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Community dynamics under environmental extremes: coastal plain wet prairie in a natural state and under restoration

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Abstract Ecological restoration is increasingly employed to restore degraded or destroyed ecosystems and evaluation of restoration success requires that natural community dynamics be understood. Wet prairies in the Southeast US have diverse plant communities subject to disturbances including fire, drought, flooding, tropical storms, and freezes. This habitat covers a fraction of its former range and reversing that trend requires ecological restoration; but, long-term data on the dynamics of this system are rare. We analyzed a 12-year plant community composition dataset from a fire-maintained Gulf of Mexico Coastal Plain wet prairie to characterize plant community dynamics and identify indicator species. The site was compared to a nearby wetland mitigation project attempting to restore a wet prairie that had been converted into slash pine (*Pinus elliottii*) plantation. The reference site had higher species richness, was dominated by *Aristida* spp., and was stable despite extreme climatic conditions. The restoration site transitioned from dense pine and understory canopy to an open, grassy community, but did not follow a trajectory toward the reference state. Restoration efforts were impeded by woody debris, accumulated duff, soil disturbance from logging, and storm surge

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from hurricanes. Continued application of prescribed fire and decomposition activity should remove the organic matter and promote establishment of wet prairie species, but on a longer time scale than expected. Although the pine plantation did not return to a typical wet prairie during the study period, the record of community dynamics of the reference wet prairie provides information on the resilience of the habitat type under prescribed fire management, and serves as a reference for restoration efforts and management of this threatened habitat.

Keywords Wet prairie · Wet savanna · Plant community dynamics · Restoration

Introduction

Ecological restoration is the process of assisting in the recovery of an ecosystem following degradation or destruction (SER 2004). Restoration projects are undertaken for a variety of reasons including improving water quality, protecting threatened and endangered species and to replace lost or destroyed wetlands, a process known as compensatory mitigation (White and Walker 1997; Matthews and Endress 2008; Gumm et al. 2011). Ecological restoration is often viewed as an accelerated succession toward a desired end point (Cortina et al. 2006). Many techniques have focused on altering vegetation, such as manual and mechanical removal of undesirable species, mowing, seeding, and planting desirable species (Mitsch et al. 1998; Clark and Wilson 2001; Meyer et al. 2010). Late successional species are often targeted for planting and seeding in order to take advantage of priority effects before non-target (often exotic) species can arrive and become established (Wilsey 2020). Often, restoration objectives require reintroducing disturbance regimes that were historical determinants of community structure such as fire and hydrologic regimes (White and Walker 1997; Suding et al. 2004). Defining success in ecological restoration can be problematic, and requires an understanding of the natural ecosystem dynamics of the target habitat.

To provide a goal or endpoint for restoration, a reference site is commonly identified and the directional changes in community composition or ecosystem processes of the restoration site are monitored over time relative to the reference condition (White and Walker 1997; SER 2004; Matthews and Spyreas 2010). Conditions of the reference site can influence the perceived restoration success if the restoration goals do not account for past and current disturbances that are occurring on the reference site (Rohr et al. 2018). It is important to understand how the reference site responds to these disturbances as successful restoration of ecological communities includes restoring ecosystem functions and community structure to a stable state that is resilient to the disturbances common to the local environment (SER 2004).

Wet prairies along the northern Gulf of Mexico are subject to a variety of disturbances including, fire, drought, flooding, and tropical storms and thus provide an opportunity to test practical approaches in applied restoration ecology. These wet prairies are located in subtropical zones and are also known as wet savannas and pitcher plant bogs. They are species-rich, fire-dependent habitats with low-nutrient sandy soils. Although wet prairies can refer collectively to a broader category of wet prairie ecosystems such as those dominated by sawgrass (*Cladium jamaicense*), this paper refers specifically to wiregrass-pitcher plant wet prairies of the coastal plain as defined by the Florida Natural Areas Inventory (Clewell et al. 2009; FNAI 2010). Wet prairies are known for their high diversity of plant species, showy flowering herbs, and carnivorous plants (Walker and Peet 1983; FNAI 2010). They once covered large areas of the Eastern Gulf of Mexico and the Southeast US Coastal Plain, but due to development and fire suppression, past estimates found only 3% remain in their natural state (Folkerts 1982; Hermann 1995; Mize et al. 2005; FNAI 2010). In response to this loss, conservation and restoration plans for management of wet prairie habitats have been established over the last 40 years (Folkerts 1982; FNAI 2010).

Restoration of wet prairies varies little from restoration of other fire-dependent savanna-type communities of the Southeastern US. Re-introduction of fire, canopy thinning, cutting and treating woody shrubs with herbicides, and flattening of beds from pine plantation establishment are all common restoration techniques (Brockway et al. 2005). However, intensive methods may alter the hydrological function of the system, particularly drainage, if not carefully applied (Trager et al. 2018). Wet prairies occupy just a fraction of their former range and yet very few studies have evaluated restoration projects in this habitat (e.g., Mize et al. 2005).

