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Pasture management, grazing, and fire interact to determine wetland provisioning in a subtropical agroecosystem

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Abstract. Wetlands in agroecosystems provide multiple ecosystem services, including provisioning services such as forage production. Here, we examine how pasture management intensity (semi-natural pastures vs. highly managed pastures (fertilized, heavily drained, planted with productive grasses), cattle exclusion (grazed vs. fenced), prescribed fire (burned vs. unburned), and their interactions affect provisioning services provided by small, isolated, and seasonally flooded wetlands in subtropical pastures and rangelands. We used a replicated, full-factorial experiment on 40 seasonally flooded wetlands located in Florida (USA), and measured standing plant biomass and annual net primary productivity in each wetland. Biomass was sorted by species to calculate species abundance of palatable and unpalatable plants. We used general linear mixed models to evaluate the effect of treatments and their interactions on biomass quantity, plant tissue nutrients (% C, % N, and % P), and forage nutritive value (using in vitro organic matter digestibility). Plant standing biomass and productivity were greatest in wetlands embedded in highly managed pastures, but in grazed wetlands, a large proportion of this biomass was unpalatable to cattle. Excluding cattle from wetlands in highly managed pastures increased productivity, standing biomass, and the amount of palatable species (~6.3 t/ha) compared to grazed wetlands (~3.3 t/ha), especially when these wetlands were also exposed to prescribed fire. Total P in plant tissue was consistently higher in wetlands within highly managed pastures, but total N responses to treatments varied between years. In vitro digestibility was higher in vegetation from wetlands within highly managed pastures, but not in fenced wetlands despite the higher amount of palatable species, suggesting that palatability and digestibility were decoupled. Subtropical wetlands in agroecosystems provide substantial provisioning services, and our study suggests that targeted management can increase these services. However, the pasture type surrounding a wetland interacts with grazing and fire management to affect provisioning services. We propose that fencing off selected wetlands (specifically in highly managed pastures) followed by low-intensity grazing with adequate resting periods could benefit ranchers and have less persistent impacts on this ecosystem.

Key words: aboveground biomass; forage nutritive value; *Juncus effusus*; Long-Term Agroecosystems Research Network; palatability; *Panicum hemitomon*; productivity; seasonal wetlands; wetland management.

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Introduction

Wetlands occupy only 6–9% of the landscape worldwide but provide considerable ecosystem services to human society (Zedler 2003, Zedler and Kercher 2005, Junk et al. 2013), especially for wetlands embedded within agroecosystems. In addition to their roles in nutrient cycling, primary production, and soil formation (i.e., supporting services), wetland embedded in agroecosystems provides vital refugia for sensitive taxa ranging from amphibians to waterfowls (Babbitt et al. 2006, Brasher et al. 2019). Agroecosystem wetlands also provide important regulating services such as nutrient sequestration, flood protection, and water and air purification, as well as cultural services. Finally, wetlands can produce a large amount of high-quality forage for livestock (i.e., provisioning service). For example, 65 small Canadian wetlands provided over three times as much forage with 77% higher protein content than the unmanaged grasslands around them (Sankowski et al. 1987). These supporting, regulating, cultural, and provisioning services together represent a large economic value (Brander et al. 2013).

Agricultural management practices have important consequences on functions and services provided by wetlands in agroecosystems (Gerakis and Kalburtji 1998, Moges et al. 2017). For instance, draining wetlands reduces local hydroperiod and water storage capacity at the watershed level (Swain et al. 2013), thus decreasing water supplies and flooding mitigation (Wamsley et al. 2010). These changes in hydrology have important consequences on vegetation and wildlife (Steinman et al. 2003, Moges et al. 2017). Grazing by domestic livestock is another pervasive land use with positive and negative effects on wetlands (Steinman et al. 2003, Marty 2015, Oles et al. 2017, Bovee et al. 2018). In Australia, grazing by livestock reduced supporting ecosystem services (i.e., habitat for organisms and biodiversity) by 20% and regulating ecosystem services by 8% across multiple sites (Eldridge and Delgado-Baquerizo 2017). Fertilizer application is another agricultural management practice with critical impacts on wetlands. The use of fertilizers can increase nutrient runoff, driving eutrophication of previously oligotrophic wetlands (Navrátilová et al. 2017, Rion et al. 2018). Eutrophication in turn may decrease species diversity, increase biodegradability of dissolved organic carbon (Mao et al. 2017), and increase decomposition through changes in litter quality, thus accelerating nutrient cycling. Finally, prescribed fire in pasturelands may also modify ecosystem services provided by wetlands embedded in those pastures. For example, Boughton et al. (2016) found that prescribed fire maintained plant diversity (a supporting service) in seasonally flooded wetlands where livestock were excluded.

