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WETLAND RESTORATION

Post-Restoration Plant Community Changes in Grazed and Ungrazed Seasonal Wetlands in Florida

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Abstract
Seasonally inundated wetlands are threatened ecosystems worldwide and increasingly important targets for wetland restoration programs. However, restoring such ecosystems is difficult, as it requires mimicking the historical shifts between dry and flooded states. In this study, we evaluate the responses of agriculturally impacted seasonal wetlands to pasture-scale hydrological restoration. We selected 15 seasonal wetlands in central Florida (10 within restoration easements and five in unrestored pastures) and excluded cattle from five of the restored wetlands. We monitored each wetland from 2011 to 2016 to document potential changes in water levels, plant species richness, beta diversity, floristic quality, and cover of obligate wetland species. Vegetation responses to restoration were gradual and subtle, becoming detectable only five years following restoration. By 2016, restored wetlands had significantly lower cover of facultative upland species and higher cover of obligate wetland species. Species richness was higher in unrestored wetlands due to the presence of many facultative upland species. Beta diversity within wetlands and floristic quality based on coefficient of conservatism were not affected by restoration. We did not find strong effects of cattle exclusion on post-restoration diversity metrics, but we observed a large increase in the native grass, *Panicum hemitomon* Schult. This study showed mixed outcomes when measured against the goals of restoring wetland communities. It also highlighted the need for more active restoration approaches to regain historical communities or promote target species (*e.g. Coleataenia abscissa* (Swallen) LeBlond). We emphasize the need for costly restoration activities to be coupled with long-term monitoring to assess success.

Keywords Hydrological restoration · Indicator species · Passive restoration · Plant species diversity · Wetland Reserve Easements

Introduction

Seasonal depressional wetlands occur worldwide and typically harbor high biodiversity with distinctive fauna and flora compared to perennial wetlands (Sharitz 2003; Paton 2005; Bagella and Caria 2012; Lukács et al. 2013). These freshwater ecosystems are characterized by fluctuating hydrology, switching between dry and wet states in response to seasonally varying rainfall and evapotranspiration rates. Like other globally distributed wetland types, seasonal wetlands are disappearing (Dahl 2014; Davidson 2014; Calhoun et al. 2017; Evans et al. 2017) and those that remain are considerably altered by human activities (Dahl 2014; Johnston and McIntyre 2019). Mitigating anthropogenic impacts through restoration is an increasingly common goal for land managers, agricultural producers and state and federal agencies. Although seasonal wetlands provide multiple ecosystem services, often at scales far exceeding what would be expected based on their size (Cohen et al. 2016; Calhoun et al. 2017; Sonnier et al. 2020), they may not be directly targeted in landscape-scale restoration programs. Even with focused attention, it may be difficult to restore seasonally varying hydrology or to predict the potential effects of the surrounding landscape, soil type, disturbance regime, and invasive species on restoration success (Zedler 2000).

Seasonal depressional wetlands (e.g., prairie potholes in the Northern Great Plains region, vernal pools in California and other Mediterranean regions, Carolina bays in the southeastern Coastal Plain) are often embedded within agricultural lands, resulting in mosaics of uplands and wetlands

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at landscape scales. For this reason, they experience direct and indirect effects of agricultural management (Swain et al. 2013), which may affect wetland size, shape, and connectivity (Johnston and McIntyre 2019), as well as plant community structure and species composition (Teuber et al. 2013; Medley et al. 2015; Boughton et al. 2016; Moges et al. 2017). For example, drainage of the surrounding lands usually decreases water level and hydroperiod (i.e. duration of inundation), but in some cases may increase water levels and hydroperiod due to consolidation drainage (McCauley et al. 2015). To improve forage quantity and forage nutritive value in pastures, farmers and ranchers often plant and fertilize more productive exotic grasses, which may then invade adjacent seasonal wetlands ((Boughton et al. 2011b). Exotic species and nutrient runoff from surrounding lands have important consequences for wetland functions and services (Olde Venterink et al. 2003; Zedler and Kercher 2004). For example, fertilization application may lead to decreased nutrient removal or decreased biodiversity (Gerakis and Kalburtji 1998).

The United States Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) has now restored millions of acres of wetlands through its Wetland Reserve Easement (WRE) program (Mausbach and Dedrick 2004; Gleason et al. 2011). When enrolled in the program, landowners retain ownership of their land, but lose development rights and must obtain compatible use authorization for cattle grazing and prescribed fire. In Florida, cattle grazing continues to be authorized in WREs due to perceived land management benefits, including exotics control and reduction of woody species. Wetland restoration through the WRE program often consists of reestablishing historical hydrology and assumes that vegetation will passively respond to changes in hydroperiod. Previous research has found that this is not always the case (Zedler 2000; Hilderbrand et al. 2005). Restoration may require additional steps, such as planting of dispersal-limited native species and/or controlling exotic species (Scheffer et al. 2001; Hobbs and Norton 2004; Suding et al. 2004). Determining restoration outcomes also requires monitoring, a step that is often overlooked in restoration planning (but see De Steven and Lowrance 2011).

In this study, we evaluated outcomes of restoration in two USDA WREs in south-central Florida, a region where there has been little assessment of wetland conservation and restoration practices (De Steven and Lowrance 2011). The site's native prairie and pine flatwoods habitats were drained and converted to cattle pasture several decades ago. The hydrology of seasonally flooded depression marshes (Florida Natural Areas Inventory [FNAI] 2010a) embedded in these pastures was highly altered by ditching and, in some cases, dredging to make them permanent water sources for cattle. Restoration measures in these two easements consisted of hydrological manipulations to mitigate the effects of ditching on both groundwater and surface water levels and to support native wetland plant species, with the further goal of restoring or enhancing wetland wildlife habitat values. Our first objective was to determine if pasture-scale hydrological restoration increased water levels in the embedded seasonal wetlands. We expected higher water levels in restored wetlands within the easements compared to wetlands in adjacent pastures outside the easements. Furthermore, we expected hydrologically restored wetlands exposed to continued grazing would have the highest water levels due to reduced evapotranspiration (Pyke and Marty 2005; Marty 2015). Second, we investigated how the passive restoration approach employed here, combined with grazing, affected native and exotic species richness, beta diversity, floristic quality, and cover of obligate wetland species. Although quantitative measures of success were not established prior to restoration, we expected increases in beta diversity, floristic quality, and cover of obligate wetland species (Sonnier et al. 2018). Removal of grazing was expected to reduce species richness due to increases in dominance of wetland grasses (Boughton et al. 2016; Sonnier et al. 2020).

