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DO LARGE, INFREQUENT DISTURBANCES RELEASE ESTUARINE WETLANDS FROM COASTAL SQUEEZING?

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DO LARGE, INFREQUENT DISTURBANCES RELEASE ESTUARINE WETLANDS FROM COASTAL SQUEEZING?

by

Jesse Fruchter

B.S., State University of New York College of Environmental Science and Forestry,

2005

A Thesis

Submitted in Partial Fulfillment of the Requirements for the Master of Science Degree

Department of Plant Biology

in the College of Science

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THESIS APPROVAL

DO LARGE, INFREQUENT DISTURBANCES RELEASE ESTUARINE WETLANDS FROM COASTAL SQUEEZING?

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Jesse Fruchter

A Thesis Submitted in Partial Fulfillment of the Requirements

for the Degree of

Master of Science

in the field of Plant Biology

Approved by:

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Southern Illinois University Carbondale

May 8, 2012

AN ABSTRACT OF THE THESIS OF

JESSE FRUCHTER, for the Master of Science degree in PLANT BIOLOGY, presented on May 8, 2012, at Southern Illinois University Carbondale.

TITLE: DO LARGE, INFREQUENT DISTURBANCES RELEASE ESTUARINE WETLANDS FROM COASTAL SQUEEZING?

MAJOR PROFESSOR: DR. LORETTA BATTAGLIA

As disturbance frequencies, intensities, and types have changed and continue to change in response to changing climate and land-use patterns, coastal communities undergo shifts in both species composition and dominant vegetation type. Over the past 100 years, fire suppression throughout the Northern Gulf of Mexico coast has resulted in shifts towards woody species dominance at the expense of marsh cover. Over the next 100 years, sea levels will rise and tropical storm activity is projected to increase; resultant changes in salinity could reduce cover of salt-intolerant fresh marsh species. Together, the effects of fire suppression upslope and rising salinities downslope could “squeeze” fresh marsh species, reducing cover and potentially threatening persistence. To mitigate the effects of fire suppression, the use of prescribed fire as a management tool to mimic historic conditions is becoming increasingly widespread and will likely gain further popularity during the 21st century. Ecological shifts that will result from changing disturbance regimes are unknown. It was hypothesized that two recent hurricanes, Ivan and Katrina in 2004 and 2005, respectively, and a prescribed fire, in 2010, differentially affected species along the estuarine gradient and drove overall shifts away from woody dominance. Overall community composition did not change significantly in the intermediate and fresh marsh zones. However, significant changes occurred in the salt and brackish marshes and in the woody-dominated fresh marsh-scrub ecotone zones. Relative to 2004, woody species abundance decreased significantly in all zones in 2006, following Hurricanes Ivan and Katrina, and 2012, following the hurricanes and fire, though woody species regeneration in the marsh-scrub ecotone had begun to occur by 2012. It is hypothesized that interacting changes in fire and tropical storm regimes could release upslope areas from coastal squeezing.

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INTRODUCTION

Abstract

During the 21st century, strong climatic shifts, including the intensification of hurricane disturbances, are projected to occur. Disturbance regime is an important factor in local-, regional-, and landscape-scale dynamics, and disturbance regime shifts resulting from climate change could drive compositional and functional shifts in coastal ecosystems, which are often the first biotic responders to these abiotic shifts. Furthermore, over the past century, fire has been suppressed from coastal systems throughout the U.S. Disruption of fire regimes has been heavily cited as a cause of woody species encroachment into prairies and savannas but the role of fire in coastal marshes has been poorly described. Native woody species are currently encroaching into fire-suppressed marshes along the northern Gulf of Mexico coast. In cases where suppression has resulted in woody species encroachment into coastal marshes, reintroduction of fire may be used to restore coastal wetlands to historical conditions. However, these wetlands will be responding not only to the reintroduction of fire but to changes in hurricane regimes as well.

A potential model for these disturbance regime shifts can be found at Weeks Bay, Alabama, U.S.A., the site of three recent, landscape-scale disturbances: (1) Hurricane Ivan, in 2004; (2) Hurricane Katrina, in 2005; and (3) a prescribed fire, in 2010. This study had one main goal: to determine the effects of projected disturbance regime shifts on coastal communities across an elevation gradient. The study analyzed how species-level responses to recent disturbances at Weeks Bay resulted in emergent

community trends, including both compositional shifts and functional shifts in species dominance.