Drainage, grazing, fertilization, and prescribed fire are management practices used in combination on wetland-rich subtropical pastures and rangelands of south-central Florida. In addition, uplands surrounding many wetlands in this region have been planted with non-native productive grass species (e.g., *Paspalum notatum*, Bahiagrass). All these management practices have resulted in two major pasture types: highly managed pastures (i.e., highly drained, fertilized, planted with non-native species, and sustaining higher stocking density) and semi-natural pastures (i.e., less drainage, no fertilization, little planting, and lower stocking density). Ranch managers face challenges when managing pastures and rangelands because wetlands comprise 15–25% of private grazing lands in Central Florida. Determining how management practices interact is particularly important because ranch managers may be more inclined to protect wetlands if a particular combination of management practices results in greater amount of more nutritious forage.

Here, we used data from a long-term ongoing wetland experiment (Boughton et al. 2016, Ho et al. 2018) to investigate the separate and combined effects of pasture management intensity (highly managed vs. semi-natural), cattle exclusion (by fencing off wetlands), and prescribed fire on wetland provisioning services. In particular, we investigated forage quantity measured as standing aboveground biomass and productivity, forage composition, and forage nutritive value. We expected productivity, forage nutritive value, and proportion of palatable species to be (1) higher in wetlands within highly managed pastures due to greater nutrient levels, (2) higher in grazed wetlands due to selection for species with high relative growth rate, especially in highly managed pastures (Cingolani et al. 2005), and (3) higher in burned wetlands due to greater soil nutrients and light availability (Knapp and Seastedt 1986). In contrast, we expected greatest aboveground (standing) biomass in ungrazed and burned wetlands due to release from cattle grazing, higher nutrients, and reduced dead biomass following prescribed fire (Knapp and Seastedt 1986). We expected higher N and P concentrations in plant tissue in wetlands embedded in highly managed pastures due to greater nutrient levels in the wetland soils, as well as higher N and P concentrations in grazed and burned wetlands. We hypothesized that the excluding livestock by fencing off wetlands would result in decreasing N availability (>C/N and <N/P) and that prescribed fire would lower N availability, especially in ungrazed and burned wetlands due to N-volatilization following fire (Blair 1997, Boughton et al. 2018).

Material and Methods

Study sites and experimental design

We studied wetlands on Buck Island Ranch, a fully operational 4,249-ha cattle ranch located in south-central Florida (27°09′ N, 81°11′ W). Buck Island Ranch is a cow–calf operation run by Archbold Biological Station. The climate is subtropical humid (Köppen climate classification) with a clear wet season (from May to November) and 60% of the 132 cm/yr mean precipitation falling during the summer rainy season. The ranch has about 600 seasonally flooded wetlands of varying size and shape.

Ranch pastures were divided into two broad management types. Highly managed pastures were fertilized annually or semi-annually with NPK from the early 1970s to 1987 (56 kg/ha as NH_4SO_4 or NH_4NO_3 and 34–90 kg/ha of P_2O_5 and K_2O) and are still fertilized semi-annually with nitrogen (~56 kg/ha). Highly managed pastures were extensively ditched to improve drainage and heavily seeded with productive and non-native grass species. Semi-natural pastures were neither fertilized nor heavily seeded with non-native species. Rotational grazing was implemented throughout the ranch with on average 2.3 months of rest in highly managed pastures and 6.6 months of rest in semi-natural pastures. All pastures and embedded wetlands were grazed at variable intensity for at least 75 yr before the start of the experiment.

In 2006, we selected 40 seasonally flooded wetlands of similar size (1–2 ha) and shape, 20 within highly managed pastures, and 20 within semi-natural pastures. Wetlands were grouped into five blocks to account for landscape variability (Kelly et al. 2015, Medley et al. 2015, Boughton et al. 2016, Appendix S1). In early 2007, 20 wetlands (10 within highly managed pastures and 10 within semi-natural pastures) were fenced off to prevent cattle grazing, but not access by native whitetail deer (*Odocoileus virginianus*) or feral pigs (*Sus scrofa*). In early 2008, 20 of the 40 wetlands were exposed to prescribed fire and subsequently burned during the dry season every 2–3 yr depending on burning permit authorization. This resulted in a 2 × 2 × 2 complete factorial design, where treatments were all combinations of management intensity (highly managed pasture vs. semi-natural), cattle exclosure (grazed vs. fenced), and prescribed fire (burned vs. unburned). Each of these eight treatments was replicated five times. Note that management intensity also implies different stocking rates between highly managed (mean 0.52 cow–calf pairs · ha^{-1}) and semi-natural pastures (mean 0.28 cow–calf pairs/ha).

Standing biomass, species relative abundance, and productivity

We harvested standing biomass in each wetland at the end of the growing season (October/November) annually from 2006 to 2009. We used five 0.25-m^{-2} circular plots to sample biomass in each wetland, stratified by wetland zone (Center, NW, NE, SE, and SW). We selected plot locations randomly and independently each year. In these five plots, we separated living plant material from dead material (litter and standing dead biomass) each year except in 2006. We then sorted live aboveground biomass by species, clipping each species at the ground level and placing individual species into separate paper bags. We dried biomass samples to constant mass and weighed them to determine relative abundance of each species in each wetland.

