restrict grazing on enrolled wetlands. More science-based information is needed on the compatibility of grazing on restored sites. Ranchers are interested in such programmes but wary about losing pasture productivity. Thus, there is a demand for information on ecological dynamics of these wetland systems and others world-wide that are embedded in grazing systems – particularly the balance between maintaining wetland ecosystem services and supporting livestock productivity.

The goal of this study was to understand the interactive impacts of ranchland management practices (i.e. pasture management intensity, grazing and prescribed fire) on plant species composition and structure of wetland ecosystems. Based on previous empirical findings, we predicted that (i) removal of top-down drivers (release from grazing and lack of prescribed fire) would result in greater shrub and non-native plant relative abundance and reduced diversity in both wetland types; (ii) vegetation composition in wetlands embedded in intensively managed pastures would not respond significantly to prescribed fire and release from grazing treatments because of initial low species richness and higher nutrients while the opposite would be true for wetlands embedded in semi-natural pastures; and (iii) plant assemblages would remain different in the two wetlands types due to the effects of pasture management intensity.

Materials and methods

STUDY AREA

We sampled wetlands at MacArthur Agro-Ecology Research Center (MAERC), a division of Archbold Expeditions, located in south-central Florida (27°09′N 81°11′W) on Buck Island Ranch, a 4170-ha commercial cattle ranch with over 600 isolated, seasonal wetlands (see Fig. S1 in Supporting Information). Wetland sizes range from 0·007 to 41·9 ha, with an average size of 0·87 ha. Annual hydroperiods range from 2 to 10 months of standing water (Steinman *et al.* 2003), driven by variation in rainfall. Average annual rainfall was ~132 cm year^{-1} with 60% falling during the summer rainy season. Two different pasture management intensities were maintained on the property, providing an opportunity to evaluate their effects on embedded wetland plant assemblages. Intensively managed pastures were fertilized with NPK (nitrogen, phosphorus, potassium) from the early 1970s to 1987 (most likely 56 kg ha^{-1} as NH_4SO_4 or NH_4NO_3 and 34–90 kg ha^{-1} of P_2O_5 and K_2O) and afterwards were fertilized annually or semi-annually with nitrogen (~56 kg ha^{-1}). Intensively managed pastures were composed primarily of the introduced forage grass, *Paspalum notatum* Flueggé, were limed regularly, extensively ditched for water drainage, had high cattle-stocking densities and were grazed most heavily in the summer wet season. Semi-natural pastures were never fertilized, were composed of a mixture of *P. notatum* and native grasses (e.g. *Andropogon* spp. L., *Axonopus* spp. P. Beauv. and *Panicum* spp. Torr.), were less extensively ditched and were grazed most heavily in the winter dry season. Grazing pressure during the study ranged from 0·57 to 1·7 cows ha^{-1} in intensively managed pasture and from 0·15 to 1·12 cows ha^{-1} in semi-natural pastures. These differences in pasture management intensity resulted in two distinct types of embedded wetlands with different biotic and abiotic attributes (Table 1). Wetland vegetation was clearly distinct from surrounding pasture vegetation.

EXPERIMENTAL DESIGN

The experiment had a 2 × 2 × 2 complete factorial design, with all possible combinations of cattle grazing (grazed or fenced to exclude cattle) and fire (prescribed burn or no burn) applied to wetlands in both semi-natural and intensively managed pastures, for a total of eight distinct treatment types. We replicated this entire design five times in 40 randomly selected wetlands of similar size (0·5–1·5 ha; Fig. S1). An individual wetland was the independent unit of statistical analysis, making this one of the largest experiments ever conducted on whole wetlands (cf. Mitsch & Day 2004). We organized complete sets of eight grazing/fire/pasture management treatments into five spatial blocks across MAERC to minimize and account for spatiotemporal variation. Sampling events were conducted by block to minimize sampling time, and we altered the order we sampled blocks each time to prevent temporal bias.

In 2006, we sampled before fences were installed or burns were conducted, although prescribed fire had occurred sporadically as part of normal ranch management before our study. Beginning in February 2007, cattle grazing was prevented in the twenty wetlands in the released from grazing treatment using standard barbed wire fencing. In contrast to cattle, which rarely crossed through fences, other mammals (e.g. white-tailed deer *Odocoileus virginianus* (Zimmermann)rabbits *Sylvilagus* sp. and feral hogs *Sus scrofa domesticus* Erxleben) readily crossed the fences. We left wetlands unfenced in the grazing treatments and often recorded cattle in and within 100 m of these wetlands.

In February 2008, we conducted prescribed burns on the twenty wetlands in the burn treatment. We ignited fires with a standard drip torch using a back fire for containment and a head fire for the main burn. Ploughed firebreaks outside wetland perimeters helped prevent burns from advancing into the surrounding pastures. Most wetlands burned readily but those dominated by *Juncus effusus* L., *Pontederia cordata* L. and *Sagittaria latifolia* Willd. were difficult to burn due to low fuel loads; in those cases, we burned the wetland using overlapping strip lines. In all cases, we estimated that 80% or more of the wetland was burned.