Methods

Study site

Our study was conducted at the 1,477-ha Archbold Reserve (27°9.1' N, 81°22.7' W; Fig. 1) located on the southwestern edge of the Lake Wales Ridge in southern peninsular Florida. Acquired by Archbold Biological Station in 2002, the Reserve comprises a mosaic of improved pastures and remnant natural communities managed with controlled burning every 2–10 years. Prior to logging and conversion to agricultural use, the site exhibited a typical transition from xeric sand pine scrub communities at higher elevation (~47 m) to mesic flatwoods and prairie-like cutthroat seep communities on the slope, then to forested wetlands (i.e., bayheads) at lower elevation (~30 m). Cutthroat seeps are rare natural communities occurring on seepage slopes associated with central Florida ridges and dominated by the state-threatened, endemic cutthroat grass (*Coleataenia abscissa*; U.S. Fish and Wildlife Service [USFWS] 1999; Florida Natural Areas Inventory [FNAI] 2010b).

The site's hydrological dynamics, including seasonally fluctuating water levels in depressional wetlands and flows to seepage-fed streams, were greatly altered by ditching between 1966 and 1981 (Fig. 1). The extensive ditch network was designed to irrigate pasture during the winter dry season and drain excess water during the summer wet

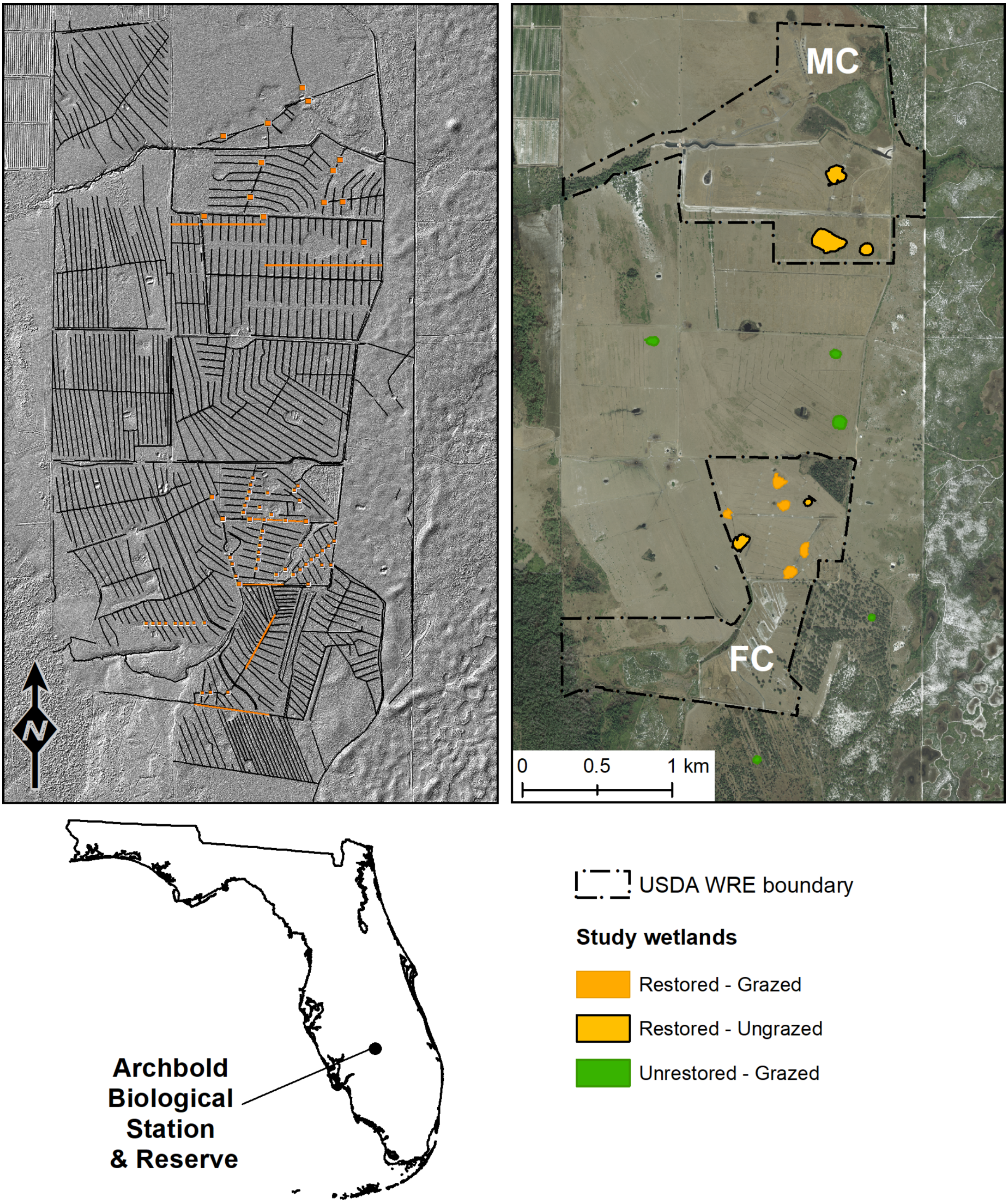

Fig. 1 Map of study area. Left panel shows the ditch network and locations of ditch plugs and land-smoothed areas (in orange) overlaid on 2006 LiDAR-derived elevations. Right panel shows the boundary of the two easements (MC in the north and FC in the south) and the locations of the 15 wetlands used in this study overlaid on 2011 aerial images. Restored wetlands are in orange, and unrestored wetlands in green

season. Irrigation ceased in the 1980s following a switch from clover (*Trifolium* spp.) and Pangola grass (*Digitaria* spp.) to other exotic forage species, primarily bahiagrass (*Paspalum notatum* Flueggé) and limpograss (*Hemarthria altissima* (Poir.) Stapf & C.E. Hubbard). Fertilization and overgrazing contributed to wetland degradation prior to 2002. Cattle grazing continued from 2003 to the present via a grazing lease with a neighboring rancher who is allowed no more than 0.62 animal units per ha of pasture. Most Reserve wetlands have been colonized to varying degrees by invasive, exotic plants, particularly torpedograss (*Panicum repens* L.) and Peruvian primrose-willow (*Ludwigia peruviana* (L.) H. Hara).