In 2016, we estimated productivity in each wetland. First, we randomly placed five 0.25-m^{-2} plots, stratified by wetland zone. We then clipped vegetation at the start of the growing season (March–April) and placed small exclosures around each plot to prevent grazing. Finally, we harvested vegetation in the plots at the peak growing season (September). Vegetation was sorted by species, dried to constant mass, and weighed. We summed the biomass of each species in each wetland to obtain total, living, and dead aboveground biomass (g/m^2). We were particularly interested in the biomass of two common obligate wetland species: the unpalatable common rush *Juncus effusus* and the palatable and preferred maidencane *Panicum hemitomon*.

Biomass composition and forage nutritive value

We classified species in three broad palatability classes based on the literature (see Appendix S2 for a list of species and palatability class), rancher's knowledge, and field observations (Tweel and Bohlen 2008). Unpalatable included clear unpalatable species (e.g., *J. effusus)* or species with low palatability (e.g., *Pontederia cordata: pickerelweed*). Palatable included species of intermediate palatability (e.g., *Hemarthria altissima: limpograss*), as well as highly palatable species (e.g., *Paspalum notatum: bahiagrass*). Unknown included 31 species (out of 176) of unknown palatability, which represented <3% of total biomass. We calculated the total biomass of unpalatable and palatable species in each wetland.

To assess plant tissue nutrients, plant biomass collected in each of the wetlands in 2006–2009 was ground and sent to the University of Georgia Stable Isotope Ecology Laboratory (Athens, Georgia, USA) to obtain plant total N (%), total C (%), total P (%), and their corresponding ratios. We also obtained total N and total P on the twelve most abundant/frequent species based on 2006–2009 biomass survey by grinding separately a small subset of the biomass of each abundant species. As such, these samples integrate multiple locations within the wetlands and whole plant tissue. In 2016, plant biomass from productivity measurements was ground and sent to the University of Florida Forage Evaluation Support Laboratory to obtain plant total N (%), total P (%), crude protein (%) content, and forage in vitro organic matter digestibility (IVOMD, %; Moore and Mott 1974).

Statistical analyses

To test our hypotheses related to biomass quantity, we assessed standing aboveground biomass (2006–2009, dead and live biomass), and productivity (2016) as a function of pasture management intensity, cattle exclosure, prescribed fire, and their interactions. When possible, we included a covariate to reflect initial conditions in these wetlands (i.e., prior to cattle exclusion and fire treatments). For example, aboveground biomass recorded in 2006 was a covariate in analyses for aboveground biomass in 2009. We used linear mixed effects models with block as a random intercept term in all analyses and analyzed years separately. To test our hypothesis related to biomass composition and forage nutritive value, we assessed cumulative relative biomass of palatable species, digestibility, N, P, and the ratios C/P, C/N, and N/P in biomass as a function of treatments. We again used linear mixed effect models with block as a random intercept term in all analyses and analyzed years separately. To explore relationship between nutrient levels in plant species tissue and species palatability, we related plant tissue total N and total P of the twelve most abundant species to their palatability status using linear models (with palatability class as explanatory variable and total N or total P as response variables).

All analyses were performed in R (R Core Team 2018) using the nlme package (Pinheiro et al. 2018). We used stepAIC and drop1 functions within the library MASS (Venables and Ripley 2002) for model simplification (Crawley 2007). We used the rsquared function within the piecewiseSEM package (Lefcheck 2016) to obtain the marginal (i.e., fixed effects) and conditional (i.e., fixed + random effects) R^2 associated with each model (Nakagawa and Schielzeth 2013). We checked for the presence of outliers, normality assumptions, and homoscedasticity by plotting model residuals and applied log-transformations accordingly.

Results

Standing biomass and productivity

Aboveground biomass varied considerably between wetlands and years. Living aboveground biomass varied 40-fold ranging from 0.40 to 16.21 t/ha, with a mean of 4.74 t/ha. Dead aboveground biomass varied 600-fold ranging from 0.01 to 6.27 t/ha, with a mean of 1.07 t/ha. We observed higher mean aboveground biomass in wetlands within highly managed pastures than wetlands within semi-natural pastures, but this pattern was statistically clear only in 2008 and 2009 (Table 1, Fig. 1 for 2009 data). On average across 2008–2009, wetlands in highly managed pastures had 26.1% more living biomass and 188.3% more dead biomass than wetlands in semi-natural pastures. Each year following cattle exclusion, we observed greater living aboveground biomass (on average + 56.4% over 2007, 2008, and 2009) and greater dead biomass (on average + 218.8% only in 2008 and 2009) in fenced wetlands compared to grazed wetlands (Table 1, Fig. 1). We did not find clear interactions between pasture types, grazing, and fire treatment on total or live biomass. However, prescribed fire and pasture type interacted to affect dead biomass in 2009 (Table 1). Prescribed fire decreased dead biomass in both fenced and grazed wetlands, but only in highly managed pastures. By 2009, dead biomass was greatest in unburned fenced wetlands embedded within highly managed pastures (2.76 ± 1.80 t/ha; Fig. 1).