The study presents an analysis of a 12-year plant community dataset from wet prairie restoration and reference sites in Northwest Florida. Our objectives were to identify reference indicator species, document the dynamics of the plant communities of the reference and restoration sites in response to disturbances, and determine if the plant community of a restoration site was moving toward reference conditions. We predicted that in response to restoration treatments, the restoration site plant community would develop and ultimately follow similar community dynamics as the reference site.

Methods

Study sites

This study was initiated in 1999 as the assessment portion of a restoration project by the Northwest Florida Water Management District (NWFWMD) on Garcon Point, Florida. The restoration site (N30°31′52.911″ W87°05′29.79″), was acquired by the state of Florida as mitigation for wetland impacts resulting from the construction of the Garcon Point Bridge in 1996 (Fig. 1). At the time of acquisition, the restoration site was a dense, shaded slash pine (*Pinus elliottii*) plantation with heavy duff accumulation. Aerial photographs dating back to 1940 confirm that the restoration site was once part of an extensive wet prairie prior to slash pine plantation establishment in the late 1960s (University of Florida Digital Collections, 2012). The development of the slash pine was visible in aerial photographs from 1974 and created a closed canopy by 1981. Aerial photographs from 1965 show an open canopy, wet prairie. Though fire history prior to project establishment is unknown, we estimated 1965 as the last year prior to the study that fire occurred since fire is generally excluded from young slash pine plantations (Hess and Tschinkel 2017). A nearby wet prairie managed by the NWFWMD (N30°31′52.91″ W87°04′41.38″) was used as a reference site based on its proximity to the restoration site and aerial photographs from 1940 indicating that the reference site has been consistently maintained as natural wet prairie (Fig. 1). The reference site is actively managed with prescribed fire.

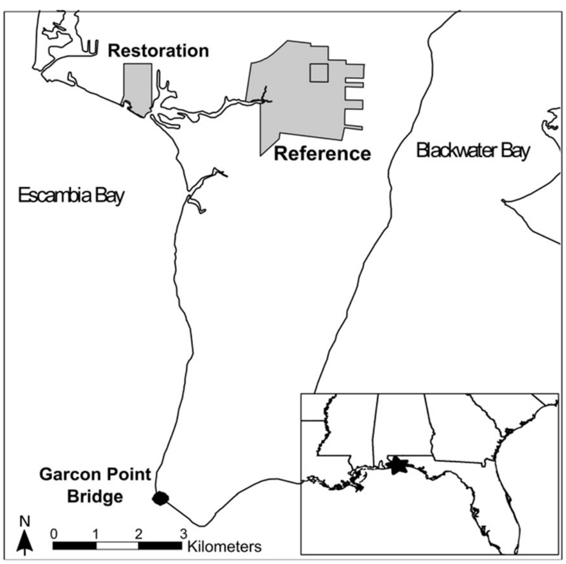

Fig. 1 Study area in northwest Florida including the reference site (right gray polygon), restoration site (left gray polygon), and Garcon Point Bridge

Data collection

Plant community surveys were conducted annually by graduate students from the University of West Florida from 1999 to 2010 at both sites. Plant identification was verified by the University of West Florida herbarium curator as needed. Three 20 × 20 m permanent plots were established at the reference site and ten at the restoration site. All plots were surveyed in July and August except in 1999 when the restoration site was surveyed in January. Each plot was divided into four 100 m^2 modules with 10, 1, 0.1, and 0.01 m^2 nested subplots and surveyed according to the vegetation survey technique for species presence, percent cover, and the coverage classes provided in Peet et al. (1998). Nested quadrats were placed in the southwest corner of each module. The midpoint of each coverage class was used for analysis. Diameter at breast height (DBH) for all woody species within each 100 m^2 module was measured and placed in size classes according to Peet et al. (1998). For woody plants less than 1.37 m tall, stems were counted and placed in the smallest size class (0–1 cm). Plant nomenclature follows the *Atlas of Florida Plants* (florida.plantatlas.usf.edu).

Restoration included logging alternate rows of slash pine to remove half of the basal area in 2004, after the annual data collection. One plot was not logged and was used as a control to determine logging effects on plant community response. In an effort to introduce wet prairie species, many of which have limited dispersal (Kirkman et al. 2004), three plots at the restoration site were seeded in 2008. Seeds were collected from another NWFWMD wet prairie site on Garcon Point in December 2006. Seed fertility of *Aristida* spp., a major component of the seed mixture, was estimated at 24%. The area was raked after seeding and approximately one inch of rain fell the following week. Fire was reintroduced to the entire restoration site with prescribed burns in February 2002 and April 2008. The reference site was burned in 1995, March 2001 and April 2008 as part of wet prairie management (Table 1).