Restoration and Study Design

USDA-NRCS completed two large hydrological restoration projects in the Frances' Creek WRE (163 ha) and Mary's Creek WRE (200 ha) easements on the Archbold Reserve during the dry season of winter 2010-spring 2011 (Fig. 1, Appendix S1). The restoration employed a passive approach and primarily entailed plugging of numerous ditches throughout each easement to render them ineffective and restore the seasonally high water table. As part of the restoration design for Frances' Creek WRE, attention was paid to blocking specific ditches that intersected seasonal wetlands, in addition to points where lateral ditches drained into larger collector ditches. We assessed restoration outcomes in 15 depressional wetlands, including 10 hydrologically restored wetlands within the boundaries of the WREs (3 in Mary's Creek, 7 in Frances' Creek) and five unrestored wetlands outside the easements (Fig. 1). We fenced cattle out of three wetlands in Mary's Creek (2009, Appendix S1) and two wetlands in Frances' Creek (2011, Appendix S1), resulting in three treatments: restored-grazed, restored-ungrazed and unrestored-grazed. We did not have unrestored, ungrazed wetlands, which prevents us from testing for an interaction between restoration and grazing. These wetlands are usually flooded 4–6 months of the year following rainfall events occurring during the wet season (late May to mid-October). Peak water depth is observed in September-October. Historically, these wetlands dried seasonally, and the goal of the restoration was not to make them permanently flooded. The 15 wetlands chosen for this experiment varied in size (ranging from 0.31 to 6.00 acres), but wetland size did not differ significantly between treatment groups at the start of the experiment (Appendix S2).

Plant Community Sampling

We randomly placed 12 1-m^2 permanent plots in each study wetland, ensuring interspersion throughout the wetland by locating three plots in each quadrant of the wetland. We sampled for the first time in May 2011, post-construction but before the wet season (funding was not available for data collection prior to 2011). We consider this initial sampling event to be a pre-restoration assessment of the vegetation communities because wetland hydrology had not yet been significantly affected by the new ditch plugs. We resampled all plots during the late dry season (22 April–2 June) in 2012 and 2014, and during the late wet season (27 October–10 November) in 2016. Within each plot, we estimated percent cover of each plant species, as well as litter and bare ground, to the nearest 5%. We also recorded signs of disturbance by cattle (trampling, cow pies) or feral pigs (*Sus scrofa* L.). We also measured depth of standing water in each plot every August.

We calculated species richness and average cover of native and exotic species at the wetland level. We also estimated the average cover of (i) obligate wetland (OBL) (ii) facultative wetland (FACW) (iii) facultative (FAC), (iv) facultative upland (FACU), and (v) obligate upland species (UPL) at the wetland level. In this study, we did not record any obligate upland species. Thus, we did not include this category in our analysis. To assess floristic quality, we calculated the mean coefficient of conservatism (CC, classification proposed by Mortellaro et al. 2012) across plots within each wetland. Coefficient of conservatism is a measure of plant fidelity to specific habitats and plant tolerance to disturbance ranging from zero to 10. It separates ubiquitous/ruderal species (CC = 0–4) from habitat specialists typical of pristine intact natural systems CC = 5–10). Exotic species are not included in this classification, but we assigned them a CC of 0 as suggested by Herman et al. (1997, 2001). Species nomenclature follows the International Plant Names Index (IPNI, https://www.ipni.org). Origin (native or exotic) and wetland indicator status follows the Atlas of Florida Plants (http://florida.plantatlas.usf.edu).

Statistical Analysis

All analyses were performed in R (R Core Team 2020). To test restoration and grazing effects on water levels (recorded in August), we compared average water depth in the three treatments using linear mixed models (LMM) with wetland as a random factor and treatment as main effect.

We tested the effect of treatments on diversity separately for each year. For mean coefficient of conservatism, native species richness, and exotic species, we used linear models with treatment as explanatory variable (one-way ANOVA). The same analysis was performed with beta diversity as response variable. We estimated beta diversity in each wetland using a distance-based approach (Anderson 2006; Anderson et al. 2006) using the package vegan. We first calculated the Bray-Curtis distance between each pair of plots (plot X species matrix) each year using the function "vegdist". Second, we used the "betadisper" function to calculate the average distance between plots from the same wetland to their centroid. Thus, we have an average distance to centroid for each wetland and for each survey year (greater distance corresponds to more heterogeneous plant community). To test the effect of treatment on cover of native, exotic, OBL, FACW, FAC, and FACU species, we used beta regression with treatment as main effect and logit link function ("betareg" function within the Betareg package).

Finally, we performed indicator species analysis on the vegetation data to identify species associated with specific treatments using importance values (Dufrêne and Legendre 1997). This was done using the "indval" function within the labdsv package and repeated for each year separately.

Results

Treatment Effects on Water Levels

Water depth measured during the wet season was highly variable both within wetlands (ranging from 1 to 96.7 cm across plots) and between wetlands (ranging from an average of 7.3 to 40.8 cm). We found that water depth measured in August was nearly two times higher in restored wetlands (31.0 ± 7.8 cm) compared to unrestored wetlands (16.4 ± 8.9 cm; $F_{1,12} = 9.4$, $p = 0.01$) and was independent of grazing treatment ($F_{1,12} = 0.01$, $p = 0.96$; Fig. 2).

Treatment Effects on Vegetation Communities

We recorded 144 plant species in the 15 wetlands, 65 of which occurred in 1% of the plots across the experiment (24 species occurred in one plot across the surveys). Across sampling events, total plot-level species richness ranged from 0 to 20 species (mean 7.9 ± 3.7 sd per plot), though only 4 plots had 0 species. At the wetland level, total species richness ranged from 14 to 45 species and averaged 28.7 ± 7.0 per wetland. Exotic species richness was generally low, ranging from 0 to 6 exotic species per wetland and averaging 1.7 ± 3.7 across all sampling events. Exotic species cover averaged 10.3% ± 19.5 across all sampling events.

We consider the first survey in May 2011 to represent pre-restoration conditions as it occurred before the first rainy season following restoration. At that time, diversity metrics were similar among treatments (Fig. 3; Table 1). In subsequent years, treatments started to diverge. Although we did not detect an effect of treatment on species richness in the first 3 years post-restoration, by 2016 unrestored-grazed wetlands had on average 8.2 more native species