Productivity varied twelvefold: between 1.96 and 24.27 $t \cdot ha^{-1} \cdot yr^{-1}$. Unlike biomass results, we observed a clear 3-way interaction among treatments on productivity (Table 1). Pasture management governed productivity response to grazing and fire. Wetlands embedded in semi-natural pastures had similarly low productivity, but wetlands embedded in highly managed pastures exhibited stronger effects of cattle exclosure and burning (Fig. 1). Productivity was highest in fenced wetlands within highly managed pastures.

Species relative abundance

In 2006, before the start of the experiment, the highly unpalatable rush *J. effusus* was the most abundant species in grazed wetlands embedded within highly managed pastures (mean 44.3% of total aboveground biomass). *Juncus effusus* remained dominant in grazed and unburned wetlands within highly managed pastures throughout the experiment. However, *Luziola fluitans* (southern watergrass), *J. effusus,* and *P. hemitomon* became co-dominant in highly managed, grazed, and burned wetlands because of experimental treatments. In contrast, wetlands in semi-natural pastures initially were

Table 1. Results of linear mixed models that tested the effect of pasture type (P), cattle exclusion (G), and prescribed fire (F) on biomass of seasonal wetlands in the Northern Everglades region, Florida, USA.

	Biomass (log_{10})				
Main effects	Total (df 1,33)	Live (df 1,33)	Dead (df 1,30)	Palatable species (df 1,31)	Productivity (df 1,28)
P	−**0.19** (0.07) *6.71**	−**0.16** (0.08) *4.29**	−**0.003** (0.19) *4.83**	−0.05 (0.08) *3.27*	**−389.1 (120.4)** *8.68**
G	−**0.23** (0.07) *10.12**	−**0.19** (0.08) *5.60**	−**0.39** (0.13) *8.88**	**−0.16 (0.06)** *7.24**	**−370.1 (120.4)** *3.86**
F			0.47 (0.19) *1.58*	−0.26 (0.08) *3.18*	−139.1 (120.4) *0.78*
P × F			−**0.59** (0.27) *4.81**	**0.30 (0.12)** *6.71**	243.0 (170.2) *0.009*
G × F					323.2 (170.2) *0.33*
P × G					434.7 (170.2) *2.25*
P × G × F					**−508.4 (240.7)** *4.46**
Covariate					
R^2 marginal	0.3	0.2	0.3	0.33	0.40
R^2 conditional	0.3	0.2	0.42	0.37	0.45

Notes: Total biomass, live biomass, dead biomass, and palatable species are from 2009 data. Productivity was obtained with 2016 data. Values are model coefficients with SE in parentheses and F values for those coefficients (in italics). Bold values identify clear differences. R squared was obtained using the approach proposed by Nakagawa and Schielzeth (2013).

$^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

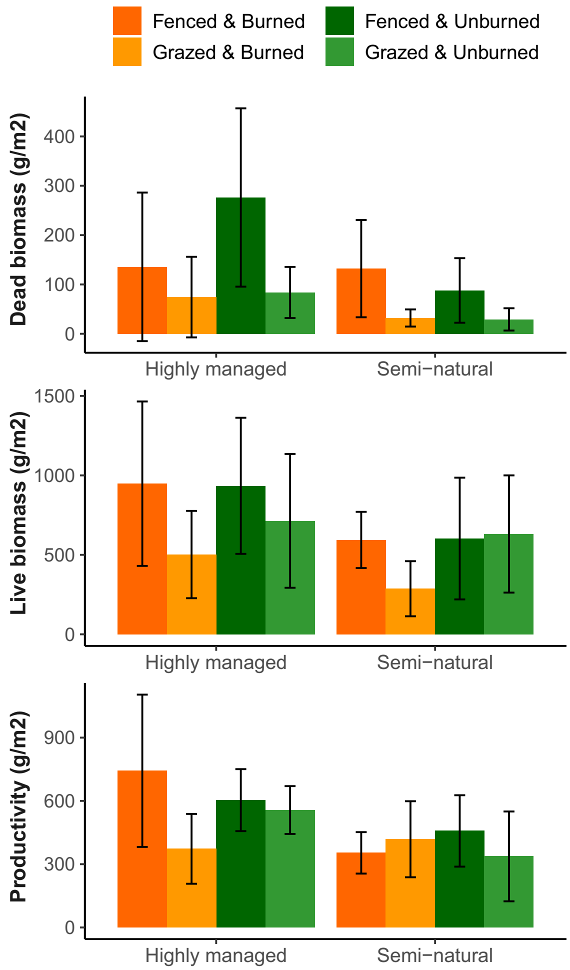

Fig. 1. Aboveground biomass and productivity responses to treatments of seasonal wetlands in the Northern Everglades region, Florida, USA. Dead biomass and live biomass in 2009 corresponds to three years after fencing and two years after the first prescribed fire. Productivity was measured in 2016, ten years after the onset of the experiment. Data are means ± SD.

