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Trade-offs and synergies in a payment-for-ecosystem services program on ranchlands in the Everglades headwaters

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Abstract. Increasingly, agriculture is recognized as valuable not only for food production, but also for regulating and supporting ecosystem services such as those encompassing biodiversity and water. Various government programs provide incentives to farmers and ranchers to maintain ecosystem services, with an emerging focus on payment-for-ecosystem services (PES) programs. However, interactions among ecosystem services, including synergies or trade-offs, at spatial scales relevant to land managers are not well understood. Here, we examined how a PES program for enhanced water retention on subtropical ranchlands in the headwaters of the Everglades affected seven indicators of ecosystem services and three indicators of disservices within wetlands (local scale) and among wetlands (wetland scale) at four different ranches. We used general linear mixed models and model selection to evaluate the feasibility of explicit, a priori hypotheses using data from 15 wetlands sampled across four participating ranches. Our study indicated that managing for increased water retention could result in both synergies and trade-offs among ecosystem services. Higher water retention increased wetland plants at both local and wetland scales and was associated with reduced mosquitoes. Trade-offs included significant declines in forage plant cover and decreases in amphibian abundance with higher water retention. Unimodal non-linear relationships described responses of macroinvertebrates, fish, mosquito, and non-native plant abundance to increasing water retention. These complex relationships indicate that optimizing water retention, provisioning services, and wetland biodiversity in ranchlands may not be straightforward. Unimodal non-linear relationships among water retention and biodiversity suggest there is a threshold of water retention that represents a trade-off for also maintaining biodiversity. Land use was an important driver of ecosystem disservices, with more intensely managed ranches having a greater potential for ecosystem disservices such as increased cover of non-native plants, abundant mosquitoes, and lower amphibian abundance. Multidisciplinary collaboration was required to design, implement, monitor, and assess this PES program for trade-offs and synergies.

Key words: agroecosystem; biodiversity; ecohydrology; grazing lands; hydrologic services; restoration; sustainability; wetlands.

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Introduction

Production of crops and livestock often degrades biodiversity, water quality, and soils (Bennett and Balvanera 2007, Kareiva et al. 2007). Alternative policies and management of agricultural lands can mitigate those effects and enhance multiple ecosystem services (Boody et al. 2005, Robertson and Swinton 2005, Swinton et al. 2006, Jordan and Warner 2010, Bommarco et al. 2013). Multifunctional agriculture management has received growing interest, including co-production of agricultural commodities and ecological services such as beneficial effects of enhancing water quality and quantity, and biodiversity (Robertson et al. 2008, Jordan and Warner 2010, Werling et al. 2014). Creating economic incentives through payment-for-ecosystem services (PES) is one emerging opportunity for multifunctional agricultural management (Swinton et al. 2007, Jordan and Warner 2010).

A market-based PES approach sets up programs to pay for services (Kroeger and Casey 2007, Bohlen et al. 2009, Farley and Costanza 2010). This approach focuses on environmental results and not just practices, encouraging producer-sellers to innovate and seek cost efficiencies to produce services (Shabman and Stephenson 2007). PES programs exist in several countries, including the United States (Bohlen et al. 2009, Ma et al. 2012), Costa Rica (Kosoy et al. 2007), Bolivia, Honduras (Kosoy et al. 2007), and Mexico (Alix-Garcia et al. 2009). PES programs range from global markets for carbon sequestration (Follett and Reed 2010) to developing regional markets for enhancing biodiversity (Günter et al. 2002), hydrologic services (Brauman et al. 2007, Bohlen et al. 2009), and greenhouse gas mitigation and scenic beauty via forest conservation (Wunder et al. 2008, Alix-Garcia et al. 2009, Arriagada et al. 2012).

But market-based PES programs are not without limits. Most PES programs focus on managing for one ecosystem service and ignore synergistic services, trade-offs, or unintended ecosystem disservices (ecosystem functions that are harmful to human well-being; von Dohren and Haase 2015). Synergies occur when increasing one ecosystem service results in increases in other services, while trade-offs occur when increasing one ecosystem service results in a reduction of another desirable service or an increase in a disservice (Bennett et al. 2009). Although research on ecosystem services has increased, understanding the interactions among ecosystem services is limited (Bennett et al. 2009, Carpenter et al. 2009, Nicholson et al. 2009), in part because measuring multiple services and disservices requires broad knowledge, for example of the underlying agriculture production, biodiversity, and ecosystem responses to fire, water, and nutrient cycles (Kremen and Ostfeld 2015). In addition, limited documentation and the cost of measuring ecosystem services hamper PES programs (Ferraro and Kiss 2002, Wunder et al. 2008).

Selecting the most informative spatial scale at which to assess synergies and trade-offs is a critical consideration for PES programs. Synergies and trade-offs among ecosystem services occur at multiple spatial scales, ranging from local to global (Kremen et al. 2007, de Groot et al. 2010, Brinson and Eckles 2011, Qiu and Turner 2013, Jessop et al. 2015, Landis et al. 2018). For farmers and ranchers managing their land, ecosystem services measured at smaller scales may be particularly relevant for making management decisions (Jessop et al. 2015, Austrheim et al. 2016, Landis et al. 2018), while policymakers may find larger scales more informative (Landis et al. 2018). Additionally, given the multitude of ecosystem services provided by ecosystems, important drivers are likely to occur at varying spatial scales depending on the service of interest (Kremen et al. 2007). For this study, we focused on both smaller spatial scales (plot, 1 m^2, and wetland scales, 0.25–31 ha) since we were interested in how ranch management of ecosystem services affected diverse stakeholders, including agricultural producers and conservation agencies, and because the ecosystem services selected for measurement were likely to be influenced by processes at local scales (e.g., competition) as well as larger scales (e.g., dispersal). Although wetland scales are most relevant for land management decisions, small plot scales enabled us to better understand mechanisms underlying spatial variability of services, given hydrological gradients, and increased understanding at small scales could be useful for developing optimal management strategies for multiple services.

Here, we evaluate synergies and trade-offs of a pilot PES program (Table 1), the Florida Ranchland Environmental Services Project (FRESP, www.fresp.org). In FRESP, sellers (i.e., willing ranchers) received payments from buyers (South Florida Water Management District), with support from other state and federal agencies, nongovernmental organizations, and universities

Table 1. Ecosystem service/disservice indicators across 15 wetlands embedded in four ranches implementing water retention projects.

Ecosystem services	Ecosystem service indicators	Disservice indicators
Provisioning services		
Forage quantity	1. Abundance of upland forage grasses (percent cover)	1. Reduced abundance of forage (percent cover)
	2. Abundance of wetland plants that are palatable and nutritious to cattle (percent cover)	
Regulating services		
Biodiversity	3. Native plant species richness and abundance (percent cover)	2. Non-native plant abundance (percent cover)
	4. Broadleaf marsh plant abundance (percent cover)	
	5. Fish richness and abundance (No./m^2)	
	6. Amphibian richness and abundance (No./m^2)	
	7. Macroinvertebrate richness and abundance (No./m^2)	3. Mosquito richness and abundance (No./m^2)
Pest regulation	5. Fish abundance (No./m^2; predation on mosquitoes)	

(Lynch and Shabman 2011*a*, *b*). The ranchers provided water-related ecosystem services (Bohlen et al. 2009): Either water retention or kilograms of nutrient (phosphorus, P) removed (Lynch and Shabman 2011*a*, *b*). Water retention is critical to reducing the amount and slowing down the delivery of water in the headwaters of the Everglades and sensitive downstream ecosystems (Lake Okeechobee and the Everglades). FRESP collected hydrologic data (surface water levels and flows) to document the water retention services purchased (Bohlen et al. 2009, Lynch and Shabman 2011*a*, *b*). Of eight projects in FRESP, seven were water retention projects and one was contracted specifically for water quality services (to reduce phosphorus loading), exhibiting completely different ecosystem trade-offs that have been addressed in another study (Shukla et al. 2017). The impacts of water retention projects on downstream nutrient loading were not evaluated (Bohlen et al. 2009), but there is evidence that water retention projects reduce nutrient runoff (Bohlen and Villapando 2011).

For many practical reasons, FRESP payments to ranchers in this study were limited to one service, levels (e.g., acre-feet) of water retention, and did not recompense or value synergies, trade-offs, or disservices. However, information on synergistic additional services delivered, trade-offs among ecosystem services, or increases in disservices was of critical interest to multiple stakeholders, including ranchers, land and water managers, health-related agencies, and the public. The research project reported here therefore capitalized on the FRESP program to collect and evaluate extensive additional data related to ecosystem services and disservices (both trade-offs and synergies).

We focus here on four ranches with water retention projects (three FRESP ranches and one other ranch with a similar water retention project). The ranches were typical of regional ranchlands with natural, geographically isolated, seasonal wetlands embedded in pasturelands and associated ditch networks (Bohlen et al. 2009). Water retention structures installed at ranches affected wetlands, which provide multiple ecosystem services and have high biodiversity (Zedler 2003). Wetlands are important to Florida ranchlands because they represent 15–25% of the regional landscape (Hiscock et al. 2003, Swain et al. 2013), are high in biodiversity and sensitive to management (Boughton et al. 2010, 2016, Kelly et al. 2015, Medley et al. 2015), and provide forage ecosystem services relevant to cattle production, hydrological and nutrient management (Bohlen and Gathumbi 2007, Ho et al. 2018), and cultural values (Swain et al. 2013).