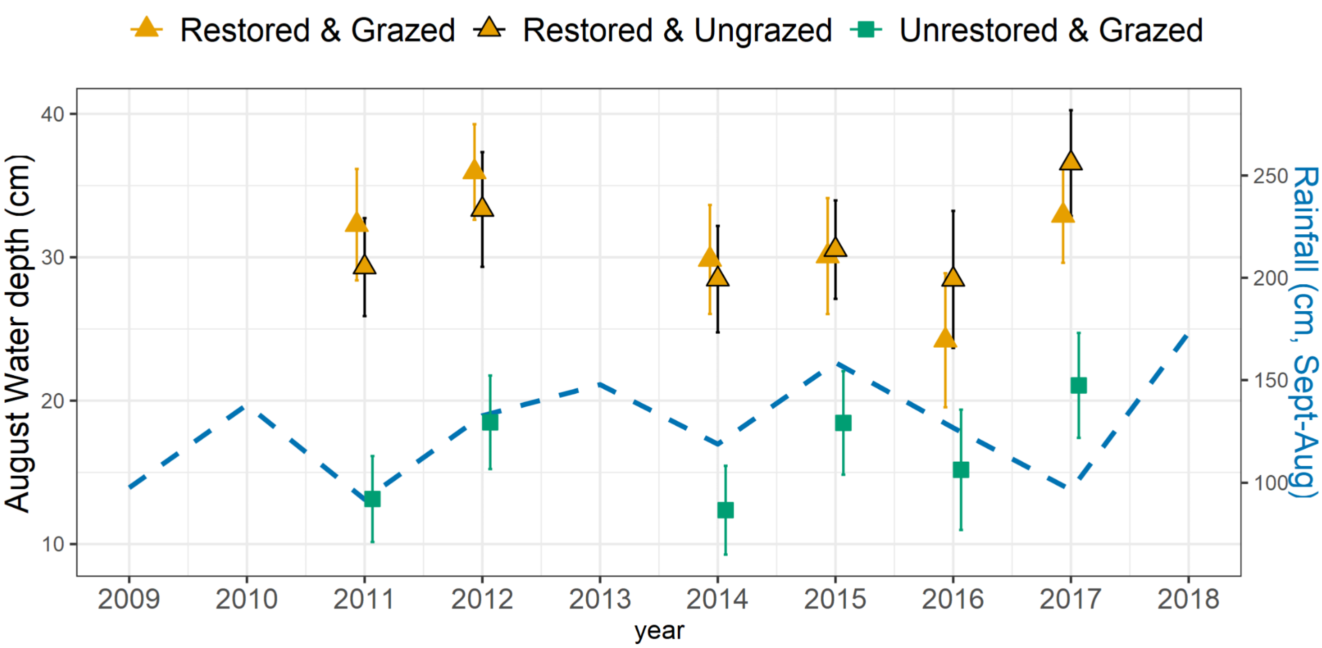

Fig. 2 Average water depth (triangle, cm ± CI) measured in August in each treatment (left y-axis) and associated yearly rainfall (cm, blue line, right y-axis). We measured water depth at 12 permanent locations within each wetland during the wet season in August 2011, 2012, 2014, 2015, 2016 and 2017. Rainfall data were obtained from a nearby climate monitoring station located in the Archbold Reserve (GPS: Latitude = 27.1828, Longitude = -81.3523) belonging to the National Centers for Environmental Information (NOAA) US Climate Reference Network (USCRN). Rainfall amount was the cumulative rainfall that occurred between September (of the previous year) and August (of the current year)

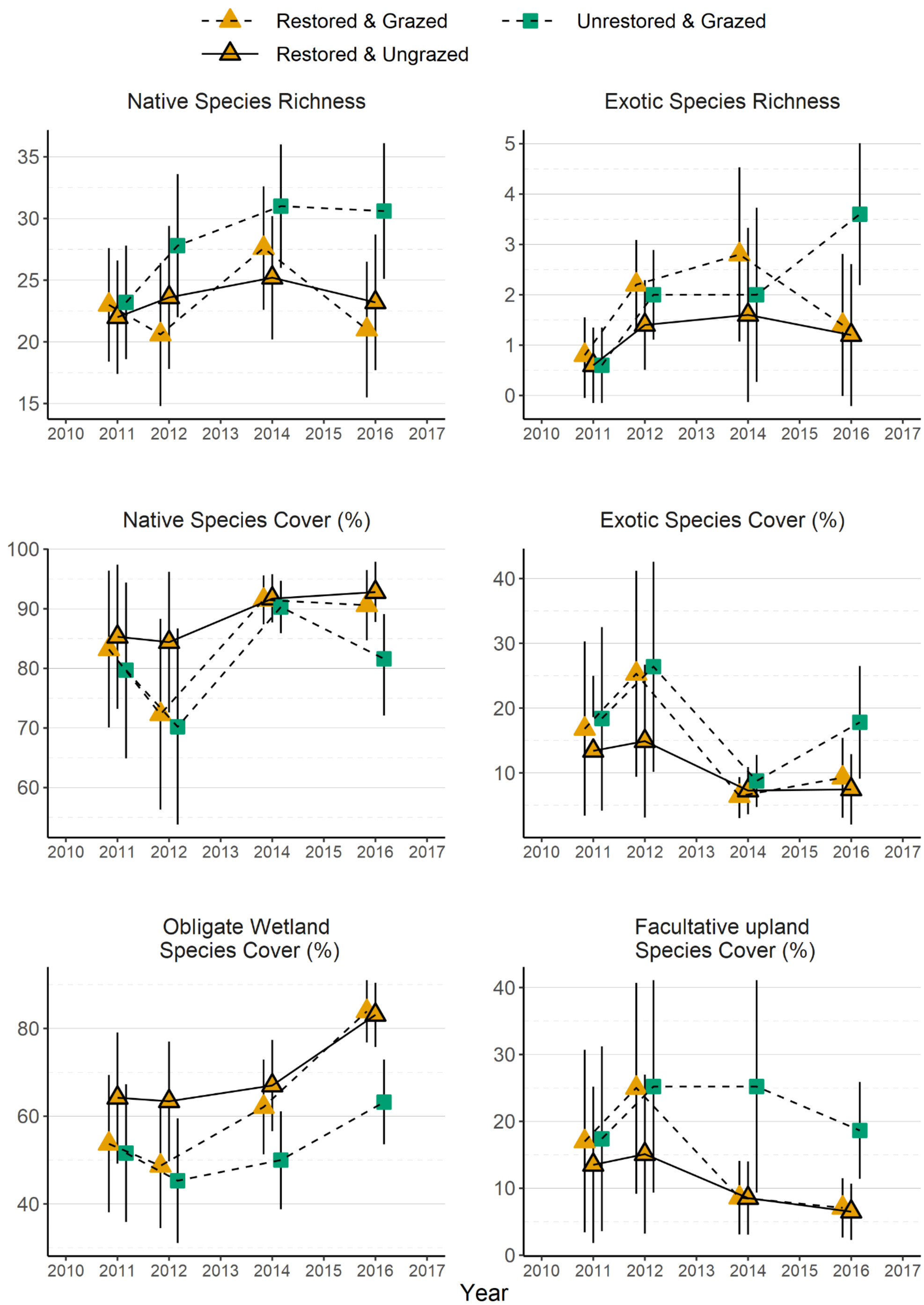

Fig. 3 Mean and confidence intervals (95%) of six diversity metrics for each year of survey and in response to hydrological restoration and cattle grazing. Diversity metrics are native species richness, exotic species richness, native cover (%), exotic cover (%), obligate wetland species cover (%) and facultative upland species cover (%)