PLANT SAMPLING

We sampled wetland vegetation at the end of the wet season during October–November. We collected species presence/absence data in 1 m^2 circular quadrats at 15 random points per wetland stratified into five zones: the wetland centre, and its north-east, north-west, south-east and south-west quadrants. Sampling points were independent each year and selected using ArcView 9.0

Table 1. Attributes of wetlands in intensively managed and semi-natural pastures. Water chemistry (total phosphorus (P) and total nitrogen (N)) was sampled in 2006, 2008 and 2009. Depth was the maximum water depth recorded in wetlands after Tropical Storm Fay in 2008. Wetland area and distances to the nearest wetland and ditch were derived from GIS shapefiles

Wetlands embedded in	Native plant richness	Non-native plant richness	Area (ha)	Distance to nearest wetland (m)	Distance to nearest ditch (m)	Max Depth (cm)	AverageWet season depth (cm)	Total P(mg L^{-1})	Total N (mg L^{-1})
Intensively-managed pasture	21·89 ± 5·54	4·99 ± 1·38	2·04 ± 0·71	108·2 ± 47·73	10·1 ± 34·13	61·4 ± 11·99	29·44 ± 6·14	0·48 ± 0·27	1·94 ± 0·54
Semi-natural pasture	30·26 ± 8·58	2·35 ± 1·88	1·78 ± 0·69	70·5 ± 57·92	58·35 ± 68·15	61·6 ± 14·19	31·59 ± 9·05	0·09 ± 0·11	1·57 ± 0·5

Values are means ± one standard deviation.

(ESRI, Redlands, CA, USA). We collected voucher specimens of each species and deposited them in the University of Central Florida and MAERC herbaria.

ANALYSIS

We divided the data set into three parts: the first set was the year of cattle exclusion only, in which the main effects of pasture management intensity and grazing (release from grazing or grazed) plus their interaction were analysed. The second set was 2 years after cattle exclusion and 1 year post-burn, and this analysis included the main effects of pasture management intensity, grazing, prescribed fire and all of their interactions. The third set was 3 years after cattle exclusion and 2 years post-burn, and likewise included the main effects of pasture management intensity, grazing, prescribed fire and all of their interactions. We treated blocks as a random factor and they were retained in all models. Results for the pre-treatment year (pasture management intensity effects only) were reported in Boughton *et al.* (2011). We used pre-treatment values of independent variables as a covariate in all analyses to account for initial condition. Thus, analyses accounted for persistent effects of prior conditions in vegetation. This approach differed from analyses of beetle assemblages in the same experiment (Kelly, Song & Jenkins 2015) because beetles reassemble annually while plants persist via perennial strategies and seed banks. We did all analyses in the R statistical environment (R Core Team, 2014) using linear mixed effects models with the package nlme (Pinheiro *et al.* 2014) and the maximum likelihood method (Crawley 2007; full models are presented in Tables S1–S3). We used model simplification to obtain the most parsimonious model (Crawley 2007). We checked dependent variables for departures of normality on the error distribution and no transformations were necessary.

We calculated species diversity metrics at the wetland level to evaluate the effects of pasture management intensity, grazing, prescribed fire and their interactions on diversity. We defined species richness as the number of different vascular plant species in the 15 plots. We calculated Shannon–Weiner diversity, species evenness and Simpson's dominance based on species frequency. We divided species into shrubs, graminoids, palatable grasses, forbs, natives and non-natives, to analyse the effects of treatments on different functional groups. We kept *Eupatorium capillifolium* (Lam.) Small separate because it responded strongly to grazing exclusion. We calculated relative abundance of plant functional groups per wetland per year as the number of occurrences of each functional group divided by the total number of occurrences.

We used non-metric multidimensional scaling (NMS) ordination in the R package vegan (Oksanen *et al.* 2015) to assess species composition across wetlands. We analysed two matrices: a presence/absence matrix and a frequency matrix. We used the Bray–Curtis distance and 400 iterations with 180 species in the ordinations. We selected the NMS axis explaining the greatest variation as the response variable to analyse the effects of experimental treatments on composition. We also calculated the average coefficient of conservatism (CC) score for each wetland for each study year to examine qualitative differences in species composition among treatments. Coefficient of conservatism scores is widely used to indicate habitat quality and restoration success (Cohen, Carstenn & Lane 2004; Brudvig *et al.* 2007; Boughton *et al.* 2010). We used CC scores from Cohen, Carstenn & Lane (2004), a study conducted on similar Florida wetlands. In this scoring system, species were assigned a score from 0 to 10, where 0 represents weedy species associated with human disturbances and 10 represents the most conservative species with affinities for areas with intact, pre-European settlement ecological processes. We used indicator species analysis in PC-Ord (Dufrêne & Legendre 1997; McCune & Grace 2002) to identify species-specific responses to treatments.

To analyse the drivers of frequency variation of *E. capillifolium*, we conducted a separate analysis on ungrazed wetlands using simple and multiple regression and employed model selection using the corrected Akaike Information Criterion (AICc; Burnham & Anderson 2002). Variables included in regressions were pasture management intensity, depth, hydroperiod, distance from ditches and roads, distance from the nearest wetland, non-native and native plant richness of wetlands in the pre-cattle exclusion year (2006), and soil total nitrogen and phosphorus. We assessed a null model and 55 alternatives, which included main effects, additive effects, and some interactions. Before model selection, we evaluated collinearity using a correlation matrix and simplified the variable set to avoid pairs that had correlation coefficients $> 0{\cdot}75$. We selected the most plausible model as the one with the lowest AICc and highest model weight.

Results

We recorded 180 plant species in the wetlands during the 4-year study, including 62 native forbs, 6 exotic forbs, 67 native grasses, 8 exotic grasses, 13 native emergent macrophytes, 2 exotic emergent macrophytes, 12 native shrubs, 3 exotic shrubs and seven species that remained unidentified (Table S4). In the year before fences were installed, wetland plant assemblage composition differed between the two pasture management intensities: NMS ordinations based on presence/absence and frequency of species showed that in both ordinations, Axis 1 (representing >95% of the variation) was related to pasture management intensity. Wetlands embedded within semi-natural pastures were in a different parameter space than those in intensively managed pastures. In all ordinations, wetlands in semi-natural pastures were more heterogeneous than those in intensively managed pastures (Fig. S2). Please see Boughton *et al.* (2011) and Medley *et al.* (2015) for more details on the response of wetland vegetation to pasture management intensity alone.