Sunlight interception by slash pine is potentially a major factor in the loss and recovery of heliophilic herbaceous species typical of wet prairie, so light intensity was measured at both sites in 2000, at the restoration site in 2002 after the prescribed burn, and in 2004 after logging to assess restoration progress. Light intensity was assessed along a north to south transect through both sites. A light meter (Fisher Scientific® traceable dual range cosine and color corrected) was held at waist height and light levels were recorded every meter along the transect. Before and after walking the transect, we took a recording in full sun, i.e., no canopy cover, to obtain an average value for 100% light transmittance.

The number of days annually with minimum temperature at or below freezing and precipitation amounts for 3, 6, and 12 months prior to each survey were obtained from the National Oceanic and Atmospheric Administration National Climatic Data Center for the stations Pensacola Regional Airport in 1999 and 2000 and Pensacola 7 NNE in 2001 through 2010. Due to close proximity, both sites were assumed to be subject to the same amount of precipitation and number of freezes throughout the study. Data for the two major hurricanes that impacted the area were obtained from the National Hurricane Center.

Data analyses

Species presence and percent coverage data were compiled for every year of the study. *Aristida* species were combined and *Rhynchospora* species were combined to avoid inconsistencies from changes in taxonomic expertise of field technicians spanning the course of the study. The data from 2005 were removed from the restoration site analyses and 2006 were removed from the reference site analyses due to concerns regarding the accuracy of the surveys at those sites during those years. Plant species were categorized as perennial and wetland species based on the USDA plants database (USDA 2013) national wetland plant list for Atlantic and Gulf Coastal Plain. Wetland species were defined as those categorized as

Table 1 Timeline of events for reference and restoration sites

Year	Reference site	Restoration site
1999	Plots established	Plots established
2000	Light intensity measured	Light intensity measured
2001	Prescribed burn	–
2002	–	Prescribed burn; Light intensity measured
2003	–	–
2004	Hurricane Ivan	Logged all but one plot; Light intensity measured; Hurricane Ivan
2005	Hurricane Dennis	Hurricane Dennis
2006	–	–
2007	–	–
2008	Prescribed burn	Prescribed burn; seeded 3 of the 9 logged plots
2009	–	–
2010	–	–

either facultative wetland or obligate wetland. To identify indicator species, species present every year of the study for each site were identified. These persistent species from the reference site were considered as potential wet prairie indicator species.

To assess whether logging produced an open canopy that allowed light penetration similar to the reference site, irradiance was compared between the reference site in 2000 and the restoration site in 2004 data with an analysis of variance (ANOVA) using R 3.6.3 (R Core Team 2020; package "car", Fox and Weisberg 2011). Restoration of plant community composition and structure at the restoration site was assessed with non-metric multidimensional scaling (nMDS) with a trajectory overlay using Primer 6 (Clarke and Gorley 2006). Bray–Curtis resemblance matrices on fourth-root transformed percent cover data of both sites were used for the nMDS. Transformations were done to account for rare and very abundant species. A 2-way analysis of similarity (ANOSIM) was conducted on the fourth-root transformed percent cover data for all of the years from the reference site and only years after logging with the no-log control plot excluded for the restoration site. Similarity percentage (SIMPER) was then run to determine which species contributed most to the dissimilarities between sites. The 20 species contributing most to the dissimilarity between the sites were then used to create a biplot with the nMDS. Species richness and evenness was compared between sites and years using repeated measures ANOVA in R. Data was split into pre-and post-hurricane prior to running the ANOVA. Evenness was estimated with a modified Hill's ratio calculated using percent coverage of each species (Alatalo 1981). Trends in the woody component of the plant communities were assessed by calculating the density of stems within each DBH size class. To determine if the restoration and reference sites exhibited similar dynamics in response to environmental conditions, correlations between the plant community composition and structure of each site over time were assessed using BEST in Primer 6 using the following variables: years since fire, total precipitation 3, 6, and 12 months prior to sampling, years since major hurricane, number of days with minimum temperature at or below freezing, and whether the canopy was open or closed (Online Resource 1).

Results

Over the course of the survey the number of days below freezing per year ranged from 7 to 23 (Online Resource 1). Annual precipitation ranged from 109 to 269 cm per year. In April 2005, extreme rain events resulted in four times the normal monthly amount of rainfall in just a few days compared to all April 1999–2010 (55.73 cm, $\bar{x}$= 12.52 ± 14.30). Category 3 Hurricanes Ivan (September 2004) and Dennis (July 2005) impacted the region after sampling in 2004 and prior to sampling in 2005. Hurricane Ivan produced little rainfall, 6.35 cm, but did result in a salt water storm surge 4.5 m above mean sea level. This storm surge directly impacted the restoration site by covering the site with salt water, salt marsh detritus, and seeds of plants such as *Baccharis halimifolia*, which became part of the community composition in post-hurricane period. Wind damage from Ivan further reduced canopy cover after logging by stripping branches and felling trees. Hurricane Dennis caused further canopy loss from wind damage at the restoration site. Hurricanes Ivan and Dennis did not produce any storm surge, downed trees, or apparent canopy damage on the reference site.