($F_{2,12}$ = 3.97, p = 0.05) and 2.3 more exotic species than restored wetlands ($F_{2,12} = 4.22$, $p = 0.04$), whether grazed or ungrazed (Fig. 3; Table 1). The exponential Shannon diversity showed a similar pattern, but even in 2016 the effect was not significant, despite a tendency for higher diversity in unrestored grazed wetlands. The cover of exotic species was low at the beginning of the study in most wetlands and remained low (< 25%) for most years, but by 2016 it tended to be higher in unrestored wetlands than in restored wetlands ($\chi^2 = 4.90$, df = 2, $p = 0.08$; Fig. 3; Table 1). Conversely, cover of native species was significantly higher in restored wetlands ($\chi^2 = 7.19$, df = 2, $p = 0.03$). We did not detect an effect of cattle grazing on the cover of exotic or native species (Fig. 3; Table 1).

Mean coefficient of conservatism did not differ significantly among treatments, regardless of inclusion of exotic species (Table 1, Appendix S3). Beta diversity was similar among treatments in all years except 2014, when it was significantly lower in restored-grazed wetlands than in unrestored-grazed wetlands ($F_{2,12} = 5.25$, $p = 0.02$; Table 1,

Table 1 Average and 95% confidence interval (CI) of each biodiversity metric in each treatment and results of model testing the effect of treatment on each biodiversity metric. For a given metric, different letters indicate statistically significant differences between treatment

Year	Restored & Grazed	Restored & Ungrazed	Unrestored & Grazed	
2011	**Estimate [95% CI]**	**Estimate [95% CI]**	**Estimate [95% CI]**	**F-value / Chisq**
Exotic SR	0.80 [-0.05, 1.55]	0.60 [-0.15, 1.35]	0.60 [-0.15, 1.35]	$F_{2,12}= 0.11$
Native SR	23.00 [18.40, 27.60]	22.00 [17.40, 26.60]	23.20 [18.60, 27.80]	$F_{2,12}= 0.09$
H’	7.74 [4.05, 11.40]	9.36 [5.66, 13.10]	9.54 [5.85, 13.20]	$F_{2,12}= 0.34$
Exotic cover[§]	16.80 [3.39, 30.30]	13.40 [18.6, 25.00]	18.4 [4.18, 32.50]	$\chi^2=0.84$, df=2
Native cover[§]	83.20 [70.10, 96.40]	85.30 [73.20, 97.40]	79.70 [64.90, 94.40]	$\chi^2=0.40$, df=2
Beta diversity	0.46 [0.37, 0.54]	0.50 [0.41, 0.58]	0.47 [0.38, 0.56]	$F_{2,12}= 0.31$
OBL cover[§]	53.70 [38.10, 69.40]	64.20 [49.20, 79.10]	51.60 [35.90, 67.30]	$\chi^2=1.45$, df=2
FACW cover[§]	32.30 [20.00, 44.60]	31.10 [19.00, 43.30]	28.90 [17.10, 40.80]	$\chi^2=0.16$, df=2
FAC cover[§]	4.16 [2.82, 5.50]	4.49 [3.10, 5.87]	4.94 [3.48, 6.40]	$\chi^2=0.91$, df=2
FACU cover[§]	17.00 [3.41, 30.7]	13.50 [1.82, 25.2]	17.40 [3.59, 31.2]	$\chi^2=0.26$, df=2
Mean CC (no exotic)	4.36 [4.03, 4.69]	4.16 [3.84, 4.49]	4.16 [3.83, 4.48]	$F_{2,12}= 0.60$
Mean CC (with exotic)	4.20 [3.81, 4.60]	4.03 [3.63, 4.42]	4.05 [3.65, 4.44]	$F_{2,12}= 0.28$
2012	**Estimate [95% CI]**	**Estimate [95% CI]**	**Estimate [95% CI]**	**F-value / Chisq**
Exotic SR	2.20 [1.31, 3.09]	1.40 [0.51, 2.29]	2.00 [1.11, 2.89]	$F_{2,12}= 1.04$
Native SR	20.60 [14.80, 26.40]	23.60 [17.80, 29.40]	27.80 [22.00, 33.60]	$F_{2,12}= 1.84$
H’	9.27 [4.14, 14.40]	10.57 [5.45, 15.70]	12.68 [7.56, 17.80]	$F_{2,12}= 0.54$
Exotic cover[§]	25.30 [9.40, 41.20]	14.90 [3.11, 26.70]	26.40 [10.17, 42.60]	$\chi^2=1.66$, df=2
Native cover[§]	72.30 [56.30, 88.30]	84.40 [72.60, 96.20]	70.20 [53.80, 86.70]	$\chi^2=2.30$, df=2
Beta diversity	0.46 [0.35, 0.57]	0.50 [0.39, 0.61]	0.48 [0.37, 0.59]	$F_{2,12}= 0.14$
OBL cover[§]	48.70 [34.50, 63.00]	63.40 [49.70, 77.00]	45.30 [31.10, 59.50]	$\chi^2=3.45$, df=2
FACW cover[§]	25.70 [17.30, 34.10]	29.40 [20.60, 38.20]	22.50 [14.50, 30.50]	$\chi^2=1.32$, df=2
FAC cover[§]	4.56 [2.29, 6.83]	5.29 [2.84, 7.73]	7.95 [4.96, 10.94]	$\chi^2=5.40^{ns}$, df=2
FACU cover[§]	25.00 [9.18, 40.70]	15.10 [3.22, 27.00]	25.20 [9.36, 41.10]	$\chi^2=1.40$, df=2
Mean CC	4.00 [3.64, 4.36]	4.36 [4.00, 4.72]	4.03 [3.67, 4.38]	$F_{2,12}= 1.52$
Mean CC (with exotic)	3.54 [3.07, 4.01]	4.11 [3.64, 4.58]	3.71 [3.24, 4.18]	$F_{2,12}= 1.85$
2014	**Estimate [95% CI]**	**Estimate [95% CI]**	**Estimate [95% CI]**	**F-value / Chisq**
Exotic SR	2.80 [1.07, 4.53]	1.60 [-0.13, 3.33]	2.00 [0.27, 3.73]	$F_{2,12}= 0.59$
Native SR	27.60 [22.60, 32.60]	25.20 [20.20, 30.20]	31.00 [26.00, 36.00]	$F_{2,12}= 1.63$
H’	13.11 [9.18, 17.00]	9.92 [6.00, 13.90]	15.93 [12.00, 19.90]	$F_{2,12}= 2.77$
Exotic cover[§]	6.43 [3.01, 9.34]	7.27 [3.62, 10.91]	8.76 [4.74, 12.78]	$\chi^2=0.82$, df=2
Native cover[§]	91.50 [87.40, 95.60]	91.70 [87.70, 95.80]	90.30 [85.90, 94.70]	$\chi^2=0.27$, df=2
Beta diversity	**0.41 [0.37, 0.46]a**	**0.46 [0.42, 0.50]ab**	**0.50 [0.46, 0.55]b**	**$F_{2,12}= 5.25$***
OBL cover[§]	62.10 [51.30, 72.90]a	67.00 [56.60, 77.40]ab	50.00 [38.80, 61.10]a	$\chi^2=4.89^{ns}$, df=2
FACW cover[§]	30.10 [22.20, 38.00]	20.90 [14.00, 27.90]	22.00 [15.00, 29.10]	$\chi^2=3.59$, df=2
FAC cover[§]	8.12 [2.28, 14.00]	10.85 [4.02, 17.70]	11.63 [4.59, 18.80]	$\chi^2=0.98$, df=2
FACU cover[§]	8.60 [3.11, 14.10]a	8.53 [3.07, 14.00]a	25.20 [9.36, 41.10]a	$\chi^2=5.24^{ns}$, df=2
Mean CC	3.71 [3.27, 4.15]	3.94 [3.49, 4.38]	4.00 [3.56, 4.45]	$F_{2,12}= 0.57$
Mean CC (with exotic)	3.34 [2.80, 3.88]	3.68 [3.14, 4.22]	3.74 [3.20, 4.29]	$F_{2,12}= 0.76$
2016	**Estimate [95% CI]**	**Estimate [95% CI]**	**Estimate [95% CI]**	**F-value / Chisq**
Exotic SR	**1.40 [-0.01, 2.81]a**	**1.20 [-0.21, 2.61]a**	**3.60 [2.19, 5.01]b**	**$F_{2,12}= 4.22$***
Native SR	**21.00 [15.50, 26.50]a**	**23.20 [17.70, 28.70]a**	**30.60 [25.10, 36.10]b**	**$F_{2,12}= 3.97$***
H’	8.62 [4.95, 12.30]	7.93 [4.25, 11.60]	13.45 [9.78, 17.10]	$F_{2,12}= 3.19^{ns}$
Exotic cover[§]	9.26 [3.08, 15.40]a	7.45 [2.03, 12.90]a	17.81 [9.10, 26.50]b	$\chi^2=4.90^{ns}$, df=2
Native cover[§]	**90.6 [84.70, 96.50]a**	**92.80 [87.80, 97.90]a**	**81.60 [72.10, 89.10]b**	**$\chi^2=7.19$*, df=2**
Beta diversity	0.46 [0.40, 0.53]	0.47 [0.40, 0.53]	0.50 [0.44, 0.57]	$F_{2,12}= 0.64$
OBL cover[§]	**83.9 [76.80, 91.0]a**	**83.10 [75.80, 90.40]a**	**63.20 [53.60, 72.90]b**	**$\chi^2=14.53$***, df=2**
FACW cover[§]	12.30 [7.74, 16.90]	12.50 [7.91, 17.20]	14.60 [9.67, 19.60]	$\chi^2=0.57$, df=2
FAC cover[§]	**4.13 [2.19, 6.07]a**	**6.09 [3.73, 8.45]ab**	**7.54 [4.93, 10.16]b**	**$\chi^2=6.24$*, df=2**