ONE YEAR OF CATTLE EXCLUSION

Cattle exclusion exerted few significant treatment effects on plant species composition and structure after 1 year (Tables S5 and S6). Relative abundance of palatable grasses was significantly greater in wetlands grazed by cattle compared to wetlands released from grazing (Table S6). Additionally, *E. capillifolium*, a native herb, responded strongly to cattle exclusion; 9 of 20 ungrazed wetlands became dominated by this species (Table S6; Fig. 2d). The most plausible model to explain the frequency of *E. capillifolium* included native plant species richness, wetland depth and distance to the nearest road (model weight 0·64; Table S7). Wetlands with increased frequency of *E. capillifolium* tended to have lower native species richness before fencing ($t = -4{\cdot}03$, $P < 0{\cdot}001$), were closer to roads ($t = 2{\cdot}94$, $P = 0{\cdot}009$) and were shallower ($t = -3{\cdot}09$, $P = 0{\cdot}007$), and the overall model was statistically significant (adjusted $R^2 = 0{\cdot}58$, $F_{3,16} = 9{\cdot}62$, $P = 0{\cdot}0007$; Table S7). Surprisingly, pasture management intensity did not appear in the top models and appeared in the ninth best model with low model weight.

TWO YEARS OF CATTLE EXCLUSION AND 1 YEAR AFTER BURNING

Multiple response variables responded to treatments in the second year. Evenness was significantly higher in wetlands within semi-natural pastures and a significant grazing × burn interaction affected non-native plant richness (Table 2). In grazed treatments, non-native richness was similar in both burned and unburned wetlands, but in the cattle exclusion treatment, burned wetlands had greater non-native richness than unburned wetlands. Burning reduced relative abundance of graminoids (Table 3). A significant grazing × burn interaction for shrub relative abundance occurred because burning increased shrub abundance in ungrazed wetlands but reduced shrubs in grazed wetlands (Fig. 2b). There was greater abundance of non-native plant species in intensively managed wetlands compared to semi-natural wetlands. *E. capillifolium* abundance remained significantly greater in ungrazed wetlands (Table 3; Fig. 2e). Finally, a significant three-way interaction between pasture management intensity, grazing and prescribed fire affected coefficient of conservatism scores (Table 3). However, the pattern was obvious; wetlands embedded in intensively managed pastures consistently had lower mean wetland CC scores than those in semi-natural pastures, with one exception: wetlands released from grazing without prescribed fire in semi-natural pastures had variable responses that overlapped all other treatments (Fig. 1c).

In all analyses, except for evenness and *E. capillifolium*, the pre-treatment covariate explained substantial variation in the response variable, evidenced by enormous F-ratios and highlighting the importance of initial condition in these wetlands (Tables 2 and 3).

Not all variables were affected in this year. Pasture management intensity, grazing and prescribed fire

Table 2. Results of linear mixed effects models of plant assemblage characteristics in response to 2 years of release from grazing and 1 year after a prescribed fire treatment. Block was a random factor in all analyses

	Richness		Native richness		Non-native richness		Shannon–Weiner diversity		Simpson's dominance		Evenness	
d.f.	1,31		1,31		1,30		1,31		1,31		1,32	
Source	Est (SE)	*F*	Est (SE)	*F*	Est (SE)	*F*	Est (SE)	*F*	Est (SE)	*F*	Est(SE)	*F*
Two years after cattle removal and 1 year after prescribed burn												
Pasture (P)	2·39 (2·0)	1·29	3·66 (2·2)	2·58	−0·95 (0·4)	**7·42**	0·08 (0·0)	0·91	0·01 (0·0)	0·58	0·02 (0·0)	**10·63**
Grazing (G)	1·11 (1·8)	0·40	1·43 (1·8)	0·66	−0·68 (0·4)	0·14	0·05 (0·1)	0·66	0·01 (0·0)	1·93	0·01 (0·0)	3·0*
Burn (B)	−1·26 (1·7)	0·53	−0·86 (1·7)	0·25	−1·09 (0·4)	2·88	−0·03 (0·1)	0·23	−0·0 (0·1)	0·20	0·00 (0·0)	0·10
Covariate 2006	0·47 (3·7)	**23·5**	**0·48 (0·1)**	**41·2**	0·81 (0·1)	**154·7**	0·53 (0·1)	**30·1**	0·55 (0·17)	**22·8**		
P × G												
P × B												
G × B					1·16 (0·58)	**3·96**						
P × G × B												
d.f.	1,31		1,31		1,31		1,31		1,31		1,28	
Three years after cattle removal and 2 years after prescribed burn												
P	−1·40 (2·1)	0·49	0·09 (2·04)	0·00	0·03 (0·34)	0·32	−0·05 (0·1)	0·35	−0·0 (0·0)	0·06	0·01 (0·0)	2·18
G	1·07 (1·86)	0·33	1·06 (1·65)	0·42	0·38 (0·25)	1·94	0·02 (0·08)	0·10	0·0 (0·0)	0·40	−0·0 (0·01)	0·85
B	−0·09 (1·8)	0·00	0·57 (1·63)	0·12	−0·88 (0·25)	**12·39**	−0·04 (0·1)	0·24	−0·0 (0·0)	0·61	0·0 (0·01)	**6·55**
Covariate 2006	0·57 (0·15)	**18·2**	0·52 (0·12)	**33·7**	0·76 (0·09)	**105·2**	0·54 (0·16)	**14·6**	0·45 (0·21)	**7·39**		
P × G											0·01 (0·01)	**5·31**
P × B											−0·03 (0·01)	2·85
G × B											−0·01 (0·01)	0·42
P × G × B											0·03 (0·02)	3·15*