The reference site had high light availability with 91% of the measured transect points receiving 100%

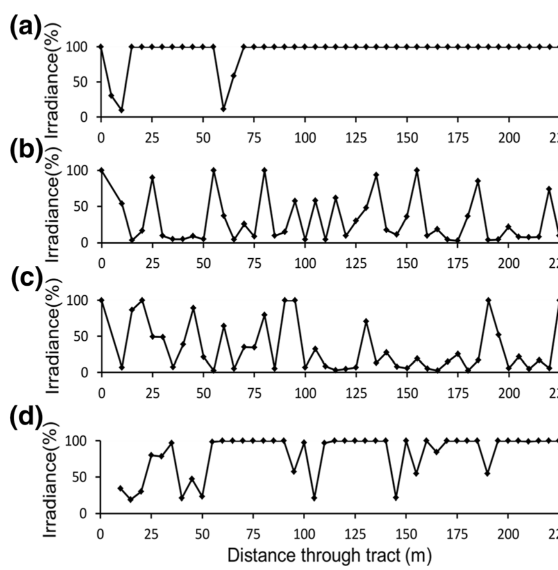

Fig. 2 Light intensity along north to south transects in the **a** reference site 2000, **b** restoration site 2000 before restoration activities, **c** restoration site 2002 after the first prescribed burn, **d** restoration site 2004 after logging and Hurricane Ivan

irradiance (Fig. 2a). In contrast, the restoration site started as a closed canopy pine forest with only 9% of measured points receiving 100% irradiance in 2000 (Fig. 2b). Light availability to the ground increased after the prescribed burn in 2002 removed much of the understory woody species (13% of transect at 100% irradiance; Fig. 2c). Logging further increased light availability at the restoration site (56% of transect at 100% irradiance; Fig. 2d), and it was no longer statistically different than the reference site when the no-log plot was excluded from analysis (ANOVA, $F_{1,\ 84} = 3.60$, $P = 0.06$).

One hundred thirty-seven species were recorded on the reference site (Online Resource 2). Most of the species found were perennials (81%) and wetland plants (85%). Five species were listed as threatened in Florida, one of which, *Sporobolus vaseyi*, is endemic to Florida. And, two species, *Platanthera integra* and *Sarracenia leucophylla*, are listed as endangered in Florida. Twenty-seven species were present all 12 years on the reference site and were considered to be indicative of natural wet prairie (complete species list with coverage can be found in Online Resource 2). One hundred fifty-four species were found on the restoration site, 83 of which were also found at the reference site. The majority of the species found at the restoration site were perennials (90%) and wetland species (74%). One species (*Triadica sebifera*) is listed as a noxious weed in Florida. Over the 12 years of monitoring, the restoration site had 16 of the 27 wet prairie indicator species defined by the reference site.

The plant community on the restoration site did not show integration with or a trajectory toward a community similar to the reference site (Fig. 3). ANOSIM of the reference site and the logged plots of the restoration site showed lack of similarity ($R = 1.0$, $P < 0.01$). According to the SIMPER analysis, *Aristida* spp. contributed the most to the dissimilarity between sites (3.72%). This species was dominant on the reference site ($\bar{x}$ coverage = 79%), but had low coverage on the restoration site after logging and hurricanes ($\bar{x}$ coverage = 0.35%) despite seeding that was done on the restoration site and being present every year at both sites. Woody species and ferns were strongly associated with the restoration site prior to logging and hurricanes (Fig. 4). After logging and hurricanes, grasses were more associated with the restoration site, though these grass species were rarely

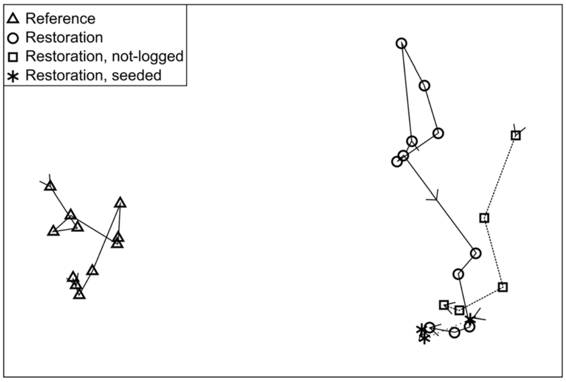

Fig. 3 nMDS of reference and restoration sites percent cover data averaged across plots per year with arrows showing site trajectories over time. Restoration site plots that were seeded and the plot that was not logged are presented as separate trajectories from the other restoration site plots. Final stress for the 2D plot was 0.07

found in the reference site. Heliophilic grasses and forbs were associated with the reference site (Fig. 4).

Woody plant species were mostly in the smallest DBH size class for both sites (Fig. 5). The reference site consistently had a greater density of smaller stemmed woody species than the restoration site. Although logging and hurricanes reduced the numbers of woody plants in the larger DBH size classes at the restoration site, they appeared to be increasing in number again by the final year of the study. The no-log plot retained a greater proportion of larger woody species even though the hurricanes produced damage and loss of trees.