Table 1 (continued)

Year	Restored & Grazed	Restored & Ungrazed	Unrestored & Grazed	
FACU cover§	**7.08 [2.64, 11.50]a**	**6.50 [2.28, 10.70]a**	**18.64 [11.42, 25.90]b**	**$\chi^2 = 11.19$**, df = 2**
Mean CC	4.28 [3.82, 4.74]	4.27 [3.81, 4.73]	4.22 [3.76, 4.67]	$F_{2,12} = 0.03$
Mean CC (with exotic)	3.97 [3.43, 4.52]	4.07 [3.52, 4.62]	3.80 [3.25, 4.35]	$F_{2,12} = 0.29$

§ beta regression with logit link function for these models; confidence intervals are asymptotic significance level: ns $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Appendix S3). The average cover of OBL and FACW species was high (> 50% when combined) in all wetlands even at the start of the experiment. Cover of OBL species was higher in restored wetlands (both grazed and ungrazed) than in unrestored-grazed wetlands in 2014 (15% higher) and 2016 (20% higher; Table 1; Fig. 3), though the effect was only statistically significant in 2016 ($\chi^2 = 14.53$, df = 2, $p < 0.001$) (Fig. 3). This was associated with lower cover of FACU species in restored wetlands in 2014 and 2016 (17% and 15% lower, respectively), though the effect was only statistically significant in 2016 ($\chi^2 = 11.19$, df = 2, p = 0.004), Table 1; Fig. 3). We observed significant effect of treatments on FAC species in 2016 ($\chi^2 = 6.24$, df = 2, p = 0.04), with higher FAC species in unrestored and grazed compared to restored and grazed wetland. Finally, we did not detect any effect of treatment on the cover of FACW species (Table 1).

Indicator Species Analysis

The three most abundant species in our study wetlands (based on average cover over all 15 wetlands and years) were *Juncus effusus* subsp. *solutus* (Fernald & Wiegand) Hämet-Ahti (14%), *Panicum hemitomon* Schult (14%), and *P. notatum* (8%). Our indicator species analysis revealed that species associated with grazed wetlands (restored or unrestored) differed among years (Table 2). Five OBL species were associated with restored-grazed wetlands, especially *J. effusus* subsp. *solutus* (2011 and 2016) and *Ludwigia repens* J.R. Forst. (2012, 2014, and 2016). Maidencane (*P. hemitomon*) was an indicator of restored-ungrazed wetlands every year; three other OBL species were also associated with restored-ungrazed wetlands but only in 2012 (*Proserpinaca pectinata* Lam.) or 2014 (*Fuirena scirpoidea* Michx., *Pontederia cordata* L.).