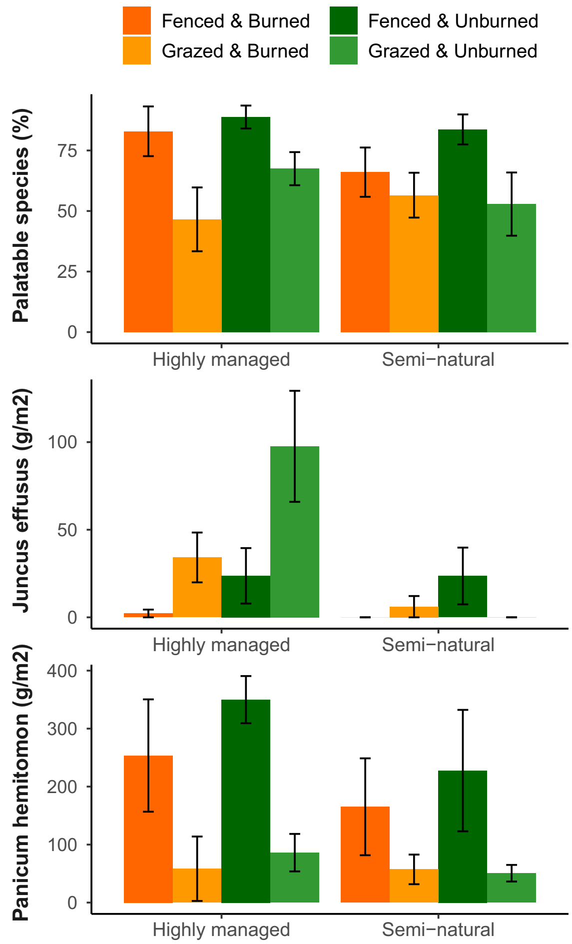

Fig. 2. Forage composition of seasonal wetlands in response to treatments ten years after the onset of the experiment (2016). Data are means ± SD.

dominated by *Pontederia cordata*, *P. hemitomon*, and *Cladium jamaicense* (sawgrass; 14%, 12.3%, and 11.2%, of biomass, respectively), when all wetlands were grazed. These three species remained dominant in grazed wetlands throughout the experiment, but three years of cattle exclusion caused *P. hemitomon* to become the dominant species (43.7% of biomass) in semi-natural pastures regardless of burning treatment. *Panicum hemitomon* also became dominant (43.3% of biomass) after cattle were excluded in wetlands in highly managed pastures regardless of burning treatment.

In 2009, relative biomass of palatable species responded clearly to cattle exclosure and exhibited a clear interaction between prescribed fire and pasture type (Table 1, Fig. 2). Relative biomass of palatable species was higher in fenced wetlands (80.3%) than in grazed wetlands (64.3%). Prescribed fires increased relative biomass of palatable species only in wetlands embedded in highly managed pastures, where palatable species comprised 8.91 t·ha^{-1} in burned wetlands, compared to 6.16 t/ha^{-1} in unburned wetlands.

Table 2. Results of linear mixed models that tested the effect of pasture type (P), cattle exclusion (G), and prescribed fire (F) on plant tissue nutrient of seasonal wetlands collected in 2009.

Main effects	Total N (log_{10}) (df 1,33)	Total C (df 1,31)	Total P (df 1,33)	C/N (log_{10}) (df 1,33)	N/P (df 1,33)
P			−**0.01*** (0.002) *52.67*		
G	**0.14*** (0.03) *16.42*	0.54 (0.34) *2.06*		−**0.14*** (0.04) *15.98*	**3.11*** (0.78) *15.72*
F		0.50 (0.35) *1.47*	−**0.004*** (0.002) *4.65*		
P × G					
P × F					
Covariate		0.08 (0.06) *2.06*			
R^2 marginal	0.25	0.13	0.55	0.25	0.23
R^2 conditional	0.4	0.13	0.62	0.4	0.44

Notes: Values are model coefficients with SE in parentheses and F values for those coefficients (in italics). Total N and C/N are (log_{10}). Bold values identify clear differences. R^2 was obtained using the approach proposed by Nakagawa and Schielzeth (2013).

$^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Plant tissue nutrients and forage nutritive value

Three years after cattle exclusion and two years after prescribed fires, plant tissue total P content was greater in wetlands within highly managed pastures but was not affected by grazing or prescribed fire treatments (Table 2, Fig. 3). However, total N (thus N/P ratio) was greater in grazed wetlands than ungrazed wetlands—independent of pasture type and prescribed fire. The N/P ratio was on average 8.78 ± 2.19 in fenced wetlands and 11.9 ± 3.34 in grazed wetlands. Total C was not impacted by any management treatments, but C/N was clearly higher in fenced wetlands and clear main effects of prescribed fire and pasture type occurred for C/P, where C/P was greater in unburned wetlands in semi-natural pastures.

In 2016, plant tissue total P was clearly higher in highly managed wetlands and was elevated in fenced wetlands, without clear interactive effects (Table 3, Fig. 4). In vitro organic matter digestibility was also clearly higher in wetlands embedded in highly managed pastures, but there was no clear evidence that prescribed fire or grazing treatments affected it. Unlike results for 2006–2009, treatments no longer clearly affected total N in 2016. The most frequent and most abundant unpalatable and palatable species did not exhibit clear differences in nutrient levels: total N ($F_{1,10}$ = 0.35, P = 0.56) and total P ($F_{1,10}$ = 1.2, P = 0.30) throughout the experiment (Appendix S3).