Degrees of freedom (d.f.), estimates (Est), standard errors (SE) and *F*-values (*F*) are presented and bold values are significant at $\alpha = 0{\cdot}05$, *non-significant at $\alpha = 0{\cdot}1$. Covariate 2006 represents the pre-treatment data of that particular variable (except evenness because initial evenness was uncorrelated with subsequent years). The results presented were subjected to model simplification (Crawley 2007); treatment combinations omitted by that process are blank.

Table 3. Linear mixed effects models of plant assemblage characteristics in response to release from grazing and prescribed fire treatments. Block was a random factor in all analyses

	Forb Rel. Abun.		Graminoid Rel. Abun.		Palatable Grass Rel. Abun.		Shrub Rel. Abun.	
d.f.	1,31		1,31		1,31		1,30	
Source	Est (SE)	*F*	Est (SE)	*F*	Est (SE)	*F*	Est (SE)	*F*
Two years after cattle removal and 1 year after prescribed burn								
Pasture (P)	−0·02 (0·0)	1·17	−0·02 (0·0)	2·03	0·04 (0·0)	**4·61**	−0·00 (0·0)	0·00
Grazing (G)	0·01 (0·0)	0·54	0·02 (0·0)	1·68	0·0 (0·0)	0·02	−0·01 (0·0)	0·01
Burn (B)	−0·0 (0·0)	0·08	0·03 (0·0)	**4·72**	−0·03 (0·0)	2·89	−0·0 (0·0)	2·45
Covariate 2006	0·82 (0·21)	**18·3**	0·48 (0·1)	**13·0**	0·57 (0·12)	**16·72**	0·54 (0·13)	**20·2**
P × G								
P × B								
G × B							0·03 (0·0)	**7·18**
P × G × B								
d.f.	1,31		1,31		1,31		1,30	
Three years after cattle removal and 2 years after prescribed burn								
P	−0·00 (0·0)	0·02	0·00 (0·0)	0·06	−0·02 (0·02)	0·60	0·00 (0·0)	0·01
G	0·02 (0·0)	1·28	0·02 (0·0)	2·21	−0·01 (0·02)	0·42	−0·01 (0·0)	0·38
B	0·03 (0·0)	3·59*	0·02 (0·0)	2·22	−0·05 (0·02)	**5·52**	−0·01 (0·0)	4·21
Covariate 2006	0·38 (0·19)	3·62*	0·30 (0·13)	**8·09**	0·43 (0·14)	**8·79**	0·39 (0·09)	**27·1**
P × G								
P × B								
G × B							0·01 (0·0)	3·09*
P × G × B								

Degrees of freedom (d.f.), estimates (Est), standard errors (SE) and *F*-values (*F*) are presented and bold values are significant at α = 0·05, * non-significant at α = 0·1. Covariate 2006 represents the pre-treatment data of that particular variable (except *Eupatorium* because initial abundance was uncorrelated with subsequent years). NMS Axis 1 (PA): Non-metric multidimensional scaling ordination Axis 1 (presence–absence matrix); NMS Axis 1 (Rel. Freq.): Non-metric multidimensional scaling ordination Axis 1 (Relative Frequency); Wetland CC score: Average coefficient of conservatism score of plant species found in each wetland. The results presented are after model simplification.

treatments did not significantly affect total plant species richness, native richness, Shannon–Weiner diversity or Simpson's dominance in the autumn following the winter burns (Table 2). Plant species composition (NMS Axis 1 scores) also did not vary significantly among treatment levels or their interactions (Table 3).

THREE YEARS OF CATTLE EXCLUSION AND 2 YEARS AFTER BURNING

Evenness was now greater in burned wetlands and there was a significant pasture management intensity × grazing interaction; within semi-natural pastures, wetlands released from grazing were less even than grazed wetlands but no difference between wetlands released from grazing and grazed wetlands occurred within intensively managed pastures (Table 2; Fig. S3). A significant pasture management intensity × burn interaction was detected on NMS Axis 1 (Table 3). Wetlands embedded in intensively managed pastures had similar NMS scores regardless of burn status, but unburned wetlands embedded in semi-natural pastures had significantly lower NMS scores than burned wetlands. Coefficient of conservatism (CC) scores was significantly lower in wetlands within intensively managed pastures, and in burned vs. unburned wetlands (Fig. 1d). Relative abundance of palatable grasses was greater in burned than in unburned wetlands, and *E. capillifolium* remained significantly more abundant in wetlands released from grazing than in wetlands grazed by cattle (Table 3; Fig. 2f). However, species richness, Shannon–Weiner diversity and Simpson's dominance still did not differ significantly among treatments (Table 2).

INDICATOR SPECIES

More plant species were associated with pasture management intensity than with the grazing and burning treatments, or their interaction (Table S8). Indicator species of intensively managed pastures tended to be non-natives, annuals or species with low coefficient of conservatism scores, while indicators of semi-natural wetlands were native species with higher coefficient of conservatism scores (Tables S8 and S4).