Plots at the restoration site averaged 29 ± 4 species prior to logging and hurricanes and 42 ± 12 species after. The no-log control plot averaged 43 ± 16 species from 2005–2010 and the seeded plots averaged 57 ± 9 species from 2008–2010. Three species introduced to the restoration site (*Helianthus heterophyllus*, *Ludwigia octovalvis*, and *Juncus validus*) were exclusively present on the seeded plots. Plots at the reference site averaged 49 ± 7 species over the 12 years of monitoring. The restoration site had significantly lower species richness than the reference site before and after hurricanes ($F_{1,\ 6} = 115.70$, $P < 0.001$; $F_{1,\ 13} = 10.08$, $P < 0.01$; Fig. 6a). However, richness increased significantly on both sites after hurricanes and logging the restoration site ($F_{1,\ 13} = 28.33$, $P < 0.001$) and was increasing at a

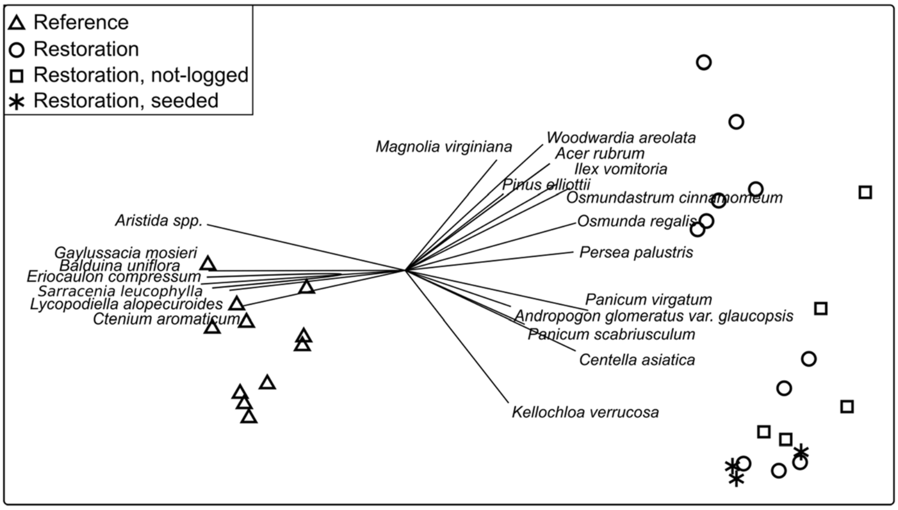

Fig. 4 nMDS of reference and restoration site percent cover data averaged across plots per year with vectors showing the twenty plants that contributed most to dissimilarity between sites. The upper right quadrant of the figure contains points from the restoration site from 1999 to 2004 and the lower right quadrant contains points from the restoration site from 2006 to 2010

greater rate on the restoration site than the reference site.

Plant community evenness on the reference site was low (Average modified Hill's ratio = 0.38 ± 0.08; where 1 is complete evenness). Dominant taxa were *Aristida* spp. and *Ilex glabra* which averaged 79 and 13% coverage per plot, respectively. The plant community on the restoration site had low evenness both pre- and post-logging and hurricanes (Average modified Hill's ratio = 0.47 ± 0.09 and 0.51 ± 0.12, respectively). *Pinus elliottii* was the dominant species present at the restoration site before logging (76% coverage), but *Kellochloa verrucosa* was the dominant species after (16% coverage).The restoration site had significantly greater evenness than the reference site both pre- and post-hurricanes ($F_{1,\,6} = 10.73$, $P = 0.02$ and $F_{1,\,10} = 18.08$, $P < 0.01$, respectively). Evenness appeared to be increasing over time before hurricanes and decreased after hurricanes on both sites (Fig. 6b).

Reference site plant community composition over time did not correlate with varying levels of precipitation 3, 6, and 12 months prior to sampling, days with minimum temperature at or below freezing, prescribed burns, or years since major hurricane (BEST, $\rho = 0.42$, $P = 0.13$). However, the restoration site plant community composition over time was significantly correlated with a combination of variables (fire, precipitation 12 months prior to sampling, hurricanes, and canopy openness) (BEST, $\rho = 0.69$, $P < 0.01$).

Discussion

Wet prairie indicator species identified in this study were also listed as present in other wet prairies throughout the Southeast US (Pullen and Plummer 1964; Folkerts 1982; Gaddy 1982; Brewer 1998) with the exception of one species: *Aronia arbutifolia*. These previous studies did not identify indicator species, but instead provided species lists. Dominance by *Aristida* spp. was seen in other wet prairie studies as well (Gaddy 1982; Walker and Peet 1983). Although *Aristida* spp. and other indicator species found in wet prairies (*Ilex glabra*, and *Gaylussacia mosieri*) can also be found in more xeric environments (Cohen et al. 2004), carnivorous plants tend to be unique to low-nutrient wet prairies and wetlands in general (Brewer et al. 2011).