Discussion

Wetlands are a substantial portion of landscapes globally and potentially provide important ecosystem services in grazing lands. Here, we evaluate how wetlands contribute to provisioning services and how pasture and rangeland management affects those services. The results of our decade-long experiment on whole wetlands demonstrate that typical practices such as grazing and prescribed fire can be manipulated to enhance or maintain wetland provisioning services. Greater understanding of wetland provisioning services may lead to greater protection and sustainable management of wetlands embedded in grazing lands.

Effect of treatments on aboveground biomass and productivity

Excluding cattle (using fencing) strongly and consistently increased live and dead aboveground plant biomass. This finding is in agreement with previous work and reflects the active removal of plant material by cattle (Milchunas et al. 1988, Jones et al. 2011, Rose et al. 2013). Aboveground biomass was generally higher in wetlands embedded within highly managed pastures, consistent with our hypothesis and known effects of fertilization on aboveground biomass (Wilson and Tilman 1991, Gough et al. 2000). However, the effect of pasture type was less consistent between years than the effect of cattle

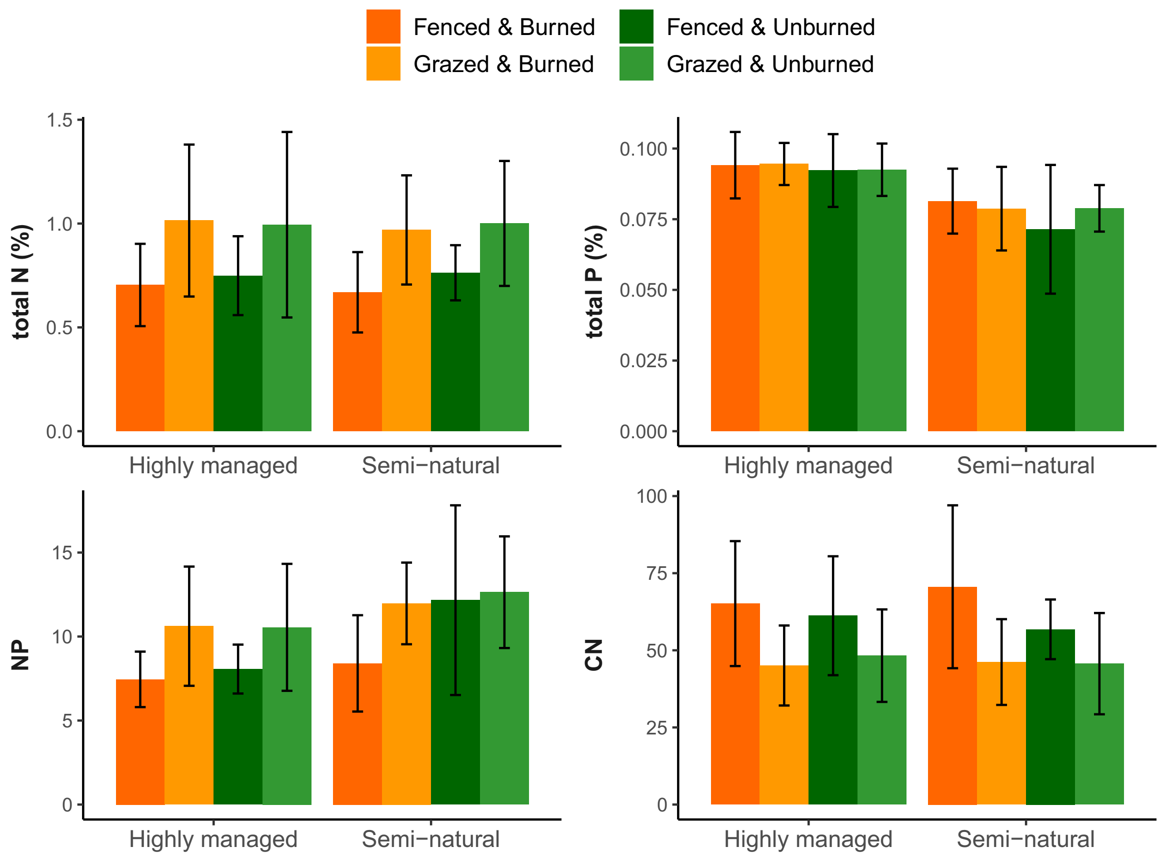

Fig. 3. Forage nutritive value (total N (%), total P (%), N/P ratio, and C/N ratio) as a function of pasture type, cattle exclusion, and prescribed fire in biomass produced in 2009 (three years following cattle exclusion and two years after the first prescribed). Data are means ± SD.

Table 3. Results of linear mixed models testing the effect of pasture type (P), cattle exclusion (G), and prescribed fire (F) on forage nutritive value of seasonal wetlands collected in 2016 using productivity protocol.