I predicted that disturbance is an important driver that maintains disclimax herbaceous dominance in coastal marshes throughout the gradient. Disturbances at Weeks Bay reduced woody species abundance, restored herbaceous dominance. I expected that hurricane-adapted woody species responded to Hurricane Ivan by dying back and resprouting, potentially enabling them to persist. However, sequential disturbances at short intervals (i.e., Hurricane Katrina and the prescribed fire) resulted in mortality and, consequently, more long-term reductions in woody species abundance. Differential species-level responses across the gradient also resulted in assemblages containing species whose ranges did not overlap prior to the disturbances. By determining how extrinsic factors impact coastal ecosystems, this study helped advance knowledge in the fields of community assembly and coastal, wetland, disturbance, and restoration ecology and provided insight into the usefulness of fire in maintaining resiliency of coastal wetlands to climate change.

Disturbances as Vital Ecosystem Processes

In the presence of natural disturbances, individual species and community associations (Pickett et al. 2009) can evolve past simple resilience to those disturbances, eventually coming to rely on them in a temporal sense to maintain resilience by periodically resetting or temporarily altering physiognomy (Paine and Levin 1981; McCook 1994; Platt and Connell 2003; Gilliam et al. 2006). Similarly, systems historically impacted by anthropogenic land use may eventually come to require human use to sustain biodiversity and resilience (Bugalho et al. 2011). Landscapes are shifting mosaics of communities in different successional seres and disruptions of historical land use patterns and disturbance regimes can impact succession by favoring late-successional community dominance across landscapes (Clark 1991).

Thus, land management that alters site and landscape successional trajectories from dynamic and shifting towards static or unidirectional can reduce ecological integrity and stability (Firn et al. 2010). Alterations include not only anthropogenic disturbances but also the disruption of natural disturbance regimes (Linder et al. 1997; Turner et al. 1998). Even stable altered ecosystem states where ecological integrity has been compromised are considered degraded (Chapin III et al. 1997; Suding et al. 2004).

Multiple States and Shifting Baselines

Landscape alteration following state changes results in shifting environmental state baselines (Pauly 1995; Folke et al. 2004); once a site has become degraded, that degraded state becomes the new baseline state. Thus, these altered landscapes are resilient to alteration both farther from and back towards their initial states (Suding and

Gross 2006a). Resilience to degradation is referred to as “good” (Marschke and Berkes 2006), “positive” (Smith and Stirling 2008), or “helpful” (Hobbs et al. in revision), whereas resilience to change back towards desirable states has been called “bad” (Marschke and Berkes 2006), “negative” (Smith and Stirling 2008), or “unhelpful” (Hobbs et al. in revision). Depending on site-specific disturbances and disruptions, more than one altered state may be possible for each site; as each of these potential altered states becomes a new baseline, that baseline state would be associated with its own unique degrees of helpful and unhelpful resilience to other potential states (Suding et al. 2004).

Unhelpful Resilience and Positive Feedback Loops

The extent of unhelpful resilience is often a function of degradation, with highly degraded sites very resistant to change back towards prior states (Suding et al. 2004). Even when restoration goals have seemingly been accomplished, stochastic events (i.e., natural or anthropogenic disturbances; see Willard and Cronin 2007) and climatic cycles (e.g., El Niño southern oscillation; see Holmgren et al. 2001) can frustrate land managers by driving systems back towards degraded states (Schooler et al. 2011). Upon reaching certain degrees of degradation, systems cross thresholds past which restoration to historical “norms” becomes impractical because unhelpful resilience acts as an impenetrable barrier (Hobbs 1999). Such barriers can result from various ongoing and future global and landscape-wide changes (e.g., global climate change, changes in anthropogenic land-use patterns). When large, infrequent disturbances (Turner and Dale 1998) become superimposed on systems already degraded by anthropogenic activity, they may render ecosystem recovery impossible (Paine et al.

1998). Thus, restoration ecologists agree that attempts to recreate historical species assemblages unsuitable for future biogeochemical landscapes are likely doomed to failure (Hobbs and Harris 2001; Frelich and Reich 2010; Schoennagel and Nelson 2011). Following state changes, unhelpful ecological resilience can be particularly strong in systems degraded by shifts in species community composition and dominance towards altered functional states (Chapin III et al. 1997) that may drive feedbacks toward biogeochemical and hydrological regime shifts (Folke et al. 2004), such as coastal systems undergoing sea level rise.