The strict definition of indicator species used in this study (presence every year), did not include other species that should also be considered. Five species (*Aletris lutea, Lobelia brevifolia*, *L. floridana*, *Lycopodiella alopecuroides*, and *Sarracenia psittacina*) were present on the reference site every year except for 2005 and were common in other studies of wet prairie

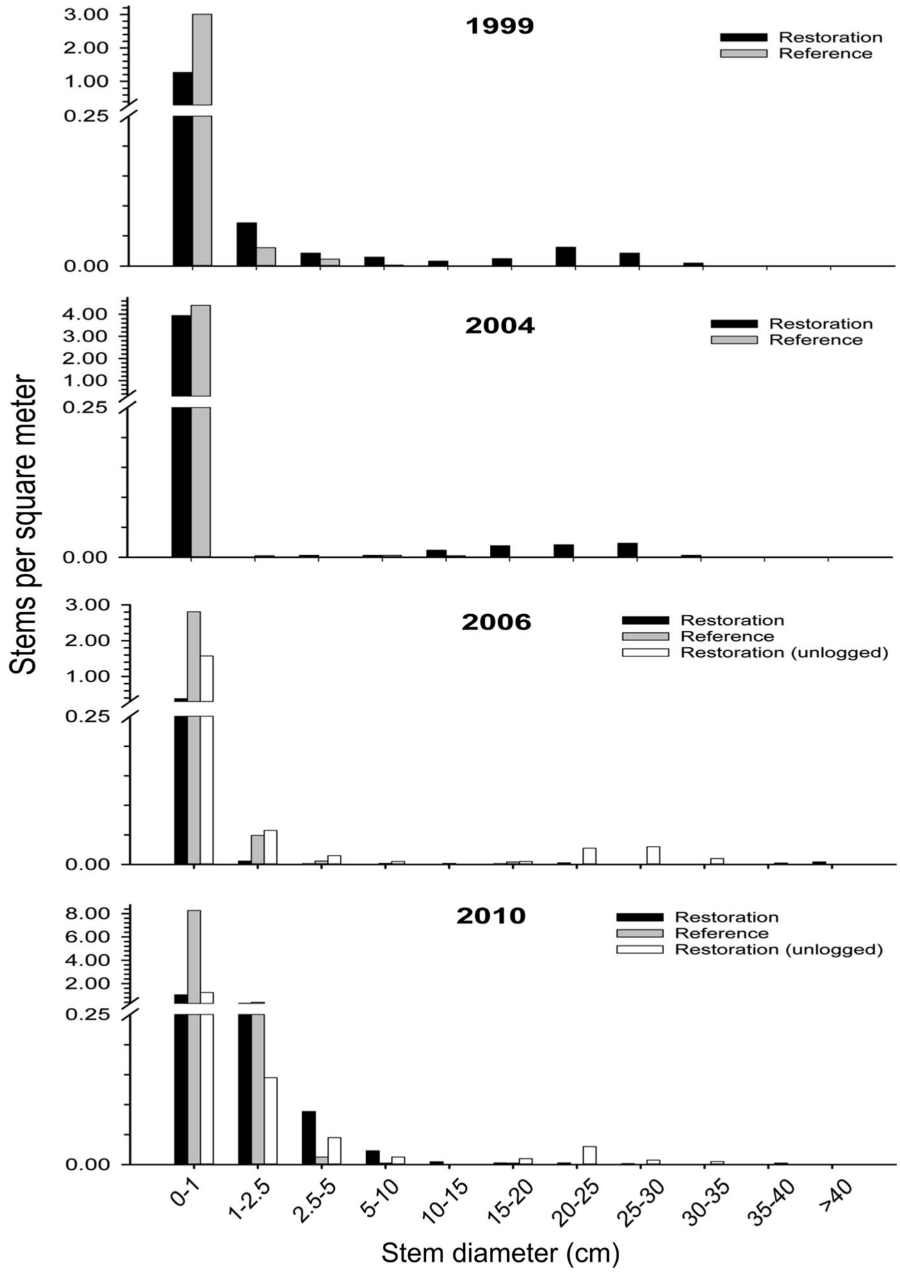

Fig. 5 Density of woody stems per plot in each DBH size class. Data shown for years 1999, project initiation, 2004, immediately prior to logging and hurricanes, 2006, immediately following logging and hurricanes, and 2010, final year of study

plant communities (Pullen and Plummer 1964; Eleuterius and Jones 1969; Brewer 1998; FNAI 2010). These species are perennials and it is likely that there were underground vegetative structures of these missing species still present in 2005 (Folkerts 1982). While the exact reason for their disappearance is unknown, they appear to have been impacted by the hurricanes. The indicator species list developed from this study can provide managers a simple way of delineating wet prairie habitat and determining success of restoration of wet prairie plant community.