We evaluated seven indicators of ecosystem services and three indicators of disservices in response to water retention both within and among wetlands (Table 1). A simple conceptual model of trade-offs and synergies was used to guide the development of a priori hypotheses (Fig. 1; Appendix S1). Indicators of ecosystem services and disservices were expected to show both

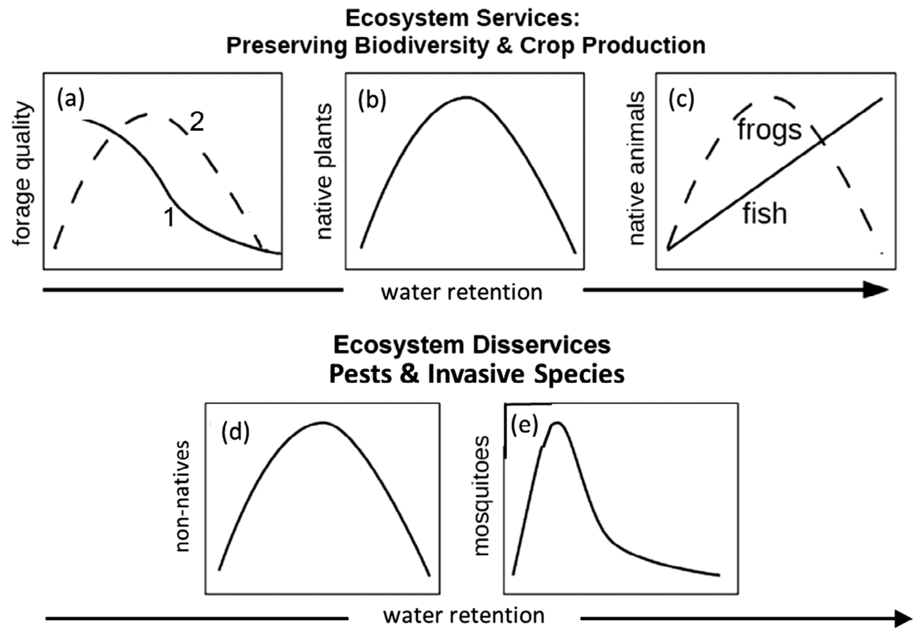

Fig. 1. Conceptual diagram of responses of indicators of ecosystem services and disservices to increased water retention on Florida ranchlands. (a) Forage quality varies with forage plants, where (1) upland forage is replaced by (2) other wetland grasses, which are replaced by low forage quality broadleaf marsh plants. (b) Native plant diversity peaks at intermediate flooding levels because more shallow/emergent wetland plant species exist than submerged/floating species. (c) Native frog diversity peaks at intermediate flooding because more frog species occur until fish predation reduces frog diversity. More non-native plants (d) and mosquitoes (e) exist at intermediate water retention, and mosquitoes will be reduced by greater fish abundance.

linear and non-linear relationships with water retention, with positive linear relationships representing synergies, negative linear relationships representing trade-offs, and non-linear unimodal relationships representing potential synergies or trade-offs depending on the level of water retention (Fig. 1). Management for water retention was expected to enhance wetland hydrology, affecting several metrics of hydrology such as depth, maximum depth, hydroperiod, and wetland connectedness, and hypotheses were developed for how indicators of ecosystem services and disservices would respond to hydrology metrics (Table 2). We tested hypotheses at two spatial scales: within wetlands, at sample points (i.e., local scale: 1 m^2), and responses among wetlands (i.e., wetland scale: 0.25–31 ha) because many of the measured ecosystem services were underpinned by biodiversity and expected to respond to processes at local scales (i.e., competition/predation) and landscape scales (i.e., dispersal; Landis et al. 2018). Percent cover of wetland plants (both grasses and broadleaf marsh plants), native and non-native plant percent cover, and abundance and richness of amphibians, aquatic macroinvertebrates, and mosquitoes were expected to peak at intermediate metrics of wetland hydrology. Fish richness and abundance were expected to increase linearly with metrics of wetland hydrology (Fig. 1c, Table 2). Abundance of upland forage plants was expected to linearly decline with increasing water retention and be replaced with wetland grasses or unpalatable wetland broadleaf marsh plants (Fig. 1a). Therefore, with increased water retention we expected synergies with one indicator of biodiversity and pest regulation (i.e., native fish abundance and lower mosquito abundance), while there were expected trade-offs with provisioning services (forage plant abundance) and other measures (native plant diversity, amphibians) if wetland water retention (and water level) was too high.

Table 2. Matrix of predictor variables (columns) and response variables (rows) of a priori hypotheses with summary results in italics.

	WW	WW/AW					AW				
Variable	*D*	MdL, MdW	GDD	Plant cover	Fish count	Non-native cover	IA	Vol	DC	DSC	TI
Upland forage cover	**Lin (−)**	Lin (−)	Lin (+)	None	None	None	Lin (−)	Lin (−)	None	None	Lin (−)
Wetland forage cover	**Quad (+)** ***WW: Lin (+)***	Quad (+)	**Lin (+)** ***WW: GDD × depth***	None	None	None	Quad (+)	Quad (+)	None	None	Quad (+)
Broadleaf marsh plant cover	**Lin (+)**	**Lin (+)** ***WW: Quad (+)***	**Lin (+)** ***both WW/AW***	None	None	None	Lin (+)	Lin (+)	None	None	**Lin (+)**
Native plant cover	**Quad (+)** ***Quad (−)***	Quad (+)	**Lin (+)** ***both WW/AW***	None	None	**Lin (−)** ***Lin (−) both WW/AW***	Quad (+)	Quad (+)	Lin (+)	None	Quad (+)
Native plant richness	**Quad (+)** ***Lin (−)***	**Quad (+)** ***Lin (−)***	NA	NA	NA	NA	NA	NA	NA	NA	NA
Fish abundance	**Lin (+)** ***Quad (+)***	Lin (+)	**Lin (+)** ***WW: D × GDD AW: TI × GDD***	Lin	None	None	Lin (+)	Lin (+)	Lin (+)	Lin (−)	**Lin (+)** ***Quad (−)***
Fish richness	**Lin (+)** ***Quad (+)***	Lin (+)	NA	NA	NA	NA	NA	NA	NA	NA	NA
Amphibian abundance	**Quad (+)** ***Lin (−)***	Quad (+)	Lin (−)	Lin (+)	Lin (−)	None	Lin (−)	Lin (−)	Lin (−)	**Lin (+)** ***Lin (−)***	**Quad (+)** ***Lin (−)***
Amphibian richness	Quad (+)	Quad (+)	NA	NA	NA	NA	NA	NA	NA	NA	NA
Macroinvertebrate abundance	**Quad (+)**	**Quad (+)** ***AW only***	Lin (−)	Lin (+)	**Lin (−)** ***WW: Lin (+)***	None	Quad (+)	Quad (+)	Quad (+)	Lin (+)	Quad (+)
Macroinvertebrate richness	Quad (+)	Quad (+)	NA	NA	NA	NA	NA	NA	NA	NA	NA
Non-native Plant cover	**Quad (+)** ***Quad (−)***	Quad (+)	Lin (+)	None	None	None	Quad (+)	Quad (+)	Lin (+)	None	Quad (+)
Mosquito abundance	**Quad (+)** ***Quad (−)***	Quad (+)	Lin (−)	Lin (+)	**Lin (−)** ***WW: fish × ranch AW: fish***	None	Quad (+)	Quad (+)	Lin (−)	Lin (+)	Quad (+)
Mosquito richness	Quad (+)	Quad (+)	NA	NA	NA	NA	NA	NA	NA	NA	NA

Notes: WW, within wetlands/local scale; AW, among wetlands/wetland scale; *D*, depth; MdL_MdW, maximum depth; GDD, growing degree days; IA, inundated area; Vol, volume; DC, days connected; DSC, days not connected; TI, time inundated; Lin, linear model; Quad, quadratic model; signs (+ or −), expected slope; Quad (+), arched curve; NA, not assessed; None, no relationship was hypothesized. A priori hypotheses were a synthesis of the groups ecological and engineering expert knowledge. In some cases, no applicable relationship was hypothesized (e.g., non-native plant cover was not expected to affect fish abundance). Bold texts indicate significant results with the relationship in italics if different from initial prediction. Ranches were expected to vary among all response variables but are omitted below for simplicity. Species richness was not assessed at the wetland scale (see text for explanation).

Materials and Methods

Study sites

We sampled fifteen wetlands of varying sizes at four ranches with similar water retention projects in the headwaters of the Everglades, a 1.062 million hectare watershed draining south into Lake Okeechobee where ranchland is the predominant land use (Swain et al. 2013; Table 3, Fig. 2). The study area has a subtropical climate, with average rainfall of 1362 mm/yr (1992–2011; National Climate Report 2012), of which about 70% falls during the wet season (May–October). Average minimum temperature of the region is 17°C, and the average maximum temperature is 29°C (1981–2010; National Climate Report 2012). The dominant soil type of the four ranches is classified as flatwood soils, which are characterized by sandy texture, nearly level topography, shallow water table, and poor drainage. Wetlands in the region are predominantly seasonally flooded emergent

Table 3. Pasture type (type) and hydrology of the 15 wetlands sampled in the study.