Resilience in Coastal Landscapes

Shifting baselines can complicate studies incorporating a resilience framework because interpretation of what constitutes resilient states begs the question that we know *a priori* the true benchmarks to which the present and future systems should be compared (Dayton et al. 1998). In reality, those benchmarks are often unclear (see the shifting baseline syndrome; Pauly 1995) and may even be continually changing. This lack of clarity is particularly apparent in tidal systems, which occur at transitional zones between marine and terrestrial systems (Odum 1988). Since prehistoric times, the combination of extreme productivity and readily exploited resources has resulted in a worldwide trend of strongly impacted coastal systems (van Andel 1990; Diamond 1997; Bird et al. 2002, Day Jr. et al. 2007). Globally, utilization of coastal areas increased during the 20th century (Nicholls et al. 2007) with approximately 23% of the global population within 100 km of shoreline and less than 100 m above sea level (Small and Nicholls 2003). As of the 2000 census, 3.0% of the U.S. population lived within the 100 year coastal flood zone, an area that accounts for only 1.3% of U.S. land area (Crowell et al. 2010). In addition to land-use changes, coastal systems are also subject to natural changes, such as short- and long-term cycles in global, regional, and local geophysical and tectonic activity, sediment accretion, erosion, sea level, and climate (Otvos 1999). As a result, shorelines and, consequently, coastal ecosystems are in a constant state of geographic flux, shifting landward or seaward based on these allogenic and autogenic processes (Anthony et al. 2009).

Eustatic (global) sea level rise has been a prevalent trend over both historic (since the last glacial maximum) and recent periods. Over the past 18,000 years, sea levels have risen as much as 120 m (Day Jr. et al. 2007); over the past 150 years, they have risen as rapidly as 1-2 mm yr^{-1} (Field et al. 2001). Current climate projections predict that sea levels will continue to rise into the 22nd century causing coastal transitions to shift landward (Carter et al. 2007). Saltwater intrusion into tidal wetlands historically dominated by freshwater vegetation may drive state changes towards more halophytic communities (Brinson et al. 1995; Michener et al. 1997). However, if there are barriers to migration by halophytic species (e.g., disjunct populations or alterations of sedimentation and flooding regimes), saltwater introduction could reduce biotic productivity and potentially drive land loss (Thomson et al. 2001). In either case, as salinities rise in areas that are currently freshwater, state changes should be highly resistant to shifts back towards salt-intolerant communities and may be more or less permanent (Brinson et al. 1995).

Transition to Alternate States in Coastal Wetlands as Site Degradation

Coastal wetlands perform many important ecological and biogeochemical functions (e.g., productivity, biodiversity, water balance, energy flow facilitation, nutrient cycling; Brinson and Rheinhardt 1996) and anthropogenically valuable ecosystem services (e.g., water quality control, nutrient retention, economically valuable aquatic, avian, and terrestrial species habitat, flood control and storm buffering, sediment stabilization; Costanza et al. 1997; Woodward and Wui 2001); as such, conversion of wetlands to open water or halophyte-dominated systems is a major shift (i.e., loss) in performance of both ecologically and anthropogenically important functions. Although saltmarshes are among the most productive ecosystems in the world (Chmura et al. 2003), productivity is just one of many ecosystem functions and is not necessarily well-correlated with other functions. In particular, productivity may be unimodally or inversely related to taxonomic richness (Grace 1999; Adler et al. 2011), which is an essential element of maintenance of functional diversity (Isbell et al. 2011). Functional diversity (e.g., diverse interactions in a diverse trophic food web) exerts important stabilizing influences on ecosystems, even where species and interactions acting in isolation do not appear to have strong impacts (McCann et al. 1998; Berlow 1999).

Community dominance shifts from relatively salt-intolerant species to relatively salt-tolerant species are likely to co-occur with declines in taxonomic and functional richness (Baldwin and Mendelssohn 1998; Waide et al. 1999) and could be part of long-term state changes along a trajectory towards land loss (Baldwin and Mendelssohn 1998; Reyes et al. 2000). As historically freshwater-dominated tidal wetlands cross critical degradation thresholds (i.e., salt introduction due to sea level rise), restoration to historical freshwater norms will become increasingly difficult because unhelpful ecological resistance (i.e., increasing salinity in conjunction with salt-intolerant physiology of dominant freshwater marsh plant species) will impede restoration efforts (Hobbs 1999; Hobbs and Harris 2001; Schoennagel and Nelson 2011). Altered biogeochemistry and hydroperiod may also lift restrictions on native and naturalized species ranges, allowing those species to invade the degraded landscape.