The stability of the unique wet prairie plant community in the reference site was remarkable considering the extremes of drought, inundation, storm events, freezing, hot summer temperatures, and recurring fire. Clearly, the species that exist there have faced considerable selective pressures and adapted to a specialized set of environmental

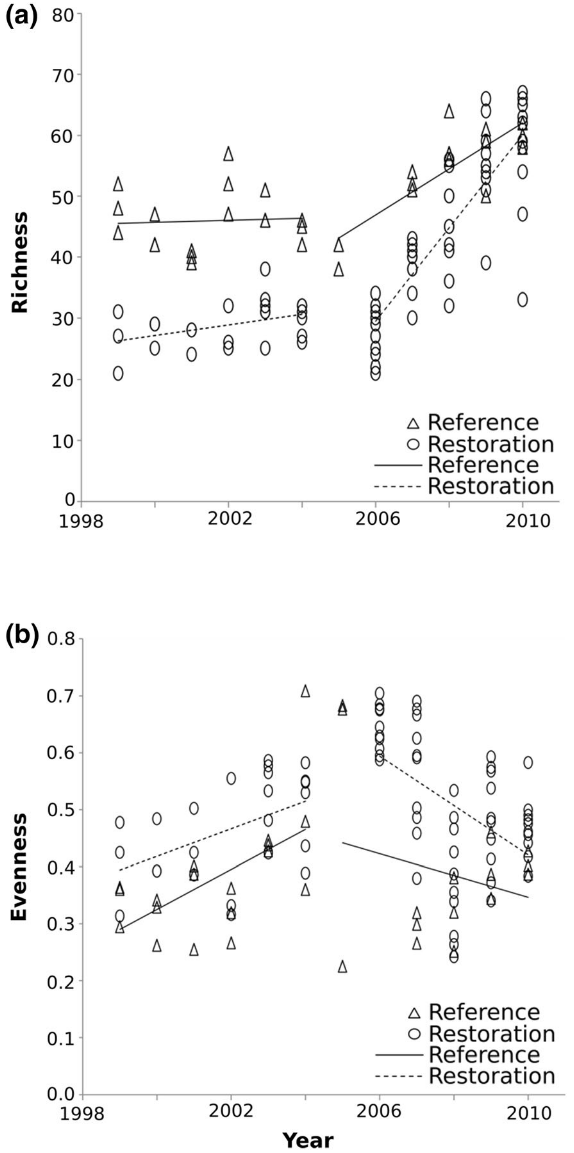

Fig. 6 **a** Species richness at the reference and restoration sites with linear trendlines for each site before and after hurricanes, **b** Evenness at the reference and restoration sites with linear trendlines for each site before and after hurricanes

constraints. Despite the observed resistance to change from the disturbances, the habitat type is easily lost by the removal of these variables, especially fire. However, the plant community composition may be affected by variables not measured in this study. In contrast, the wet prairie converted to pine plantation, where restoration was attempted, was characterized by constant change in the plant community, never reaching a stable end point during the course of the study.

Wet prairie restoration

Restoration efforts did not restore the plant community on the restoration site to wet prairie habitat within the study period, though a heliophytic grass-dominated community did develop. The amount and duration of alteration to a site is directly linked to the speed of restoration of wet prairies (Mize et al. 2005). This community was clearly very different than the initial state, but lacking similarity in composition to the reference site. Reintroduction of fire, though recommended and an important part of restoration (White and Walker 1997; Suding et al. 2004; Trager et al. 2018), was not enough to restore the plant community. The prescribed burn in 2002 killed many of the understory trees and shrubs allowing sunlight to reach the ground. However, not all woody plants were killed and the plant community composition rebounded by the following year to look very similar to the first year of sampling. Additional prescribed burns reduced fire intolerant woody species and shade adapted wetland species such as *Osmundastrum cinnamomeum* and *Osmunda regalis*, but they were still present on the site. The density of larger DBH woody stems appeared to be increasing again by the final year of study suggesting that fire may need to be applied more frequently to the site to reduce woody plant competition (Folkerts 1982). However, downed timber on the restoration site from the hurricanes could alter how future fires impact the site by simultaneously increasing light availability due to canopy reduction for herbaceous plants that act as fuel and by creating barriers to fire spread from large woody debris (Cannon et al. 2017). The low organic accumulation in wet prairies due to recurring fire has probably not yet been achieved on the restoration site due to the legacy of debris from logging and hurricanes. Removal of this organic material by fire creates a considerable smoke risk, and proximity of the site to an interstate highway limits burning until conditions are ideal.