Of the significant indicator species for grazed or wetlands released from grazing, most were associated with grazed wetlands and tended to be short species including

Eupatorium Rel. Abun.		Non-native Rel. Abun.		NMS Axis 1 (PA)		NMS Axis 1 (Rel. Freq.)		Wetland CC score	
1,32		1,31		1,27		1,31		1,27	
Est (SE)	*F*	Est (SE)	*F*	Est (SE)	*F*	Est (SE)	*F*	Est (SE)	*F*
−0·0 (0·0)	0·04	−0·05 (0·02)	**5·01**	0·18 (0·1)	**4·04**	0·11 (0·1)	1·33	0·37 (0·17)	**5·43**
−0·03 (0·0)	**10·78**	−0·01 (0·01)	0·21	0·12 (0·1)	0·79	0·04 (0·05)	0·71	0·27 (0·14)	1·01
−0·0 (0·0)	1·92	−0·00 (0·01)	0·09	0·02 (0·1)	0·18	0·01 (0·05)	0·03	0·14 (0·14)	0·02
		0·76 (0·08)	**278·2**	0·96	**630·3**	0·94 (0·07)	**680·4**	0·82 (0·1)	**330·1**
				−0·16 (0·12)	0·01			−0·31 (0·2)	0·08
				−0·07 (0·12)	0·91			−0·23 (0·2)	0·79
				−0·12 (0·12)	0·00			−0·42 (0·2)	0·29
				0·31 (0·16)	3·57*			0·69 (0·28)	**6·03**
1,32		1,31		1,30		1,27		1,31	
0·00 (0·0)	0·41	−0·03 (0·02)	3·77*	0·00 (0·1)	3·44*	0·06 (0·13)	2·13	0·19 (0·08)	**8·48**
−0·02 (0·0)	**7·21**	0·01 (0·01)	0·99	−0·02 (0·05)	0·11	0·02 (0·1)	0·55	−0·09 (0·06)	2·05
−0·00 (0·0)	0·37	−0·01 (0·01)	0·22	−0·11 (0·07)	0·03	−0·04 (0·1)	0·53	0·13 (0·06)	**5·29**
		0·83 (0·08)	**278·6**	0·94 (0·09)	**405·9**	0·91 (0·1)	**536·1**	0·77 (0·07)	**402·0**
						−0·11 (0·14)	0·40		
				0·21 (0·09)	**4·88**	0·02 (0·15)	3·98*		
						−0·19 (0·14)	0·03		
						0·35 (0·2)	3·05*		

three graminoids (*Eleocharis vivipara, Kyllingia brevifolius and Luziola fluitans*) and five forbs (*Bacopa caroliniana, Diodia virginiana, Ludwigia repens, Pontederia cordata and Sagittaria graminea*). Only the native herb, *E. capillifolium* was a significant indicator of wetlands released from grazing. Species associated with burned wetlands include the graminoids *Sacciolepis striata* Nash and *Cladium mariscus* (L.) Pohl *jamaicense* (Crantz) Kük., and the shrub *Cephalanthus occidentalis* L. Two grasses*, S. striata* and *Leersia hexandra* Sw., were associated with wetlands released from grazing and subject to prescribed fire.

Discussion

Our experiment demonstrated that pasture management intensity had a strong influence on plant community metrics, but synergistic effects of pasture management intensity, cattle grazing and prescribed fire were uncommon. Overall, for the last 2 years of the study, only four of the 90 possible two-way interactions analysed were significant, and only one of 30 three-way interactions was significant. Most significant main effects were associated with pasture management intensity, followed by prescribed burning. Vegetation responses were strongly constrained by initial conditions, as indicated by large F-ratios associated with pre-treatment covariates, suggesting that pre-existing conditions continue to have strong effects after 3 years of treatment.

Pasture management intensity continued to dominate vegetation, despite other strong treatments throughout our 4-year study. Before conversion of surrounding uplands into pastures, studied wetlands were similar to depression wetlands typical of dry and wet prairie ecosystems (Swain *et al.* 2013). Pasture management intensity decreased floristic conservation value of wetlands, as indicated by lower species richness and coefficient of conservation scores (also see Lopez & Fennessy 2002; Cohen, Carstenn & Lane 2004; Boughton *et al.* 2010). In a previous study, soil P was significantly associated with wetland vegetation composition in intensively managed pastures explaining ~25% of the variation (Boughton *et al.* 2010); clearly, factors beyond nutrient loading are important to fully represent pasture management intensity. Wetlands embedded in intensively managed pastures also tend to be more ditched, and more often grazed and trampled by cattle in the growing season (Medley *et al.* 2015). As a result, those wetlands are also more often dominated by a characteristic outer zone of *Juncus effusus*, which has low forage value and is difficult to remove by prescribed fire,