ID	Ranch and type	Size (ha)	GW well	Ditched	Grazing	V (m^3)	TSI (d)	DSC (d)	DC (d)	Max depth (m)	Depth (cm)	TI (d)	IA (m^2)
	3												
1	IM	0.66	IW	No	Yes	1106.0	0.0	357.7	0.0	30.7	22.1	75.7	5122.1
						±686	±0	±210	±0	±3	±4	±12	±1779
2	IM	0.78	IW	Yes	Yes	1388.3	0.0	347.9	0.0	29.9	19.7	37.3	6658.2
						±855	±0	±224	±0	±10	±8	±16	±1642
3	IM	0.39	IW	Yes	No	575.0	2.3	359.0	0.0	34.3	19.8	57.0	2983.6
						±276	±4	±243	±0	±8	±5	±9	±945
4	IM	0.57	600 m	No	No	2452.2	0.0	30.7	0.0	46.7	29.8	152.3	6842.1
						±634	±0	±11	±0	±13	±NA	±64	±6
5	SN	0.74	700 m	Yes	No	1061.5	0.0	0.0	187.3	24.3	13.1	191.6	6575.5
						±137	±0	±0	±74	±5	±5	±93	±737
6	SN	0.24	300 m	No	Yes	760.8	0.0	0.0	188.8	27.7	13.6	204.3	3858.3
						±247	±0	±0	±90	±8	±10	±93	±660
7	SN	0.63	IW	Yes	No	849.6	0.0	0.0	259.2	37.2	15.0	199.0	5388.4
						±348	±0	±0	±47	±9	±9	±102	±335
8	SN	0.37	IW	Yes	Yes	1113.0	0.0	0.0	201.0	29.2	16.6	204.3	5350.0
						±254	±0	±0	±70	±2	±8	±93	±828
	1												
9	SN	4.45	50 m	Yes	Yes	4501.5	17.1	5.2	11.3	26.3	12.6	19.9	28,170.4
						±284	±1	±1	±10	±10	±8	±0.6	±9461
10	SN	1.28	IW	Yes	Yes	1235.4	5.9	1.4	65.3	26.8	15.6	66.6	9051.9
						±351	±7	±2	±38	±10	±10	±48	±106
11	SN	4.56	126 m	Yes	Yes	11,279.0	17.1	7.0	53.7	27.8	17.9	25.1	40,221.8
						±3040	±4	±5	±22	±4	±10	±7	±2119
	2												
12	IM	6.55	216 m	Yes	Yes	7157.5	1.2	2.7	8.5	20.9	13.4	77.6	46,420.6
						±662	±2	±0.1	±3	±2	±2	±49	±5868
13	IM	31.06	IW	Yes	Yes	27,111.7	0.0	1.6	9.1	19.5	12.6	82.6	176,338.9
						±13,498	±0	±2	±3	±2	±0.1	±47	±34,079
	4												
14	IM	12.9	IW	Yes	Yes	18,570.8	0.0	34.8	7.3	43.6	21.6	103.8	92,457.6
						±5053	±0	±38	±10	±6	±3	±44	±17,615
15	IM	7.5	IW	Yes	Yes	2229.8	0.0	3.0	36.5	17.0	10.7	60.0	24,108.1
						±1386	±0	±4	±52	±20	±11	±42	±13,986

Notes: V, volume; TSI, time since inundated; DSC, days since connected; DC, days connected; Max depth, maximum depth; TI, time inundated; IA, inundated area; IM, intensively managed pasture; SN, semi-native; GW, groundwater; IW, in wetland. Hydrology values are mean±SD for the three study years (2010–2012).

freshwater marshes or forested/shrub wetlands (National Wetlands Inventory 2014). Wetlands are defined as isolated because they are geographically distinct systems embedded in grasslands and separated from other aquatic bodies (DeLaune and Reddy 2008, Cohen et al. 2016). The natural geographic isolation is altered in Florida ranchlands because many wetlands were ditched so that some wetlands are connected via ditches during the wet season. Also, overland flow during large storm events can temporarily connect wetlands.

All ranches included in the study were cow-calf operations and included both intensively managed and semi-natural pastures (Ranch 1, three wetlands; Ranch 2, two wetlands; Ranch 3, Archbold Biological Station's Buck Island Ranch [BIR], eight wetlands; and Ranch 4, two wetlands). A detailed description of the FRESP ranches and their water retention projects can be found in Bohlen et al. (2009), but briefly, both the Ranch 1 and Ranch 2 projects installed culvert riser structures with boards (weirs) in ditches that drain pastures to retain water and restore

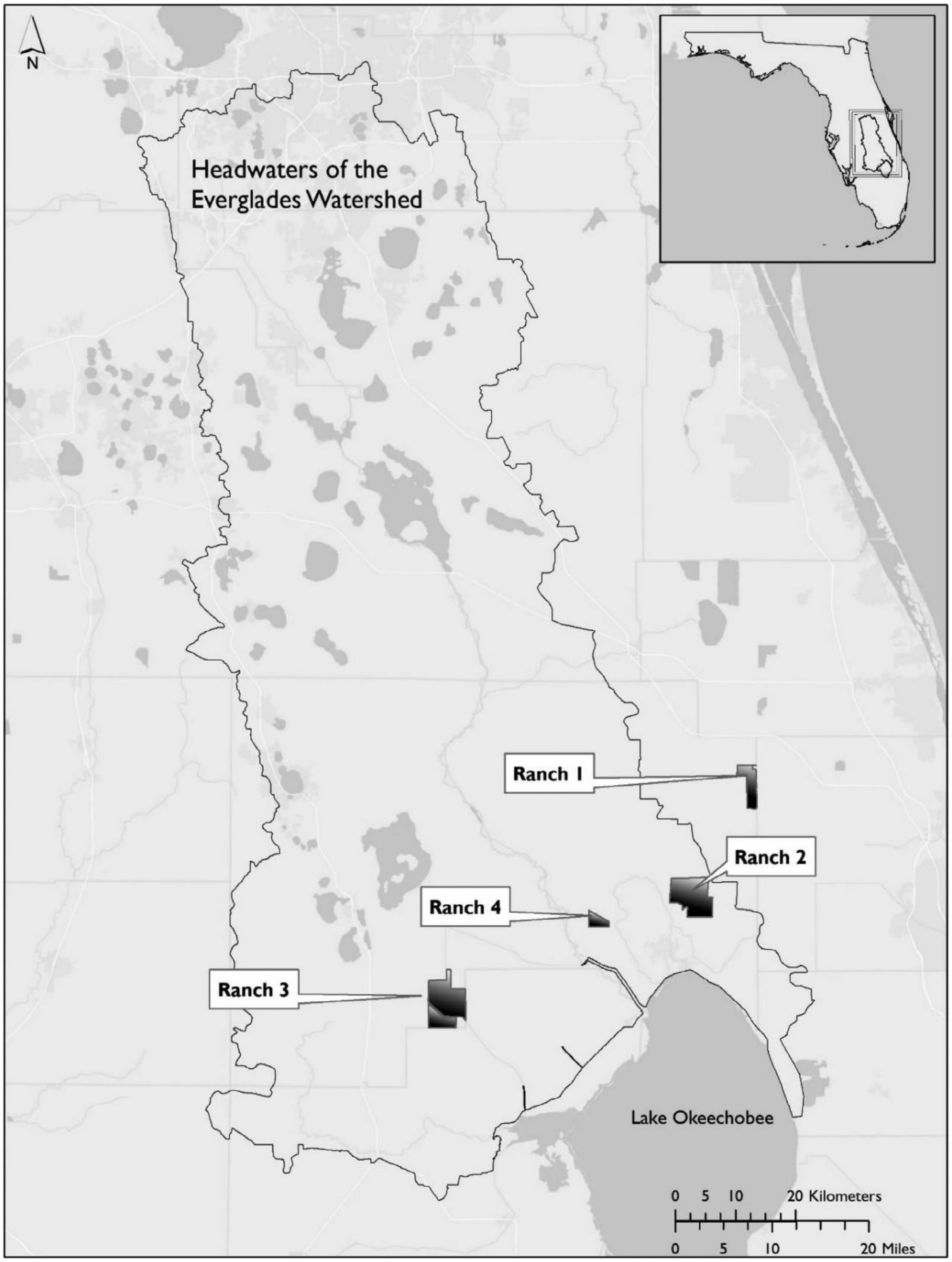

Fig. 2. Locations of the four ranches sampled in this study relative to Lake Okeechobee, within the headwaters of the Everglades, in south central Florida, USA.

flood regime in large, shallow depressional freshwater marshes (Bohlen et al. 2009). The FRESP water retention project at Ranch 3 retained water in a ditch network utilizing 42 culverts with riser structures on a 1133-ha area of pasture with numerous embedded wetlands (Bohlen et al. 2009). At Ranch 4, the water retention project also used culvert with riser structures downstream of wetlands, similar to the basic design at Ranch 1 and Ranch 2 (Wu et al. 2016). Ranch 4 was not enrolled in FRESP but had a similar water retention project and was selected for inclusion in the study for its existing hydrological data collection and modeling for the site (Wu et al. 2016).