Discussion

Hydrological Response

We observed higher water levels in wetlands located in the two restoration easements compared to nearby unrestored wetlands, suggesting that ditch plugging did have the desired outcome of mitigating the drainage effects of the extensive ditch network. Because our data set was limited to instantaneous measurements rather than continuous measurements, we could not estimate duration of inundation. Hydroperiod was found to be strongly correlated to hydroperiod in nearby seasonal wetlands located in scrub habitats (Rothermel, *unpublished data*). However, this correlation does not always exist (Brooks and Hayashi 2002) even in similar wetland types (Medley et al. 2015). Thus, while we observed higher water levels in restored wetlands, the degree to which restoration of these seepage slope wetlands extended their hydroperiods is unclear.

We did not observe a difference in water levels between grazed and ungrazed wetlands. This contradicts previous studies showing that grazing by livestock might increase water levels and hydroperiod in wetlands (Pyke and Marty 2005; Marty 2015) by removing plant biomass and thus decreasing evapotranspiration during the growth period. A study of wetlands on a nearby cattle ranch showed that fenced wetlands have higher biomass than grazed wetlands (Sonnier et al. 2020), potentially resulting in different levels of evapotranspiration. However, grazed wetlands may have greater amounts of open water and thus higher evaporation in this subtropical environment, potentially masking the influence of grazing on evapotranspiration. Additionally, grazed wetlands were dominated by *J. effusus* subsp. *solutus*, which is unpalatable to cattle and thus grazing is likely to have less impact on evapotranspiration in these wetlands.

Hydrological restoration within WREs maintained the seasonal nature of these wetlands. Ditch plugging was sufficient to increase water levels, but it did not go so far as creating permanently ponded wetlands. This is important because retention of dry/wet cycles may achieve optimal production of diverse services over the long term (Euliss et al. 2008), which can be overlooked when restoration focuses on improving habitat for wildlife, especially waterfowl (De Steven and Gramling 2012). Complete ditch filling was not necessary to improve hydrology of these seepage slope wetlands, and the associated soil disturbance might have facilitated non-native species invasion. However, our data did not allow us to determine if these wetlands remained wet later into the dry season, which could be seen

Table 2 Results of the indicator species analysis performed on each year separately. Treatments are restored and grazed (R&G), restored and ungrazed (R&U), and unrestored and grazed (U&G).

Year	Treatment	Species	Wetland status	CC	Indicator value	p-value	Species frequency
2011							
	R&G	*Axonopus furcatus*	OBL	1	0.84	0.03	11
		Juncus effusus subsp. *solutus*	OBL	5	0.61	0.03	15
	R&U	*Panicum hemitomon*	OBL	4	0.67	0.04	15
	U&G	*Polygonum hydropiperoides*	OBL	3	0.69	0.04	14
2012							
	R&G	*Ludwigia repens*	OBL	4	0.63	0.02	15
		Proserpinaca pectinata	OBL	7	0.86	0.01	8
	R&U	*Panicum hemitomon*	OBL	4	0.67	0.04	15
	U&G	*NA*					
2014							
	R&G	*Ludwigia repens*	OBL	4	0.76	0.01	15
		Eleocharis vivipara	OBL	2	0.64	0.03	10
	R&U	*Fuirena scirpoidea*	OBL	5	0.77	0.04	6
		Panicum hemitomon	OBL	4	0.71	0.02	14
		Pontederia cordata	OBL	3	0.70	0.05	6
	U&G	*Coleataenia abscissa*	FACW	6	0.94	0.01	9
		Solidago fistulosa	FAC	5	0.83	0.01	8
		Xyris spp			0.66	0.03	5
2016							
	R&G	*Limnobium spongia*	OBL	5	0.73	0.00	10
		Juncus effusus subsp. *solutus*	OBL	5	0.61	0.04	11
		Ludwigia repens	OBL	4	0.57	0.05	13
	R&U	*Panicum hemitomon*	OBL	4	0.56	0.04	15
	U&G	*Edrastima uniflora*	FACW	4	1.00	0.00	5
		Axonopus furcatus	OBL	1	0.90	0.00	7
		Hydrocotyle umbellata	OBL	4	0.72	0.02	15

as an additional benefit of wetland restoration for easements on cattle ranches (Boughton et al. 2019).

Species Diversity and Floristic Quality Responses

In this study, we observed both lower native and exotic species richness in restored wetlands. This trend was observed in the 2014 surveys, but it was only significant in 2016. This suggests that despite restoration rapidly impacting water levels, vegetation response was gradual. It is also possible, that we detected this significant effect only in 2016, because we sampled plant communities during the wet season. Nevertheless, this result agrees with previous work showing that increasing water levels resulted in decline in plant richness in similar seasonal wetlands (Boughton et al. 2019). We think this result was driven by rare species as the effect of treatments disappeared when we removed species occurring in less than 1% of the plots or when we accounted for species cover using the exponential of Shannon diversity. Additionally, despite native species being more numerous in unrestored wetlands, their cumulative cover was still lower in unrestored wetlands compared to restored wetlands whether grazed or ungrazed. Many species found in unrestored wetlands were FACU and to a lesser extent FAC species and their cover was higher in unrestored wetlands, suggesting they benefited from the drier conditions in these wetlands.

Native species richness observed in our study site was similar to native richness recorded in other seasonal wetlands embedded in improved pastures in south-central Florida (Boughton et al. 2016, Sonnier et al. 2023), but lower than in wetlands within semi-native pastures (Boughton et al. 2016, Sonnier et al. 2023). Exotic species richness was slightly lower than in other seasonal wetlands embedded in improved pastures (Boughton et al. 2016, Sonnier et al. 2023), which could be due to differences in land-use and invasion history or because there has been more active control of exotics like *L. peruviana* on the Archbold Reserve. Exotic species richness and exotic cover were both lower in restored wetlands. These results suggest that unrestored wetlands might be more prone to exotic species invasions. Surprisingly, we did not observe an effect of grazing on species richness in restored wetlands; this is in contrast to a positive effect of low-intensity grazing on species richness reported in other studies (Marty 2015; Boughton et al. 2016; Bovee et al. 2018; Sonnier et al. 2023).

Floristic quality indices are considered good indicators of vegetation development (Taddeo and Dronova 2018) and have been shown to follow increasing trajectories after restoration (Cohen et al. 2004; Bourdaghs et al. 2006; Matthews et al. 2009). In our study, however, neither the mean coefficient of conservatism nor beta diversity varied among treatments. Beta diversity also remained relatively stable throughout the duration of the experiment. This is in contrast to a similar study that found increased beta diversity and floristic quality following wetland restoration in bahiagrass pastures and shallow marsh systems at another ranch in Florida (Sonnier et al. 2018). We believe this is because the hydrology and plant communities of our study wetlands were in a less altered state prior to restoration, resulting in less pronounced changes in community composition post-restoration.