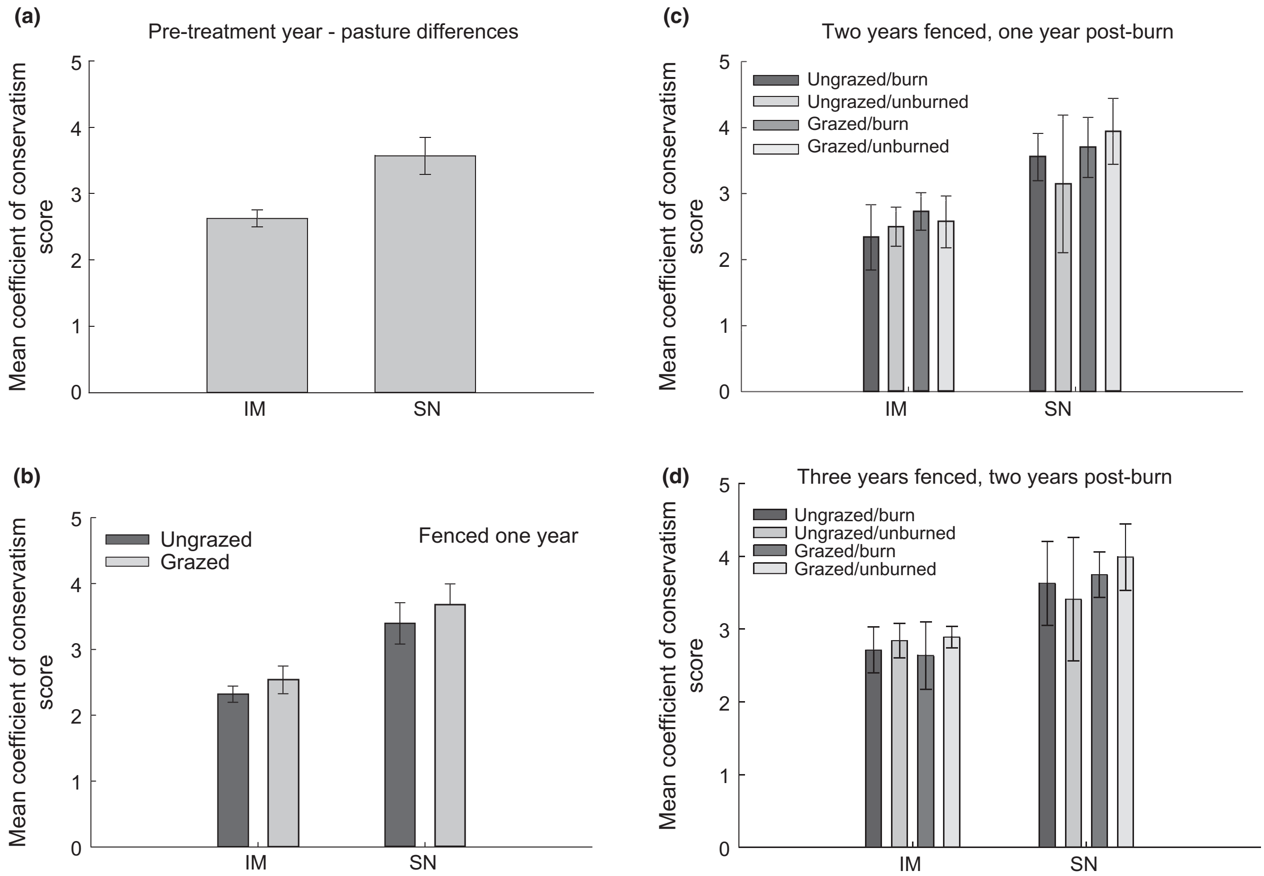

Fig. 1. (a) Before release from grazing and prescribed fire treatments were implemented, the wetland mean coefficient of conservatism (CC) score differed significantly among pasture management intensities: intensively managed (IM) and semi-natural (SN). (b) One year after release from grazing, cattle exclusion had no effect on CC scores, but pasture management intensity differences still existed (pasture: $F_{1,32} = 23{\cdot}28$, $P < 0{\cdot}0001$). (c) Two years after release from grazing, and 1 year post-prescribed fire, there was a significant three-way interaction (pasture × grazing × burn, $F_{1,27} = 6{\cdot}03$, $P = 0{\cdot}02$) for CC score with all treatments in wetlands embedded within intensively managed pastures having similar mean CC scores while wetlands released from grazing and without prescribed fire in semi-natural pastures had the lowest CC scores. (d) The third year after cattle exclusion, there was a significant main effect of pasture management intensity and prescribed fire, with lower CC scores in intensively managed wetlands ($F_{1,31} = 8{\cdot}48$, $P = 0{\cdot}007$) and in wetlands with prescribed fire ($F_{1,31} = 5{\cdot}29$, $P = 0{\cdot}03$). Data are means and 95% CI.

mowing or roller chopping; indeed, *J. effusus* was identified as a significant indicator species of wetlands in intensively managed pastures. The strong association of *J. effusus* (and other species) with wetlands embedded in intensively managed pastures and the partial effects of other strong experimental treatments applied here indicate that ranchland wetlands existed in alternate stable states (Beisner, Haydon & Cuddington 2003).

Pasture management intensity constrained the effects of grazing and prescribed fire on vegetation attributes. Floristic quality (i.e. CC scores) of wetlands in semi-natural pastures was initially higher than in intensively managed wetlands, and generally remained that way despite other treatments. However, semi-natural wetlands protected from both grazing and prescribed fire had highly variable CC scores and a mean indistinguishable from other treatments, including wetlands in intensively managed pastures. This suggests that CC scores may decrease in semi-natural wetlands when both top-down factors are removed. Similar outcomes for vegetation evenness and composition (NMS Axis 1 scores) support the inference that release from the 'filters' of pasture management intensity, grazing and fire permitted wetland vegetation composition to diverge, including some reductions in CC scores if species with low scores became more prevalent.