Overall, wetlands were embedded in two pasture types, intensively managed to semi-natural, and varied in size (Table 3). Intensively managed pastures (usually referred to as improved pastures) were typically planted with non-native forage grasses, have a history of fertilization and liming, and had higher stocking rates. Semi-natural pastures contained both native and non-native grasses, have no history of fertilization, and had lower stocking rates. In general, wetlands within intensively managed pastures are typically nutrient-rich because they have been exposed to fertilizer runoff from surrounding pastures, while wetlands embedded in semi-natural wetlands were oligotrophic (Gathumbi et al. 2005, Boughton et al. 2010). All but four wetlands were grazed by cattle during the project period (Table 3). We did not analyze animal use days but all intensively managed and semi-natural pastures that were grazed used typical stocking rates for these pasture types (Swain et al. 2007, Boughton et al. 2016). In no instance did we observe wetlands that were heavily overgrazed or trampled by cattle.

All wetlands selected for inclusion in the study were geographically isolated (though most were ditched), natural, depressional, and seasonally flooded wetlands (Table 3). We sampled wetlands when they contained water, several times (range 1–9; median = 6) each wet season (May–November) for two years (May 2010–February 2012), where timing of sampling depended on hydroperiods and access. The period of sampling included both a prolonged dry period at Ranch 3 and extensive, short-term flooding at Ranch 1, so that sampling encompassed a wide range of hydrological conditions.

Hydrology

During each sampling event, water depth to the nearest cm (Table 4; 1, Depth [*D*]) was measured with a meter stick at all sampled plots and wetland perimeters were mapped using a Trimble GeoXT GPS (Trimble, Westminster, Colorado, USA) by walking along the water's edge and

Table 4. Hydrological variables, spatial scale, and definition.

Variable	Spatial scale	Definition
Depth (*D*)	Within wetlands, local scale (m^2)	Depth in cm at a meter square plot, measured in field
Inundation area (IA)	Among wetlands, wetland scale	Area (ha) of water on wetland footprint on sampling date, obtained from ArcGIS using field measured perimeters of wetted area, wetland topography, and wetland water depth
Water volume (*V*)	Among wetlands, wetland scale	Volume (m^3) of water in wetland on the sampling date, obtained from ArcGIS using field measured perimeters of wetted area, wetland topography, and wetland water depth
Hydroperiod (TI)	Among wetlands, wetland scale	The number of days the wetland held water previous to the sampling date. The number of days the wetland had held water at a depth of at least 15 cm (6 inches). The TI was adjusted using a regression intercept to account for the number of days water was present before sampling occurred. This adjustment was important for the analysis of biota
Time since inundated (TSI)	Among wetlands, wetland scale	Number of days dry until the wetland filled on the sampling date
Days connected (DC)	Among wetlands, wetland scale	Number of days the wetland was hydrologically connected via ditches on sampling date. A wetland was considered connected if the water level in the ditch was the same as the wetland water level, and the number of previous DC was summed for each sampling date
Days since connected (DSC)	Among wetlands, wetland scale	Number of days not connected via ditches on sampling date
MaxdepthL (MdL)	Within wetlands, local scale (m^2)	The difference between the point elevation (meter square plot) and the nearest upland elevation (cm) obtained from ArcGIS
MaxdepthW (MdW)	Among wetlands, wetland scale	Maximum depth (cm) of all of the meter square sampling points in a wetland recorded on the sampling date

Notes: All variables except depth (*D*) were derived. Spatial resolution of local scale is meter square plots sampled within wetlands. Spatial scale of wetland scale is given by wetland sizes in Table 3.

creating polygons. Shallow groundwater wells (~3 m belowground surface) with pressure transducers (KPSI 550) were installed in 10 wetlands, and water level and temperature were recorded every 15 min. The remaining five wetlands had a groundwater well within at least 700 m that was used for analysis (Table 3). Groundwater well data were manually downloaded every 2–3 months. Eight (2–9 in Table 4) wetland hydrological variables were derived, representing within wetland (local scale) and among wetland (wetland scale) hydrology using a combination of manual depth measurements, groundwater wells, GPS data of wetland perimeters and wetland bathymetry, LiDAR, and ArcGIS (Table 4). Accurate DEMs (digital elevation models) were based on LIDAR data collected earlier and developed for the Ranch 3 and Ranch 4 (Guzha and Shukla 2012, Wu et al. 2016). For Ranch 3 and Ranch 4, LIDAR data were collected and processed by NCALM (National Center for Airborne Laser Mapping) at the University of Florida with an estimated vertical accuracy of 10–20 cm (Ranch 3 flown in April 2006 and Ranch 4 in May 2008; in both instances, wetlands were dry). The DEMs for the other two sites, Ranch 1 and Ranch 2, were developed from data collected using a Trimble S6 Total Station (Trimble) in July 2013. Measurements of D taken within wetlands, GPS-based wetland perimeters, and the DEMs were combined using ArcGIS to estimate inundation area (2, IA) for each sampling date. Wetland volume (3, V) was determined using the average of measured depths, GPS-based wetland perimeters, and the DEM within ArcGIS for each sampling date.

Hydroperiod (4, time inundated; TI, in days) was derived from groundwater well data (Table 3) and the lowest recorded elevation of the wetland (see Table 4 for definitions). Conversely, the time since inundated (5, TSI, days) at each sampling date reflected preceding dry conditions in the seasonal wetlands (Table 4). Two additional temporal variables represented hydrological connectivity for each sampling event. The bottom elevation of ditches and calculated water levels in ditches draining wetlands were used to estimate previous days connected (6, DC; Table 4). Similarly, previous days since last hydrological connection to a ditch (7, DSC) was estimated for every sampling date to show how many days the wetland had been hydrologically disconnected from the drainage network. Maximum depth (8, MdL; Table 4) for local scale analyses (i.e., within each wetland) was calculated as the average difference in elevation (from LiDAR or DEM) of each individual plot location from the elevation at the edge of the wetland. Maximum depth (9, MdW; Table 4) for among wetland (wetland scale) analyses was the maximum depth recorded among all plots sampled in a wetland on a sampling date.

Ecology

We used stratified random sampling to quantify species richness and abundance of native and non-native plants, forage, broadleaf marsh plants, mosquitoes, fishes, and amphibians at each wetland. The number of sampling points depended on wetland size, ranging from six sampling points for wetlands that were 1–2 ha to 18 points for the largest wetland of 31 ha, for a total of 132 points each sampling event (if all wetlands contained water). Sampling points were randomly stratified by wetland zones (edge and center), and within each wetland zone, we sampled within three depth strata: 1–15 cm, 16–30 cm, and 31–45 cm, which incorporated most of the wetland depth range and over time resulted in sampling a range of depths within each zone. We randomly selected sampling points for each sampling event with ArcGIS and georeferenced each sampling point using Trimble GeoXT GPS (Trimble). For each random sampling point, data on plants, fish, frogs, and insects were all collected within 5 m of the point.

In total, 11 sampling events occurred, and 664 plots were sampled. In 2010 and 2011, sampling events took place in the early (April, May), mid (June–August), and late wet season (September–November), and in 2012, two sampling events occurred during the wet dry season (January and February 2012).

Forage quality and biodiversity sampling.—For plants, we surveyed circular 1-m^2 quadrats centered at the randomly generated sampling point to determine species richness and percent cover. We identified plants in the field or collected them for later identification (vouchers are kept at the BIR herbarium). Percent cover for individual species was assigned to one of seven classes of a modified Daubenmire scale (Daubenmire 1959, 1968; 1: 0–1%, 2: 2–5%, 3: 6–25%, 4: 26–50%, 5: 51–75%, 6: 76–95%, 7: 96–100%). The midpoints of the cover classes were used in analyses. We estimated upland forage cover by combining cover estimates for upland grasses (grasses with a wetland indicator status of FAC [facultative] and FACU [facultative upland]): *Paspalum urvillei, Paspalum notatum, Paspalum conjugatum, Digitaria serotina, Cynodon dactylon, Aristida patula, Andropogon virginicus*, and *Andropogon* sp. (Note that upland forage cover contains important planted forages such as *P. notatum* and *C. dactylon.*) Wetland forage cover combined estimates of planted and native wetland grasses known to be palatable and selected by cattle (palatable grasses with a wetland indicator status of FACW [facultative wetland] and OBL [obligate wetland]): *Sacciolepis striata, Paspalidium geminatum, Paspalum distichum, Paspalum acuminatum, Panicum sp., Panicum rigidulum, Panicum repens, Panicum longifolium, Panicum hemitomon, Panicum dichotomum, Hymenachne amplexicaulis, Hemarthria altissima, Echinochloa walteri, Dichanthelium erectifolium, Axonopus fissifolius, Axonopus furcatus*, and *Aristida palustris*. To understand the pattern of broadleaf marsh plants that are found in deeper water conditions, percent cover of four species were combined: *Sagittaria graminea, Sagittaria lancifolia, Pontederia cordata*, and *Thalia geniculata*.