Main effects	Total N (df 1,31)	Total P (df 1,31)	IVOMD (df 1,31)
P	−0.008 (0.07) 0.04	**−0.08 (0.01)** **52.04***	**−5.64 (2.14)** *6.82**
G	−0.09 (0.08) 1.68	**−0.02 (0.01)** **4.28***	1.76 (2.15) 0.68
F	0.08 (0.08) 1.37	−0.001 (0.01) 0.01	0.51 (2.14) 0.06
R^2 marginal	0.07	0.60	0.17
R^2 conditional	0.14	0.60	0.17

Notes: Values are model coefficients with SE in parentheses and *F* values for those coefficients (in italics). Bold values identify clear differences. R^2 was obtained using the approach proposed by Nakagawa and Schielzeth (2013).
$^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

exclusion, consistent with top-down grazing having greater effect on plant biomass than bottom-up land management effects. We expected that prescribed fire would positively affect biomass. Instead, prescribed fire primarily reduced dead biomass in fenced wetlands, with little effect on live biomass.

Clear three-way interaction among treatments reflected past grazing effects on productivity, consistent with other research showing the importance of interactions between grazing and other environmental drivers on grasslands and wetlands (Fuhlendorf and Engle 2004, Kotze 2013, Jansen et al. 2019). We expected that prescribed fire would positively affect productivity through increases in both soil nutrients and light (Blair 1997). Instead, prescribed fire effects were contingent on pasture type and grazing

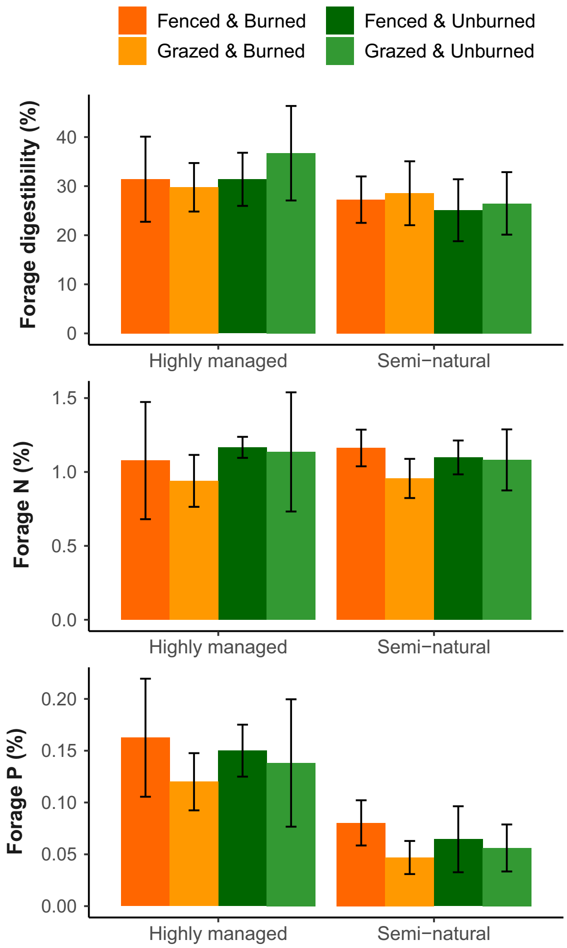

Fig. 4. Forage nutritive value as a function of pasture type, cattle exclusion, and prescribed fire in biomass produced in 2016. Data are means ± SD.

treatment, where burned and grazed wetlands within highly managed pastures had lower productivity compared to burned and fenced wetlands. By design productivity measurements obtained in 2016 reflected effects of past grazing, but not grazing effects in that year. The way we measured productivity did not allow investigating compensatory regrowth due to grazing. Because of this, our estimate of productivity might have underestimated true annual net primary productivity.

Interactive effects of fire and grazing on vegetation are a well-known phenomenon (Fuhlendorf and Engle 2004). In our study, burned wetlands within highly managed pastures may experience higher grazing pressure due to higher stocking rates and lower resting periods than semi-natural pastures. Interestingly, fire and grazing treatment effects on productivity and standing biomass in wetlands in semi-natural pastures were lower or null compared to those in highly managed pastures, which reflects long-term consequences of past management differences between pasture types.

Effect of treatments on species relative abundance and forage nutritive value

Relative abundance shifted among wetland species in response to cattle exclusion and to a lesser extent prescribed fire in highly managed pastures. Treatments that shifted away from status quo conditions (i.e., fencing, burning) increased the proportion of palatable species in both wetland types (semi-natural and highly managed). For example, the unpalatable common rush (*J. effusus)* dominated highly managed and grazed wetlands. After cattle exclusion, it was replaced by the more palatable and preferred grass, *P. hemitomon*. *J. effusus* was identified as a refuge under grazing pressure (Boughton et al. 2011), with many palatable species surviving/growing under its canopy. When cattle were excluded, these species competed with *J. effusus* and in the case of *P. hemitomon* outcompeted *J. effusus* due to high growth rate and clonal traits (Boughton et al. 2011).