Grazing and prescribed fire are commonly manipulated 'top-down' factors in ecosystem management and restoration (Bond & Keeley 2005; Marty 2005; Davies, Svejcar & Bates 2009), including in subtropical ranchlands of south Florida. Both disturbances have strong effects on species and trait composition of terrestrial grassland plant assemblages and when these disturbances are removed from or added to a community, species composition is expected to shift in predictable ways, depending on life history, canopy height and architecture (Collins & Smith 2006; Diaz *et al.* 2007; Spasojevic *et al.* 2010; Boughton, Bohlen & Steele 2013). However,

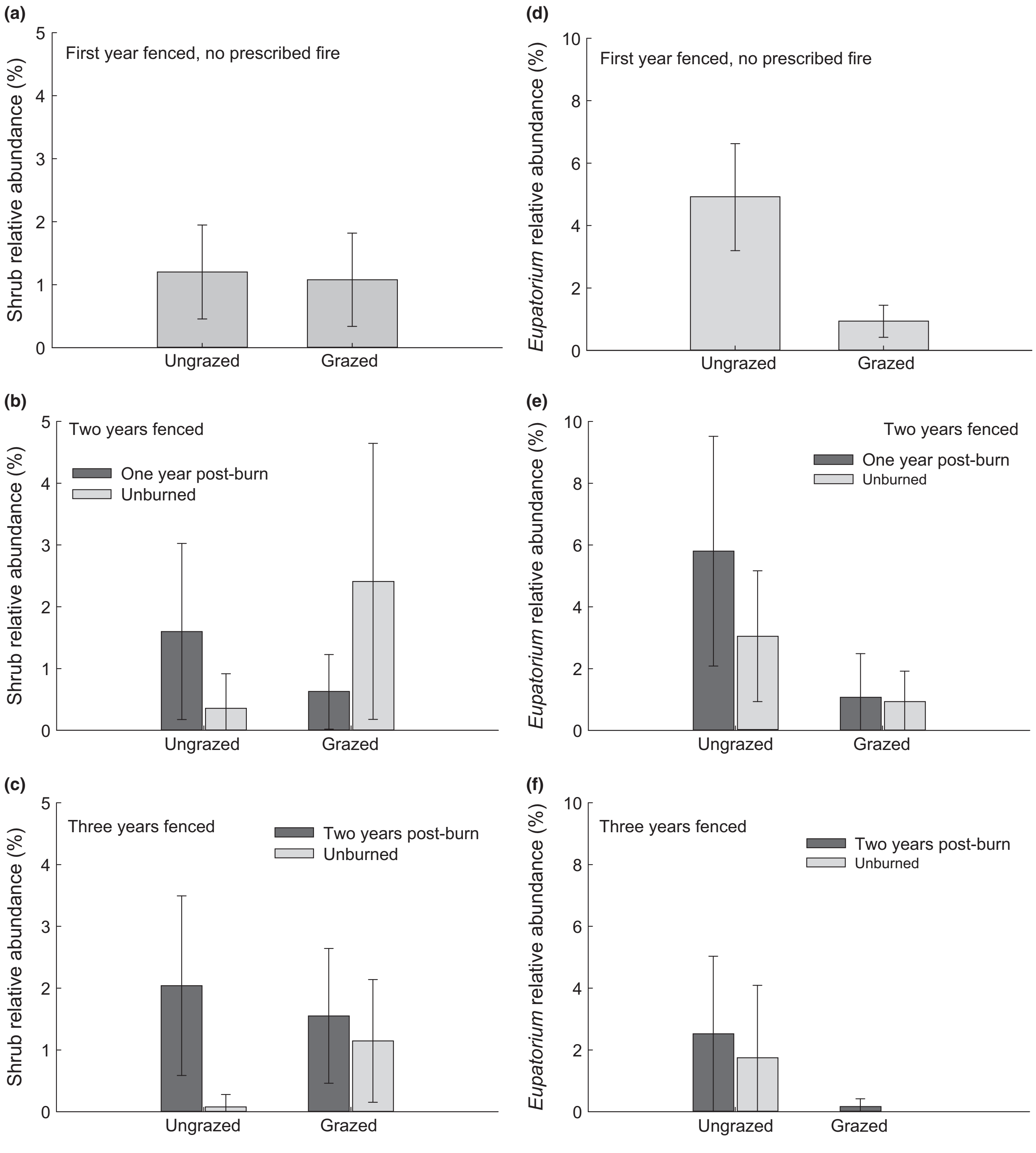

Fig. 2. (a) Grazed wetlands and wetlands released from grazing did not differ significantly in shrub relative abundance 1 year after cattle exclusion ($F_{1,32}$ = 1·20, P = 0·28). (b) A significant grazing × burn interaction affected shrub relative abundance 2 years after release from grazing and 1 year after a prescribed fire ($F_{1,30}$ = 7·18, P = 0·01). (c) Three years after release from grazing and 2 years post-prescribed fire, there was a weakly significant grazing × burn interaction ($F_{1,30}$ = 3·09, P = 0·09) on shrub relative abundance. (d) Wetlands released from grazing had significantly greater relative abundance of *Eupatorium capillifolium* 1 year after cattle exclusion ($F_{1,33}$ = 22·09, P < 0·0001). (e and f) Wetlands released from grazing had significantly greater abundance of *E. capillifolium* two ($F_{1,32}$ = 10·78, P = 0·003) and three ($F_{1,32}$ = 7·21, P = 0·01) years after cattle exclusion. Data are means and 95% CI.

vegetation may not change rapidly when conditions result in plant assemblages that are species poor or dominated by slow responding species such as *J. effusus* (Browning and Archer 2011; Davies *et al.* 2011; Spasojevic *et al.* 2010).

Instead, our experiment demonstrates that manipulating grazing and fire will not quickly return wetland vegetation in intensively managed pastures to a state more similar to those in semi-natural pastures. Two wetland restoration possibilities exist. Most simply, cattle exclosure and prescribed fire may require more time to consistently counter the legacy bottom-up effects of pasture management intensity. Otherwise, wetlands in intensively managed pastures may be irreversibly shifted to an alternative stable state (Beisner, Haydon & Cuddington 2003) because past nutrient loading will persist, and/or perennial vegetation (e.g. *J. effusus*) will persist even if nutrient status was to be reversed (Suding, Gross & Houseman 2004). Past work suggests that release from grazing may reduce *J. effusus,* the dominant species in grazed wetlands (Tweel & Bohlen 2008). However, seed banks of *J. effusus* and other annual species were extremely abundant within wetlands of intensively managed pastures (Franks & Boughton unpublished data); even if nutrient status was restored, *J. effusus* may still dominate intensively managed wetlands. Longer-term studies will be needed to assess persistence of *J. effusus* after long-term grazing exclusion.