When sampling vertebrates and invertebrates, we avoided the area disturbed by plant sampling and selected a location within 5 m of the georeferenced sampling point and at the same water depth. We collected mosquito larvae and pupae with standardized 1 m dip net (0.5-mm mesh) samples. We preserved specimens in ~50% isopropanol and transported them to the laboratory, where all mosquito samples were isolated, counted, and identified to species using Darsie and Ward (2005) and Cutwa-Francis and O'Meara (2008). We collected fishes, amphibians, and macroinvertebrates using one box sampler per sample point (0.54 m diameter × 0.6 m high) and repeatedly dipnetted (0.5-cm mesh) the trapped water column until two consecutive sweeps yielded no vertebrates or invertebrates. We identified, staged, sexed, measured, and released all fishes and amphibians at their point of capture (see Appendix S4 for a full species list). From box samples, we also collected macroinvertebrates, identified them to genus or family, and then released them (Appendix S4).

Hypothesis testing

We predicted that depth (within wetlands) and TI (among wetlands) would be the most important hydrological variables to organisms (Table 2). However, we expected other variables might be important at the local and wetland levels (Table 2). We included inundation area (IA), volume (*V*), maximum water depth (MdL, MdW), and temporal and connectivity parameters (DC, DSC) in our statistical models to explain variation among wetlands. We expected that the relative importance of these hydrological variables would differ among ranches because their landscape context and management intensity varied. Thus, we expected a ranch-scale effect for all organisms, based on our expectation that the combination of land use history, management practices, and geographic position of a ranch would substantially influence wetland community composition (Babbitt et al. 2009, Boughton et al. 2010, Medley et al. 2015).

Of the 19 predictor variables available, some were relevant to local scale analyses, others to wetland-scale analyses, and some to both analyses (Table 2), and thus, we used different independent variables for analyses within and among wetland spatial scales. Collinearity of all variables was assessed prior to analyses.

*Within wetlands: Local scale analyses.—*We evaluated up to seven variables (Table 2) in local scale models: two hydrological variables (*D* and MdL), one seasonal variable (growing degree days, GDD), ranch (a categorical variable), and where applicable, variables describing biotic interactions (i.e., plant cover, native plant cover, nonnative plant cover, fish counts). Variables that applied to wetland scales (e.g., TI) were not used in local scale analyses. Some polynomial models tested the non-linear hypotheses as depicted in Table 2.

*Among wetlands: Wetland-scale analyses.—*Wetland-scale analyses used up to 10 variables, including six hydrological variables, all of which applied to whole wetlands, but not to local sampling points: TI (adjusted for an additional 17 d based on the regression intercept); IA; *V*; DC; DSC; and MdW recorded on a sampling date (Table 2). When applicable, we again included ranch and GDD and variables describing biotic interactions at the wetland level: mean plant cover, mean native plant cover, mean non-native plant cover, and mean fish counts. We also tested non-linear hypotheses (Table 2).

Statistical approach

We used model selection based on Akaike's information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2001) to identify the most parsimonious and informative models given the hypotheses proposed. For local scale models, we used generalized linear mixed-effects models for abundances, where wetlands were treated as random effects across the landscape and within ranches. We used negative binomial, Gaussian, or zero-inflated negative binomial distributions where applicable. We analyzed species richness in response to *D* and MdL using quantile regressions, which split the data by sequential quantile regions and are useful for identifying limiting factors and when the response variable is known to be affected by more than one factor and when not all factors are measured (Cade and Noon 2003). Quantile regression was used instead of simple regressions due to wedge-shaped patterns in richness data. Quantile regressions were not used for among wetland models because analyses were not possible with 15 wetlands and limited variation existed for species richness for most organisms at the wetland scale.

Potential models included additive and interactive effects in linear and non-linear curves as appropriate to hypotheses and are all listed in Table 2, although we included interactions only if we expected them to be important. All sets of models were compared to a null model that included an intercept term only and univariate models that contained only each independent variable. All analyses were conducted in R v. 2.15.3 using glmmADMB (Fournier et al. 2012) and bbmle (Bolker 2014) for both point scale and wetland-scale analysis of counts and plant cover. For richness analyses, we used quantile regressions based on the R library quantreg (Koenker 2005). For models that included non-linear effects, we used quadratic functions and general additive models in R and plot3D to visualize results.

Results

General description of hydrology and diversity

Wetland hydrology varied across ranches and years (Table 3; Appendix S2). Overall, average depth (*D*) measured was 16.7 cm and average annual TI was 111 d (range = 19.5–285 d/yr), average volume (*V*) was 4888 m^3 (range = 324–36,656 m^3), average TSI was 2.3 d (range 0–19.8 d), average days since connected (DSC) was 88 d (range 0–635 d), average DC was 74.3 d (range = 0–302 d), average maximum depth (wetland scale, MdW) was 30.4 cm (range 3–58 cm), and average inundated area (IA) was 27,034 ha (range 1988–200,436 ha; Appendix S2).

Across all wetlands, we identified 259 species: 201 plant species (176 native, 17 non-native, 8 unknown), 11 amphibians (all native, 10 frogs and 1 salamander), 10 fishes (9 native, 1 non-native), 15 species of mosquitoes, and 22 macroinvertebrates (Appendix S3–S5).

In general, the expectation that local *D* and TI would be the most important hydrological variables was supported. In three cases, other hydrological variables were significant; maximum depth (MdL [maximum depth, local scale] and MdW) explained variation in broadleaf marsh plant cover at the local scale and macroinvertebrate abundance at the wetland scale and DSC (number of days not connected via a ditch) explained variation in amphibian abundance at the wetland scale.

Overall, 11 of our a priori hypotheses were accepted, but in 14 instances, results were different than expected and there was no evidence for many of the hypotheses (Table 2).

Within wetland, local scale analyses

*Forage and plant community.—1. Forage cover: Upland and wetland forage.—*At the local scale, upland forage plant percent cover declined with greater water *D*, consistent with our a priori hypothesis (Table 2). The most plausible model included a negative linear function of *D* (-0.01 ± 0.003; coefficients ± standard error from GLMMs are presented and used throughout below), Ranch, native cover, and an interactive effect between native cover and Ranch (Table 5). As expected, there was a significant Ranch effect. Upland forage percent cover at Ranch 3 (-0.51 ± 0.24) was significantly lower than at Ranch 1, which in turn was significantly lower than at Ranch 2 (2.41 ± 0.27). Upland forage percent cover at Ranch 4 did not differ significantly from Ranch 1 (−0.45 ± 0.28). Upland forage percent cover was negatively associated with native plants at Ranch 2, but this relationship was absent at the other three Ranches (native cover × Ranch: −0.02 ± 0.003).

2. *Wetland forage cover.*—The relationship of wetland forage species to water retention did not support the predicted unimodal effect of water retention. Instead, wetland forage percent cover was most plausibly a positive linear function of D (1.93 ± 0.39), GDD (1.53 ± 0.30), and an interaction between GDD and D (−0.07 ± 0.01; Table 5). Early in the season, wetland forage increased with increasing D, while later in the season, wetland forage decreased with D.

3. *Broadleaf marsh plant cover.*—The most plausible model for broadleaf marsh plant percent cover contained a positive linear effect of D and a quadratic effect of MdL (Table 5). Abundance of broadleaf marsh plants at the local scale was positively linearly related to D (0.006 ± 0.003) and had a positive quadratic (arched) relationship with MdL ($[1.98 \pm 0.51]x + [-1.62 \pm 0.85]x^2$). Broadleaf marsh plant cover was greatest in plots with intermediate MdL.

4. *Native plant cover and richness.*—The most plausible model for native plant percent cover included a positive effect of GDD (0.84 ± 0.17), a negative effect of non-native plant cover (−0.74 ± 0.06), and a marginally significant negative quadratic effect of D ($[-0.59 \pm 0.34]x + [0.01 \pm 0.007]x^2$; Table 5). These effects were consistent across Ranches. Native plant cover increased with the length of the growing season, and non-native cover was negatively associated with native cover. The negative quadratic relationship of native plant cover with D was opposite to our expectations.

Native plant species richness was assessed with quantile regression and responded negatively to increasing D in quantiles of 0.5 and higher, and to increasing MdL in quantiles of

Table 5. Most parsimonious and informative models from the Akaike information criterion (AIC) model selection with AIC attributes.