Microtopography from logging equipment, large amounts of logging and storm debris, and salt deposition from hurricane storm surge could have contributed to the increased species richness on the restoration site, but on a trajectory independent of the community composition found at the reference site. Vehicular damage consisting of deep ruts in the soil surface can alter the hydrologic regime of surrounding area leaving some portions inundated with water for longer periods of time and other portions drier than typical, both of which can be detrimental to the vegetation (Mize et al. 2005). Within site variation was greater on the restoration site as compared to the reference site reflecting random dominance as ruderal colonizers became temporary dominants. Invasive and exotic species are successful at colonizing disturbed areas, such as restoration sites, and can prevent the recruitment of native species (Kulmatiski 2006). The restoration site has several dominant species that are typically found in disturbed areas: *Andropogon glomeratus*, *Baccharis halimifolia*, and *Eupatorium capillifolium* (Tobe et al. 1998), all of which increased following logging and hurricanes. It was also noted that species responding to the restoration efforts sometimes did so initially as monotypic patches rather than the interdispersed species distribution found at the reference site.

The limited dispersal capabilities of many reference site indicator species certainly retarded recovery (Campbell et al. 2003; Kirkman et al. 2004). Seeding of plots on the restoration site potentially introduced three new species, *Helianthus heterophyllus*, *Ludwigia octovalvis*, and *Juncus validus*, although coverage was low and they did not spread to other plots. *Aristida* spp. did not increase as a result of seeding as was expected, and this plant may be a keystone species that aids the low, fast fires required to remove organic matter and return limited nutrients to the soil. Seeding efforts were probably hindered by the poor germination conditions likely present on the site. Restoration efforts focused on planting *Aristida* spp. without accompanying native species could result in greater *Aristida* spp. survival and growth (Aschenbach et al. 2010) and might accelerate the dominance of this important taxa at the restoration site, but soil conditions would likely need to be addressed. The continued spread and perpetuation of *Aristida* spp. would require periodic early summer (May–June) prescribed fire as part of land management to stimulate flowering and seed production (Fill et al. 2012). While the high abundance of *Aristida* spp. was stable on the reference site, coverage of *Aristida* spp. decreased on the restoration site following logging and hurricanes. This is likely directly linked to logging debris, physical soil disturbance, and the storm surge and smothering wrack from hurricane events. *Aristida* spp. is known to respond negatively to both storm surge and wrack application in upland pine savannas (Tate and Battaglia 2013) and is sensitive to compaction by vehicle wheels. However, Abbott and Battaglia (2015) found that *Aristida* spp. in a coastal wet prairie increased in cover after experimental storm surge application, potentially due to the higher water table diluting the extra salts.

Species richness and evenness showed similar dynamics at both sites, though the reference site had higher richness and the restoration site had greater evenness. The increase in richness seen at both sites is consistent with other studies that show an increase in richness after disturbance (Kershaw and Mallik 2013; Abella et al. 2018). However, the plant community composition over time showed differing responses to environmental conditions. The reference site plant community was not correlated with any environmental variable examined. Species found on the reference site appeared uniquely suited to the extreme environmental conditions of the wet prairie that we measured. Characteristics of the dominant taxa cannot be overlooked (Polley et al. 2007). *Aristida* spp. is tolerant to fire, one of the major disturbances, and facilitates fire by the production of combustible dry litter (Hillebrand et al. 2008; Beckage et al. 2009; Grman et al. 2010). The major difference between the two sites was proximity to surface water that allowed hurricane storm surge ($\sim$ 4.5 m with Ivan) and the associated salt and organic wrack to impact the restoration site but not the reference site (Hillebrand et al. 2008; Tate and Battaglia 2013; Abbott and Battaglia 2015). Correlations between plant community composition over time on the restoration site with fire and canopy openness were expected as both were implemented to alter the plant community. The correlation found between the restoration site plant community composition over time and years since hurricane is not surprising given the amount of damage that occurred on the site following the two major hurricanes. However, the exact responses of the plant community to the hurricanes and to logging are difficult to resolve since they both occurred in the same year between sampling efforts. The correlation of the restoration site plant community over time with the amount of precipitation 12 months prior to sampling is unexplained, but likely related to the continued successional processes and sequential dominance of species responding to site alterations.

Though frequent prescribed fire and timber management to produce an open canopy have been shown to increase ground species richness (Platt et al. 2006) and promote succession-based restoration in upland pine savannas (Robertson, unpublished data), restoration is seldom the simple trajectory that is often expected (Cortina et al. 2006). Despite not reaching a stable community state within the time frame of this study, the plant community dynamics seen at the reference and restoration sites in this study can aid in planning and evaluating future wet prairie restoration efforts. Reintroduction of fire to the site and logging to produce an open canopy, low-risk restoration steps, are important for shifting the community composition toward an herbaceous-dominated system (Trager et al. 2018). Seeding of the restoration site with wet prairie species had limited effect and was probably premature given the amount of organic accumulation and soil disturbance at the site. Developing the physical conditions suitable for wet prairie species would likely have been more conducive to seeding effort success. As sea level rise continues, the potential for storm surge impacts, even if infrequent, may be a factor to consider prior to investing in salt sensitive community restoration activities. The unique features and location of the restoration site, including the accumulated effects of long-term pine plantation status and proximity to Escambia Bay may mean longer time frame for restoration, and perhaps the ultimate community structure endpoint will be different than our intended reference site.

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Data availability Data available upon request.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

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