Our study highlights that management of grazing and fire regime increased in biomass and forage quality for cattle ranching, especially in highly managed pastures. Using the same experiments, Boughton et al. (2016) found that excluding cattle and implementing prescribed fire did not measurably affect the diversity and floristic quality of wetlands embedded within highly managed pastures. Together, these results suggest that fire and cattle exclusion may not affect which species are present in these wetlands, but their relative abundance. Our study also indicates that 1–2 yr of cattle exclusion enables strong recovery of wetland vegetation that is higher quality forage for subsequent grazing.

Forage of wetlands in highly managed pastures had greater in vitro organic matter (IVOMD), but grazing or fire treatments did not affect IVOMD. Further, there was no effect of the treatments on crude protein. A better understanding of the relationship between palatability, IVOMD, crude protein, and plant tissue nutrients would help to assess management effects (i.e., experimental treatments here) on forage value. In our study, both palatable and unpalatable species had high N and P in plant tissue. For example, *Persicaria* spp (*Persicaria punctata* and *Persicaria hydropiperoides*: knotweeds) had high levels of tissue P, but were completely avoided by cattle and as such were abundant in grazed wetlands, especially in highly managed pastures. Additionally, *J. effusus* contained N and P tissue levels similar to *P. hemitomon* and other palatable grasses. Thus, N and P tissue levels are not good proxies for palatability. Further, IVOMD did not differ between fenced and grazed wetlands, so digestibility seems decoupled from palatability in our study. We think the presence of aerenchyma (e.g., *J. effusus*) or presence of secondary compounds (e.g., *Polygonum* spp.: knotweeds) in leaf tissue could explain why species with average N and P concentrations are not desired/palatable to cattle. Because we did not measure aerenchyma and secondary compounds in plant tissue, we cannot test this hypothesis. Thus, further research should investigate the relationship secondary compounds and palatability in wetland species.

Plant tissue nutrients and implications for wetland nutrient cycling

After 3 yr of experimental fencing and 2 yr following prescribed fire, plant N/P ratio was on average 8.78 (± 2.19) in fenced wetlands, suggesting that these wetlands were N-limited (N/P < 10; Güsewell et al. 2003, Güsewell 2004). In contrast, N/P in grazed wetlands was on average 11.9 (± 3.34), suggesting that these wetlands were not clearly limited by either N or P (10 < N/P < 20; Güsewell et al. 2003, Güsewell 2004). Despite no nutrient limitations, grazed wetlands within highly managed pastures had lower productivity and were dominated by unpalatable species (e.g., *J. effusus*, *P. punctatum*) adopting an avoiding strategy (Briske 1996, Díaz et al. 2001). This contrasts with previous studies on grasslands which found that grazing promoted unpalatable species in low nutrient systems, but promoted palatable species with high relative growth rate when nutrients were non-limiting (Milchunas et al. 1988, Cingolani et al. 2005). It is possible that productive and palatable species that are also able to cope with flooding were filtered out due to overgrazing in wetlands within highly managed pastures.

Nutrients are returned and imported by grazers via urine and excrement, which is readily decomposed and speeds N cycling to increase N availability (Hobbs et al. 1991, Augustine 2003, Cech et al. 2008). This process explains the higher N/P ratio observed in grazed wetlands. Similarly, it explains greater plant tissue C/N ratio in fenced wetlands than in grazed wetlands and in turn is often associated with lower decomposition rates. Finally, C/P ratio in wetlands within semi-natural pastures was greater than in wetlands of highly managed pastures. Greater P availability in highly managed pastures is a legacy effect of P-fertilization that ended in 1987 (Swain et al. 2007, Ho et al. 2018).

Economic implications and future management

It is important for agriculture, environmental sustainability, biodiversity, and ecosystem services that management of wetlands on grazing lands is optimized. Greater understanding of wetland provisioning services may lead to greater protection and sustainable management of wetlands embedded in grazing lands. Our study showed that biomass quantity and palatability positively responded to cattle exclusion within 2–3 yr. Based on our results, we estimated a gain of 5.9 t/ha of palatable forage three years after excluding cattle. Considering that 12% (510 ha) of our study site is covered by seasonal wetlands, this would represent a gain of 3.0 t of palatable forage, roughly equivalent to 705 animal unit months per year. Recently, the fences around our wetlands were replaced at a cost of US $32,000 and their expected lifetime is 12 yr. Our twenty fenced wetlands had a total area of 34.5 ha, which is expected to generate 203.5 t of palatable forage in every 3-yr cycle, for a total of 814.2 t of palatable forage during the fences' lifetime. At the current price for silage (US $35–40 per ton; G. Lollis, *personal communication*) another high-quality fodder, the expected benefit of fencing these wetlands for 12 yr is US $28,497–$32,568, yielding a benefit–cost ratio of 089–1.02. Thus, this provisioning service alone may not justify fencing every small wetland. However, fencing larger circular wetlands is more favorable because area, which determine forage yield, increases as a squared term of wetland circumference. This approach could be subsidized by agency incentive programs and could be applied primarily to wetlands within highly managed pastures dominated by *J. effusus* or other unpalatable species. Future research should investigate what grazing regime could then be applied to these wetlands to prevent a return to wetlands dominated by unpalatable species.

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