Ecosystem service/disservice indicator	Top model	No. models assessed with AIC_c	ΔAIC_c	AIC_c weight	Null model ΔAIC_c and AIC_c weight
Local, within wetland scale					
Upland forage cover	~D + natcov + ranch + ranch:natcov	39	0.19	0.47	92.95, <0.001
Wetland forage cover	~D + gdd + D:gdd	23	0	0.53	20.73, <0.001
Broadleaf marsh plant cover	~D + MdL + MdL2	23	0.19	0.2	18.48, <0.001
Native plant cover	~D + $D$2 + gdd + noncov	37	0	0.46	158.28, <0.001
Fish abundance	~D + $D$2 + gdd + D:gdd + $D$2:gdd	28	0	0.54	18.53, <0.001
Amphibian abundance	~D + ranch	47	2.19	0.06	14.36, <0.001
Macroinvertebrate abundance	~D + $D$2 + fishct + D:fishct + $D$2:fishct	47	0	0.68	15.29, <0.001
Non-native plant cover	~D + $D$2 + natcov + ranch + ranch:natcov	42	0	1.0	236.5, <0.001
Mosquito abundance	~D + $D$2 + fishct + ranch + ranch:fishct	47	0	0.99	33.62, <0.001
Wetland, among wetland scale					
Upland forage cover	~natcov + ranch + natcov:ranch	19	0	0.61	20.17, <0.001
Wetland forage cover	~1 (null model)	21	0	0.13	0, 0.13
Broadleaf marsh plant cover	~TI + gdd	28	0	0.32	5.49, 0.02
Native plant cover	~noncov + gdd	30	0	0.69	35.58, <0.001
Fish abundance	~TI + TI 2 + gdd + TI:gdd + TI2:gdd	46	0	0.99	25.24, <0.001
Amphibian abundance	~TI + DSC + ranch	22	0	0.61	7.18, 0.02
Macroinvertebrate abundance	~MdW + MdW2	47	0	0.13	4.79, 0.01
Non-native plant cover	~natcov + ranch	18	0	0.79	15.67, 0.0003
Mosquito abundance	~fishct	9	0	0.26	0.18, 0.24

Notes: D, depth; natcov, native plant cover; noncov, non-native plant cover; fishct, fish abundance; TI, time inundated; gdd, growing degree days; DSC, days since connected; MdL, maxdepth local scale; MdW, maxdepth wetland scale; AIC_c, Akaike's information criterion corrected for small sample size.

0.25 and higher (Fig. 3; *D*: $\tau = 0.25$, $t = 0$, $P = 1.0$, $\tau = 0.50$, $t = -5.4$, $P < 0.001$, $\tau = 0.75$, $t = -7.4$, $P < 0.001$, $\tau = 0.95$, $t = -7.3$, $P < 0.001$; MdL: $\tau = 0.25$, $t = -4.3$, $P < 0.001$, $\tau = 0.50$, $t = -6.8$, $P < 0.001$, $\tau = 0.75$, $t = -7.8$, $P < 0.001$, $\tau = 0.95$, $t = -5.9$, $P < 0.001$). This was due to the wedge-shaped richness-*D* and richness-MdL relationships, with substantial variation in richness in shallow waters, and suggests a limiting constraint of water depth on richness.

*Vertebrates and invertebrates.—1. Fish abundance and richness.—*Unlike the a priori hypothesis of a positive linear relationship, local scale fish abundance responded to *D* as a positive (arched) quadratic function ($[0.62 \pm 0.20]x + [-0.02 \pm 0.005]x^2$), GDD ($0.2 \pm 0.06$), and a *D* and GDD interaction (-0.02 ± 0.007; Fig. 4b, Table 5). Seasonality interacted with *D*, so that sample events later in the year (greater GDD) also exhibited greater peak abundance at intermediate Ds. However, the peak shape was broader, indicating that fish were more dispersed across depths later in the season. This pattern appeared generally across Ranches, because Ranch effects were not included in the most plausible model.

Quantile regression showed a quadratic relationship of fish species richness to water depth for the 75th quantile of the data, showing that fish richness tended to be greater in shallower water, peaking between 20 and 30 cm (*D*: $\tau = 0.75$ ($[t = 2.5]x + [t = -3.2]x^2$), $P = 0.001$. MdL was not related to fish richness.

*2. Amphibian abundance and richness.—*Amphibian abundance did not follow our a priori hypothesis, but instead had a significant negative linear relationship with *D* (-0.04 ± 0.01; Fig. 4a, Table 5). More amphibians were collected in shallower waters at the local scale. The model also contained a significant effect of Ranch where Ranch 3 and Ranch 4 were significantly different

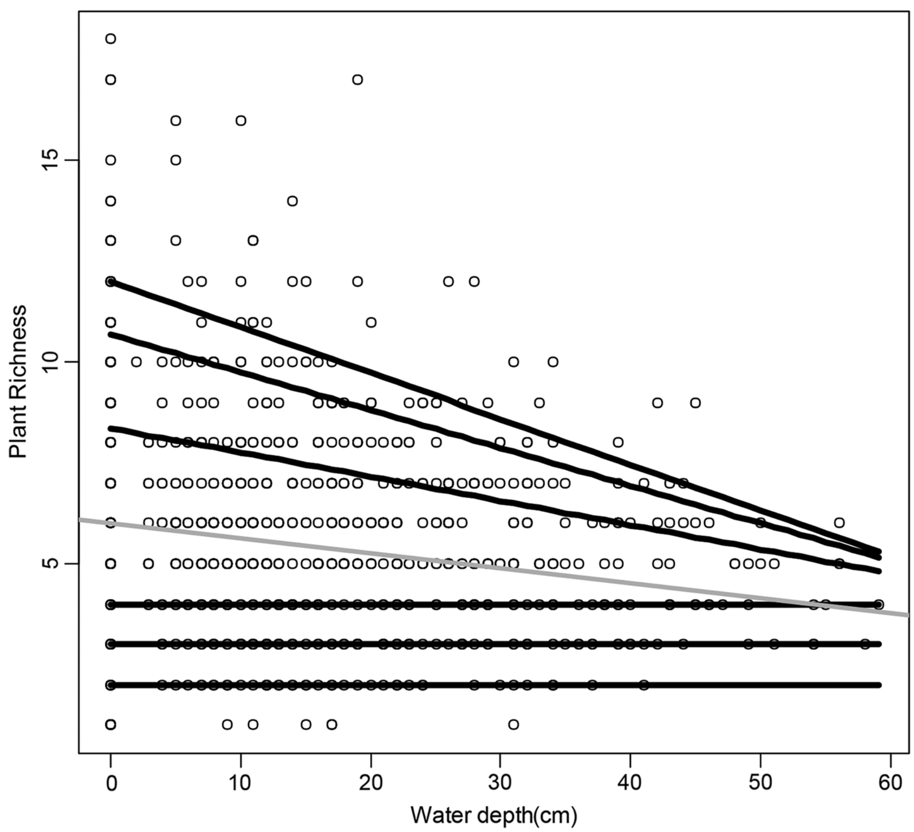

Fig. 3. Quantile regression of plant richness in response to water depth at the local scale (within wetlands). The negative linear relationship was significant for quantiles of 0.5 and higher.

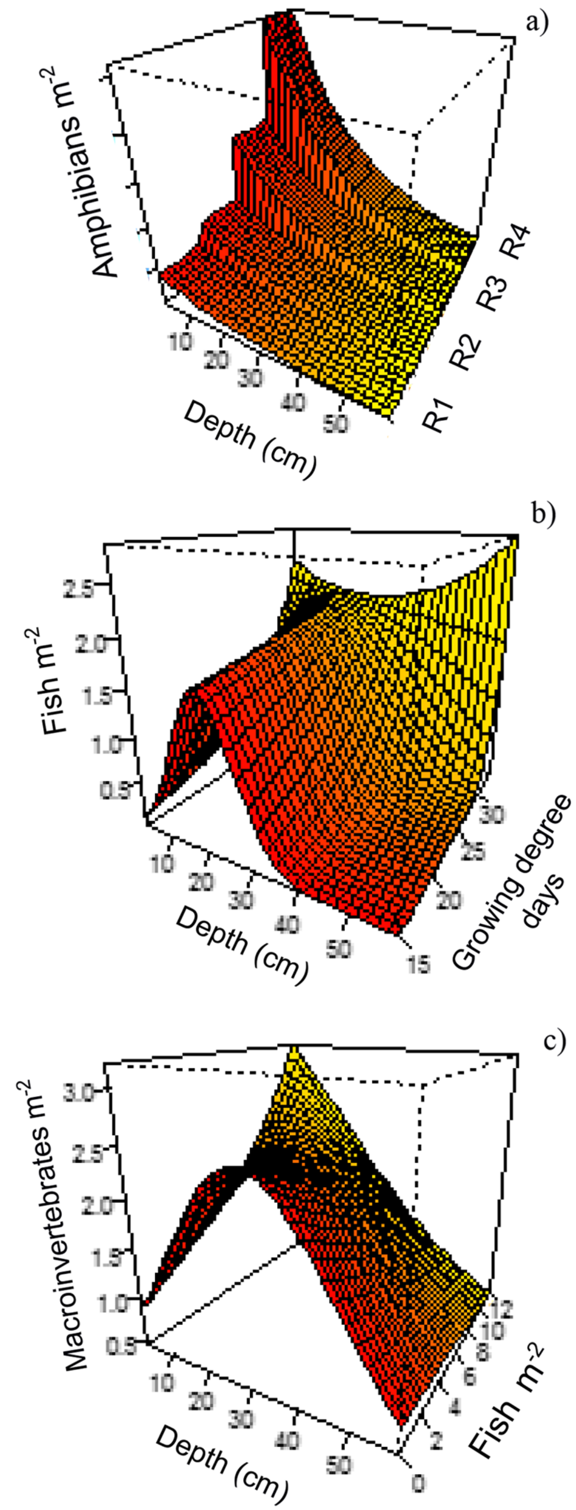

Fig. 4. Plots of local scale, within wetland relationships. (a) Amphibian abundance as a function of depth among ranches. Depth had a uniformly negative effect on amphibian abundance across all ranches, although Ranches 3 and 4 had significantly greater amphibian abundances than Ranches 1 and 2. (b) Fish abundance as a function of water depth across growing degree days. (c) Macroinvertebrate abundance as a function of water depth and fish abundance.

from Ranch 1, while Ranch 2 was not. Ranches differed in abundances because Ranch 1 and Ranch 2 had generally lower amphibian abundances than Ranch 3 and Ranch 4 (Fig. 4a). Amphibian species richness was independent of D and MdL at all quantiles.