The strongest response to release from grazing was that of the native herb, *E. capillifolium,* which was a significant indicator of wetlands released from grazing regardless of management intensity in the surrounding pasture. We suspect that the timing of cattle exclusion contributed to dominance of *E. capillifolium* in degraded wetlands. Our initial plan was to complete cattle exclusion fence construction by the onset of the wet season, when wetlands would fill with water. Instead, fences were completed ahead of schedule and cattle were excluded midway through the dry season. This timing left trampled, muddy wetlands without water and exposed and allowed *E. capillifolium* to establish and grow. In addition, the following wet season was a drought, so that wet season inundation and aquatic vegetation did not hinder *E. capillifolium*. A similar event was observed in the Francis Marion National Forest, South Carolina, USA, in the late 1990s (J. Fauth, pers. obs.). Timing of cattle exclusion relative to the hydrological cycle therefore may be critical to near-term wetland restoration efforts.

We predicted that release from grazing and lack of prescribed fire would increase non-native plant abundances and decrease vegetation diversity in both wetland types. Instead, non-native abundance remained consistently higher in intensively managed wetlands and was not affected by release from grazing or prescribed fire. In semi-natural wetlands, non-native richness increased significantly when released from grazing and with prescribed fire. Implementing prescribed fire in wetlands that are released from grazing can result in non-native invasion mediated through increased litter, which results in increased fire-induced mortality of perennial vegetation (Davies, Svejcar & Bates 2009). Non-native invasion (as a greater portion of vegetation) was supported here by no significant changes in total plant species richness, Shannon–Weiner diversity or Simpson's dominance.

Contrary to conventional wisdom that pastures and their embedded wetlands should be burned to prevent shrub encroachment (Middleton 2006), shrubs were most abundant in wetlands released from grazing but burned. This synergistic effect was primarily due to the response of the native wetland shrub, *Cephalanthus occidentalis*, which was significantly associated with burned wetlands. It remains to be seen whether slower-growing shrubs increase in number when released from grazing and not burned, or whether shrubs continue to be associated with burned wetlands. Other studies have found that grazing exclosures, draining and fire suppression favour recruitment of trees and shrubs (Peroni & Abrahamson 1986; Landman & Menges 1999; Middleton, Holsten & Diggelen 2006). Season of burn can also affect shrub abundance (Watts & Tanner 2006; Boughton, Bohlen & Steele 2013). We burned wetlands in the dormant season (February) to mimic ranching practices, but results may differ if prescribed fires were conducted in the natural May/June burn season, which appears to reduce shrubs more effectively than winter burns (Watts & Tanner 2006; Boughton, Bohlen & Steele 2013).

CONSERVATION IMPLICATIONS

Our study shows that wetland vegetation previously altered by increased pasture management intensity largely resisted common restoration management techniques including release from grazing and prescribed fire, at least in the short term. This result suggests that either more time may be required for restoration outcomes to overcome lag effects (Boughton, Bohlen & Steele 2013) or that alternative stable states exist. On the other hand, vegetation in wetlands not exposed to fertilizers and surrounded by semi-natural pastures was more responsive to top-down factors such as prescribed fire and release from grazing. Our short-term results suggest that removing both of the top-down factors of grazing and prescribed fire removes 'filters' that otherwise maintain vegetation evenness and floristic quality. It is important to note that prescribed fire was only implemented once during this study and that repeated prescribed fire over time may have a cumulatively larger impact on species composition. Future studies should examine how intensity and seasonality of grazing and fire affect wetland vegetation, and track long-term responses to evaluate lag effects.

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Data accessibility

Functional group data with wetland IDs, treatments, block and year are archived in Dryad Digital Repository doi:10.5061/dryad.92bv3

(Boughton *et al.* 2015). Diversity data with wetland IDs, treatments, block and year are archived in Dryad Digital Repository doi:10.5061/dryad.92bv3. R scripts are uploaded as online supporting information.

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Supporting Information

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

Table S1 Full models for all diversity and functional group variables from the first year after release from grazing.

Table S2 Full models for all diversity and functional group variables from the second year after release from grazing and 1 year after prescribed fire.

Table S3 Full models for all diversity and functional group variables from the third year after release from grazing and 2 years after prescribed fire.

Table S4 Mean percentage frequency of plant species among pasture management intensity, grazing and prescribed fire treatments 3 years after fencing and 2 years post-fire.

Table S5 Results of linear mixed effects models for the first year after removal of cattle for richness and diversity measures.

Table S6 Results of linear mixed effects models for the first year after removal of cattle for functional groups and composition measures.

Table S7 Full Akaike Information Criterion model selection details.

Table S8 Indicator species analysis results for pasture management intensity, release from grazing, prescribed fire and grazing × fire treatments.

Fig. S1 A map showing MacArthur Agro-ecology Research Center and the layout of the forty experimental wetlands and their treatments and blocks.

Fig. S2 Non-metric multi-dimensional scaling ordination of forty wetlands over the 4 years of the study.

Fig. S3 The effect of pasture management intensity, release from grazing, and prescribed fire on plant species evenness in the third year after release from grazing and 1 year post-burn.