As expected, we observed higher cover of OBL species in restored wetlands (e.g., *Limnobium spongia* (Bosc) Rich. ex Steud., *P. hemitomon, J. effusus* subsp. *solutus, P. cordata*). This increase was gradual and only statistically significant during the last survey in 2016. It was associated with a decrease in FACU species (e.g., *P. notatum, Cyperus retrorsus* Chapm.) and to a lesser extent a decrease in FAC species, whereas FACW species remained the same between treatments. We do not think the difference in timing of the 2016 survey versus previous years' surveys (wet season instead of dry season) contributed to this pattern. Seasonal turnover exists in our wetlands, but it is limited and often due to free-floating plant species presence during the wet season. Several free-floating species (*Lemna* spp., *Utricularia* spp., and *Salvinia minima* Baker) were only observed in our 2016 surveys. Removing these species from our analysis did not change the outcome; for example, we still found a significant effect of treatment on cover of OBL species in 2016 ($\chi2 = 15.97$, $p < 0.001$), with higher cover of obligate species in restored wetlands (grazed or ungrazed) compared to unrestored wetlands. Additionally, the increase in OBL species cover in restored wetlands was already apparent in 2014, although it was not significant. The increase in OBL species was faster in Mary's Creek WRE, where wetlands exhibited an early increase in *P. hemitomon* cover, likely because cattle were excluded from the three Mary's Creek wetlands in 2009, 2 years before cattle were excluded from the two restored wetlands in Frances Creek WRE.

Indicator Species Analysis

Several obligate, native wetland species were associated with hydrologically restored wetlands that were still grazed, most notably soft rush (*J. effusus* subsp. *solutus*) and creeping primrose-willow (*L. repens*). *J. effusus* subsp. *solutus* was particularly abundant in grazed wetlands (whether restored or not) and is characteristic of seasonal wetlands within improved pastures throughout central Florida (Boughton et al. 2016; Sonnier et al. 2020). *J. effusus* subsp. *solutus* performs better under nutrient fertilization typically occurring in improved pastures and because it is unpalatable to cattle (Boughton et al. 2011a; Sonnier et al. 2020). As its common name suggests, *L. repens* is a low-growing, small-leaved herbaceous plant that probably benefits from grazing of taller plants by cattle.

Interestingly, the indicator species associated with unrestored wetlands did not overlap between years even though plots were permanent. This might suggest that unrestored-grazed wetlands experience more turnover than both restored-grazed and restored-ungrazed wetlands, which may be related to the pattern and timing of cattle grazing and less restrictive hydrology for plant species. In contrast, *P. hemitomon* was a consistent indicator of restored-ungrazed wetlands in our study, suggesting less turnover in these communities. We think this result is primarily driven by cessation of cattle grazing rather than an effect of restoration per se. Indeed, *P. hemitomon* is palatable and highly preferred by cattle and fencing wetlands has been shown to increase the cover and biomass of *P. hemitomon*, sometimes resulting in a monospecific stand (Sonnier et al. 2020). The fast recovery of *P. hemitomon* in our study wetlands is most likely due to the facilitative interactions between *J. effusus* and *P. hemitomon* under grazed conditions, where the unpalatable *J. effusus* provides associational resistance to *P. hemitomon* (Boughton et al. 2011a). *P. hemitomon* is a clonal native species that was found to be infrequent or absent in wetlands undergoing restoration in South Carolina and required active planting for recovery (De Steven et al. 2010).

C. abscissa, a restricted endemic grass constitutive of the historical communities at Archbold Reserve, was found at low abundance in 11 of the 15 wetlands. We did not observe a significant increase in cover of cutthroat grass following restoration. Cutthroat grass is a facultative wetland species that was probably a dominant species bordering most seasonal wetlands on this site and also occurred in the understory of adjacent flatwoods (Yahr et al. 2000). A small-scale experimental reintroduction of cutthroat grass in another former cutthroat seep site on the Reserve failed, likely due to poor seed germination (Tucker et al. 2017). Thus, active restoration employing alternative techniques, such as outplanting of plugs, is likely needed to restore cover of this species (Sinclair et al. 2020).

Conclusion

This study presents 5 years of post-restoration monitoring to evaluate the responses of seasonal wetlands exposed to pasture-scale hydrological restoration as part of the USDA's WRE program. Our results emphasize the need for costly restoration activities to be coupled with long-term monitoring to assess success. We found vegetation responses to restoration were slow and subtle, with changes in plant communities only becoming detectable 5 years following restoration. These projects showed encouraging but mixed outcomes when measured against the goals of restoring wetland hydrology, increasing floristic value of wetland plant communities, and increasing cover of obligate wetland species. Strategic placement of ditch plugs (vs. complete ditch filling) effectively increased wetland depths in restored wetlands, although more continuous monitoring of water levels would be needed to assess hydroperiods. By 2016, the cover of facultative upland species declined in restored wetlands, whereas obligate wetland species cover increased. Facultative wetland species did not increase, which suggests that hydrological restoration was only partially successful or that more active approaches are needed to regain these species, as is likely the case with cutthroat grass, a historically dominant species on central Florida seepage slopes. In contrast to studies elsewhere, floristic value and beta diversity of these wetland plant communities did not respond to restoration, suggesting indicators of restoration success must be tailored to wetland type. Total species richness was greater in unrestored wetlands, suggesting that this metric is not useful for assessing restoration success (SER 2004; Piqueray et al. 2011; Rydgren et al. 2020). We did not find strong effects of continued cattle grazing on post-restoration vegetation assemblage responses, except for a large increase in the native grass, maidencane, when cattle were excluded. Future studies should investigate wetland functional consequences of plant community changes, as well as responses of other assemblages (e.g., amphibians, fishes, birds) to grazing and hydrological restoration.

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Author contribution Order of authors reflects relative contributions. GS performed the statistical analyses and wrote the manuscript with contributions from all co-authors. BBR initiated and maintained the experiment and collected data with help from RCT and GS. RCT led data management and quality control. BBR and EHB secured funding for analysis and write-up. All authors read and approved the final manuscript.

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Data Availability Data associated to this manuscript will be made publicly available through the Environmental Data Initiative (EDI) portal.

Declarations

Ethics Approval Not applicable.

Consent to Participate Not applicable.

Consent to Publish The Authors hereby consent to publication of the Work.

Plant Reproducibility Not applicable.

Clinical Trials Registration Not applicable.

Gels and Blots/ Image Manipulation Not applicable.

Plant Nomenclature International Plant name Index (IPNI, https://www.ipni.org).

Conflict of interest /Competing interests The Authors do not have any conflict of interest regarding the work presented in this manuscript.

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