3. Macroinvertebrate abundance and richness.—Abundance of macroinvertebrates was a positive quadratic function of D at local scales ($[0.08 \pm 0.02]x + [-0.001 \pm 0.0004]x^2$) (Fig. 4c) and the effect of D interacted with fish abundance (-0.008 ± 0.05; Table 5). Macroinvertebrate abundance also was positively correlated with fish abundance (0.1 ± 0.05). Thus, macroinvertebrates responded positively and quadratically to hydrologic conditions, irrespective of Ranch site, like the case for fishes. However, species richness of macroinvertebrates did not vary significantly with D or MdL at any quantile.

Indicators of ecosystem disservices.—1. Non-native plant cover.—Contrary to our a priori hypothesis, the most plausible model for non-native plants included a highly significant negative quadratic effect (i.e., basin-shaped) of D ($[-0.82 \pm 0.19]x + [0.02 \pm 0.004]x^2$), as well as significant effect of Ranch and significant interaction between Ranch and native cover. This finding suggests greater non-native cover at either shallower or deeper depths and reflects the diversity and wide tolerance of regional non-native plant species. Ranch management and landscape position also influenced non-native cover which was negatively associated with native cover at three Ranches (Ranch 3, Ranch 4, and Ranch 2) with the largest effect size at Ranch 4 (-0.48 ± 0.06).

2. Mosquito abundance and richness.—A priori, we expected mosquito abundance to peak at shallow depths. Instead, mosquitoes were most abundance in the shallowest waters sampled, and most plausibly modeled with a negative quadratic relationship (i.e., basin-shaped) with D ($[-0.06 \pm 0.03]x + [0.001 \pm 0.007]x^2$) that differed among Ranches. That model also included a significant interaction between fish abundance and Ranch site. Ranch 4 (2.09 ± 0.91) and Ranch 2 (5.29 ± 0.87) had significantly more mosquitoes than Ranch 1, which did not differ significantly from Ranch 3 (0.91 ± 0.64). Those abundances at Ranch 2 were also significantly (-1.45 ± 0.35) related to lower fish abundances in the very shallow waters sampled there. In contrast, fish abundances had no more than a marginal effect on mosquitoes at other Ranches (Ranch 3 -0.04 ± 0.19 and Ranch 4 -0.41 ± 0.25). Overall, our data support a significant negative effect of D for mosquito abundances, though the effect of D varied among Ranches and with fish abundances. Mosquito species richness did not vary significantly with D or MdL for any quantiles.

Among wetlands, wetland scale

Forage and plant community metrics.—1. Forage cover: Upland and wetland forage.—The most plausible model for upland forage percent cover at the wetland scale contained the effects of native cover, Ranch, and their interaction; no hydrological variables were in the most plausible models (Table 5). Upland forage cover varied in response to Ranch (Ranch 2 was the only Ranch with a significantly greater effect size than Ranch 1), all other Ranches did not differ, and there was an interaction between native cover and Ranch (-0.044 ± 0.01); upland forage and native cover were negatively associated at Ranch 2 but not at other Ranches. For wetland forage species, the most plausible model was the null model (Table 5), but there were 8 other models similar in plausibility (i.e., $\Delta AIC \leq 2$). However, all models were weak, precluding interpretation.

2. Broadleaf marsh plant cover.—Broadleaf marsh plant percent cover was most plausibly modeled by TI (0.003 ± 0.001) and GDD (0.02 ± 0.01; Fig. 5a, Table 5). Wetlands with longer hydroperiods had greater abundance of emergent wetland plants.

3. Native plant cover.—Analyses at the wetland scale were consistent with local scale analyses: Non-native plant percent cover had a significant negative effect on native plant cover (-0.02 ± 0.003) and GDD (0.01 ± 0.006) had a significant positive effect (Table 5). No hydrological variables were retained in the most plausible model.

Vertebrate and invertebrate metrics.—1. Fish abundance.—Contrary to a priori expectation, fish abundance was explained by a model with a negative quadratic (basin-shaped) relationship with TI ($[-0.3 \pm .07]x + [0.002 \pm 0.0004]x^2$), a negative effect of GDD (-0.23 ± 0.07), and an interaction between quadratic TI and GDD (0.01 ± 0.002; Fig. 5c, Table 5). Differences among Ranches were not included in the most plausible model.

2. Amphibian abundance.—Two temporally related variables negatively and significantly affected amphibian abundances among wetlands but did not support the a priori hypothesis; abundance was negatively related to TI (-0.007 ± 0.003) and DSC (-0.005 ± 0.002), with differences among Ranches (Fig. 5b, Table 5). Consistent with local scale analyses, Ranch 1 wetlands had a marginally negative effect on amphibian abundances, while all other Ranches had positive effects, with two of them significantly different from Ranch 1 (Ranch 3 and Ranch 4). Ranch 1 wetlands appeared to be oligotrophic, presumably reducing amphibian populations by resource limitation. The number of days the wetland had been disconnected from the ditch network was negatively related to amphibian abundance, consistent with drier wetlands having less amphibians.

3. Macroinvertebrate abundance.—As expected, the most plausible model included a positive quadratic effect of MdW in a wetland ($[0.08 \pm 0.03]x + [-0.001 \pm 0.0004]x^2$). Thus, more macroinvertebrates were observed in wetlands with intermediate maximum depths (Fig. 5d).

Indicators of ecosystem disservices.—1. Non-native plant cover.—Non-native plant cover differed among Ranches, and all Ranches had significantly greater effect sizes than Ranch 1 (Ranch 3, 1.01 ± 0.44; Ranch 4, 2.4 ± 0.64; Ranch 2, 1.44 ± 0.58). There was also a negative linear effect of native plant cover on non-native plant cover (-0.02 ± 0.005) signifying potential competition between natives and non-natives. Two

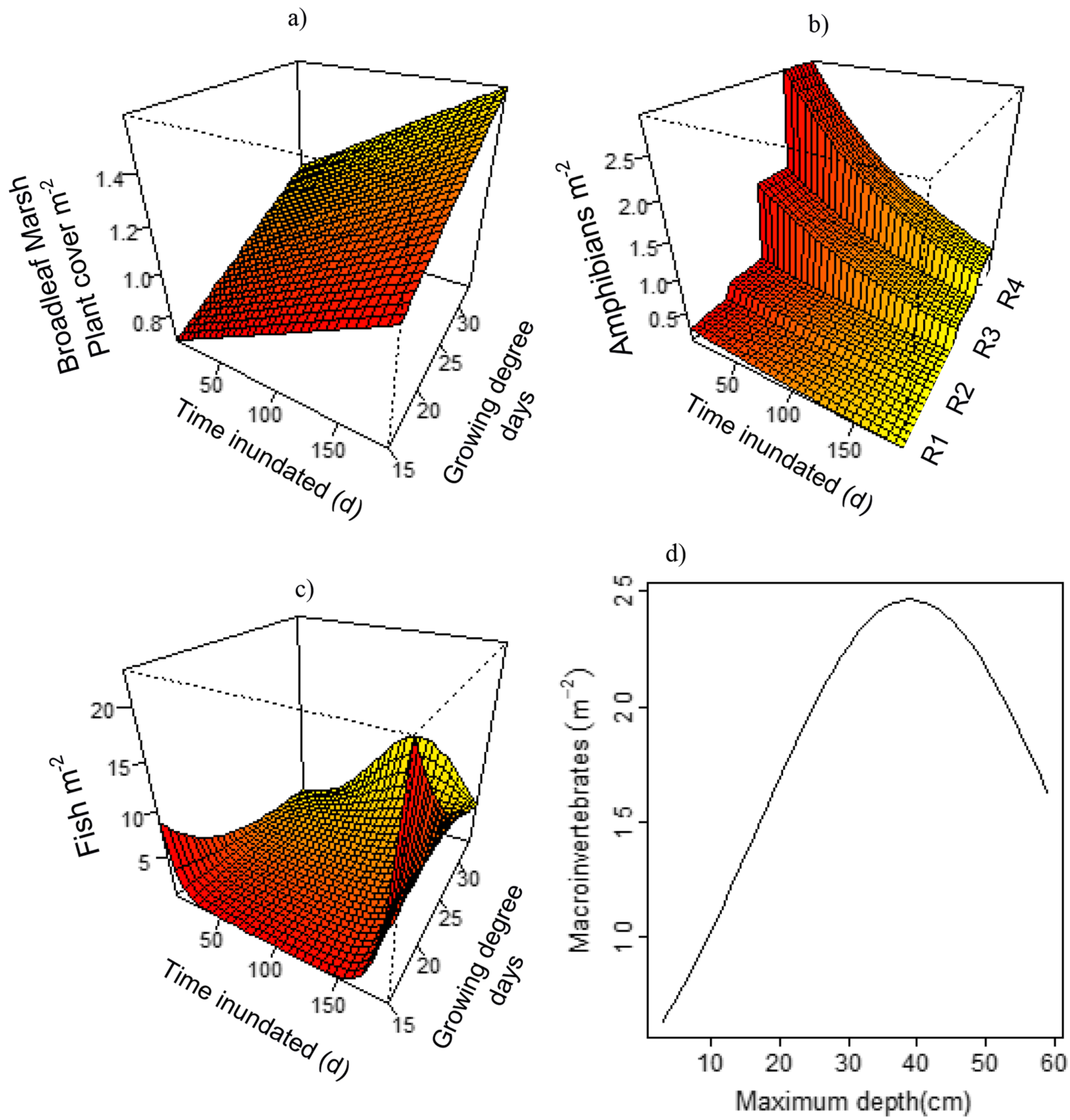

Fig. 5. Plots of wetland scale, among wetland relationships. (a) Broadleaf marsh plant cover increased with time inundated (TI) and growing degree days (GDD). (b) Amphibians decreased with TI and differed among ranches. (c) Fish abundance was explained by a model with a negative quadratic relationship with TI, a negative effect of GDD, and an interaction among the two variables. (d) More macroinvertebrates were observed in wetlands with intermediate maximum depths.

Ranches, Ranch 4 and Ranch 2, had especially large positive coefficients and highly significant effects on non-native plant cover compared to Ranch 1. Thus, native plants may be resisting non-native plants in some wetlands, depending on Ranch management practices and/or landscape context.

2. *Mosquito abundance.—*The most plausible model among wetlands contained only fish abundance, where greater fish abundance was

negatively related to mosquito abundance (-0.09 ± 0.06).

Discussion

Managing for increased water retention could result in both synergies and trade-offs among ecosystem services, both within and among wetlands. At both spatial scales, increased water retention is associated with increased wetland broadleaf marsh plant cover and reduced mosquito abundances. However, most biodiversity metrics are highest at low or intermediate water retention. Our data suggest that higher levels of water retention may reduce native plant richness and fish richness. Furthermore, amphibian abundance and both fish and macroinvertebrates were more abundant at intermediate depths within wetlands. Conversely, non-native plant cover was greater where water depth was either shallow or deep. We also detected a trade-off between water retention and provisioning services. Upland forage cover, which is directly linked with beef production, declined with increasing water depth within wetlands. Palatable wetland grasses would not likely offset the entire loss of upland forage if wetlands expanded due to water retention.

These complex relationships indicate that optimizing water retention, provisioning services, and wetland biodiversity in ranchlands is not straightforward. Ranchers likely require strategies for maintaining provisioning services while providing water retention and would need to monitor outcomes carefully. The trade-off between provisioning and regulating services is common in agricultural production landscapes (Bennett and Balvanera 2007, Carpenter et al. 2009, Qiu and Turner 2013). In contrast, non-linear relationships among water retention and biodiversity suggest there is a range of intermediate retention levels of water retention that also maintain biodiversity. Mixed strategies are required in areas such as the headwaters of the Everglades where downstream water quantity and quality are major environmental and social issues and less biodiverse wetlands could be managed to retain water and remove nutrients, at the expense of biodiversity. But these projects should be balanced with other offsetting projects managed at intermediate retention levels for biodiversity support. Our results here provide the vital relationships between ecological responses (measured by ecologists) and hydrological measures (derived by hydrologists) essential to decision support tools to identify and prioritize optimal water retention scenarios where different stakeholders can evaluate the extent to which water retention projects provide for both biodiversity and desired levels of water retention. The relationships found here are used to develop a decision support tool (Engel 2014) that will allow us to offer specific hydrological management recommendations for a given goal or suite of goals. Our study emphasized the importance of spatial scale in quantifying the impact of water retention on ecosystem services provided by wetlands. Site-specific effects (i.e., the ranch-scale effect) were important to ecosystem services and disservices provided by wetlands. Land use history and landscape context are known to be important drivers of ecosystem services in other studies (Daily 1997, Polasky et al. 2011, Qiu and Turner 2013, Jessop et al. 2015, Landis et al. 2018). For example, Jessop et al. (2015) showed that restored wetlands closer to riparian areas had greater plant, avian, and anuran conservation value than did wetlands further from these areas. In addition, land use history affects ecosystem services at both local (e.g., by altering resource availability for pollinators) and landscape scales (e.g., fragmentation affects dispersal (Kremen et al. 2007, Landis et al. 2018). It is likely in our study that land use history drives processes at both local and landscape scales that affect the biodiversity indicators (plants, amphibians, fish, and macroinvertebrates). For example, Boughton et al. (2010, 2016) showed that wetlands in more intensively managed pastures have lower wetland plant diversity compared to wetlands embedded in semi-natural pastures. Medley et al. (2015) also showed that pasture type was a strong driver of amphibian composition. Therefore, land use history has important consequences for the delivery of ecosystem services and is important for strategically identifying ranches and wetlands to participate in PES programs.

The impacts of water retention on nutrient loading or other regulating services such as greenhouse gases and carbon sequestration were not feasible to assess in the water retention FRESP projects or this study. Detailed monitoring of carbon and nutrients (especially N and P) budgets in PES programs should be a priority, especially in regions with sensitive ecosystems downstream (e.g., the Everglades). During the FRESP pilot program, the documentation team concluded that measuring the impacts of water retention projects on nutrient loading would not be cost effective, given the flat landscape, sandy soils, and seepage-driven hydrology and lack of baseline data. At least five years of pre- and post-water retention coupled with concurrent control sites would be required to assess the water quality impacts of water retention projects, and these data did not exist for the FRESP projects. Bohlen and Villapando (2011) had existing baseline data before initiating an experimental water retention project and found that retaining water on pastures and ditch networks significantly reduced N leaving the pastures. They also found that P loads were 27% lower in pastures with reduced flow compared to pastures with unobstructed flow, but the difference was not statistically significant due to variable water tables among years. The differences among years were attributed to higher water table conditions that triggered increased P release from soils (Bohlen and Villapando 2011).

Increased water retention in seasonal wetlands and pastures could enhance carbon sequestration by altering C inputs and decomposition rates. Jessop et al. (2015) found that more surface water storage in wetlands caused slower decomposition and thus wetlands could act as important carbon sinks. However, wet soils and flooding events on subtropical pastures are an important source of methane (Chamberlain et al. 2015, 2017) and methane emissions may, in part, offset greenhouse sink strength (Allard et al. 2007, Soussana et al. 2007, Dengel et al. 2011). Chamberlain et al. (2017) estimated that water retained in the PES program on Ranch 3 accounted for a total of 2–11% of annual intensively managed pasture GHG emissions. Further studies are warranted to assess these ecosystem services across regional water retention projects and account for the different types of projects and land management.

In the context of larger goals for Everglades restoration, water retention projects on private ranches are only one tool in the Everglades restoration toolbox of projects that includes large reservoirs and regional storm treatment areas to slow water flow and nutrient loading from the headwaters of the Everglades to Lake Okeechobee. It will take a multitude of projects north and south of the lake to effect benefits for the downstream estuaries and the Everglades (Graham et al. 2015). The FRESP pilot project has now been scaled up by the South Florida Water Management District (SFWMD) to the Northern Everglades PES program (NEPES) with 9217 ha on 13 participating ranches as well as four other ranch projects in operation or under construction on 21,790 ha encompassed within the SFWMD's Dispersed Water Management program (e.g., Northern Everglades Public-Private Partnership program, NE-PPP). If adopted regionally, these dispersed water management projects still provide only a small proportion of water storage needs for the Everglades watershed, and the current focus is on large storage reservoirs south of the lake (Graham et al. 2015). However, as well as downstream watershed ecosystem services, including water retention and nutrient reductions, dispersed water projects also provide multiple services on-site including wetland restoration, increasing water retention and availability, nutrient reductions, and wetland species habitats (Shukla et al. 2017). PES payments may also reduce undesirable land use change at scale. In this study, the PES payments to BIR allowed the ranch to generate net revenues annually rather than lose money overall. For private ranchers, PES payments may represent enough financial incentive to avoid converting entire ranches to more intensive agriculture or development.

For the long-term success of PES programs, it is crucial to understand trade-offs and synergies associated with managing for one ecosystem service. In our study system, ranchers were paid by state water managers to retain water in existing wetlands and ditches, with the common assumption that other beneficial services would result (e.g., increased wetland plants and aquatic biodiversity). Our results partially support this assumption; wetland plants increased with water retention, but plant diversity was highest and wetland vertebrates and invertebrates were most abundant in shallow to intermediate wetland habitat. However, increasing shallow water habitat has trade-offs, including lower overall water retention, loss of forage, potential increases in non-natives, and increased mosquitoes, especially in wetlands surrounded by intensively managed pastures. Loss of forage and increased mosquitoes economically impact ranchers, who should consider these risks when negotiating payments with state water managers. The spatial extent of depths of wetland habitat in a PES program would be an important detail for program planning.

Finally, this project would not have been possible without a unique collaboration of ranchers, ecologists, hydrologists, engineers, and policymakers. Multidisciplinary collaboration was required to design, implement, and monitor this PES program as well as to assess multiple ecosystem services and begin to evaluate trade-offs and synergies. We argue that multidisciplinary collaboration such as this is required for ecologically and economically sustainable water management and the success of PES programs that affect multiple stakeholders.

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