Native Species Range Expansions as Invasions

While invasions are generally thought to occur as the results of exotic species introductions, species native to an area also have invasive potential (Davis et al. 2000). Upon being released from conditions that have otherwise prevented colonization or limited persistence and abundance, such as fire, weather, and biogeochemical disturbances (Canham and Marks 1985) or competition, disease, predators, and parasites (Shea and Chesson 2002), the range expansions and marked increases in abundance of species otherwise considered “native” may occur (Archer 1989). These native species expansions are functionally similar to exotic species invasions (Thompson et al. 1995; Burke and Grime 1996) and critical thresholds exist at which increasing abundance of historically limited landscape modulating species negatively affect unmodulated landscape-dependent native species (Shachak et al. 2008), potentially decreasing system stability and driving state changes (Suding et al. 2005; Pujol and Pannell 2008). Although species range expansions and contractions have occurred naturally since pre-historic times (Teed 2000) due to modification of disturbance regime through climate change and anthropogenic use patterns (Pickett and Cadenasso 1995; Millar and Woolfenden 1999; Jetz et al. 2008), rates of changes since European settlement greatly exceed rates of changes prior to European settlement (Kirkpatrick and Barton 1997).

Fire and Disturbance as Fundamentally Important Ecological Drivers

Although Holdridge (1947) based the vegetation types in biomes exclusively on climate factors, disturbance has long been considered an important factor in community succession at local, regional, and landscape levels (Loucks 1970; Grime 1973; Denslow 1980; Grace 1999; Prach and Walker 2011). In many systems, fire and other disturbances are important drivers of succession and community assembly (Cattelino et al. 1979; Bond and Keeley 2005). By providing canopy gaps, which increase light availability (Schlesinger and Gill 1980), and altering nutrient cycling and transformation rates, fire removes many of the biological filters that limit the growth and dominance of shade-intolerant species and early successional communities (White and Pickett 1985; Reich et al. 2001; Bond et al. 2003; Suding and Gross 2006b).

Adaptations to Fire and Fire as a Mechanism for Maintenance of Herbaceous Dominance

Although specific ecological responses to disturbances depend on the characteristics of the species and communities in question, a common adaptation in disturbance-adapted species is the capacity to vegetatively reproduce. Prairie grasses adapted to frequent fire and grazing often recolonize areas by rhizomes, which give rise to tillers (McKendrick et al. 1975; Vinton and Hartnett 1992; Walsh 1994). Similarly, woody species adaptations to disturbance include sprouting responses. Disturbances that induce sprouting responses in woody species vary with the local and regional historical disturbance regimes; while almost all woody plant are capable of replacing defoliated tissue following herbivory, species adapted to more intense disturbances also sprout vigorously from roots or rhizomes following losses of apical meristems and other physical damage by surface fire, windthrow, or biological disturbances (Paciorek et al. 2000; Bond and Midgley 2001). Species that are adapted to particularly hot crown or ground fires may forego sprouting responses and instead germinate readily on mineral soil (Oliver 1980).

In addition to adaptive responses to local and regional fire regimes, species have also evolved mechanisms to alter those regimes (Mutch 1970; Bond and Keeley 2005). Late-successional, shade-tolerant species, (e.g., sugar maple, *Acer saccharum*) shade out other species, which reduces the fuel bed and limits fire behavior (Peterson and Reich 2001). Other species have evolved mechanisms by which they actually increase fire intensity, frequency, or severity. Brush stands, comprised of short, scrubby woody species, enable stand-replacing crown fires (Turner and Romme 1994), the litter of pine savanna tree species with high foliar carbon content decomposes slowly, promoting low-severity surface fires (Hendricks et al. 2002), and herbaceous species in grasslands and savannas that burn frequently may occur in high stem densities, an evolutionary trait allowing them to carry fire quickly and over expansive areas (Hobbs and Huenneke 1992). When fire promotes herbaceous communities, it also limits the spread of woody species. A combination of natural nutrient cycling, climate, herbivory, and disturbance regimes allows herbaceous plant communities to maintain dominance over other vegetation types at certain sites (Van Auken 2009). Anthropogenic land use has been an important influence on ecosystems in areas settled by humans (Ellis and

Ramankutty 2008) and anthropogenic disturbances, such as fire and grazing, are often considered part of the system's historical disturbance regime (Guyette et al. 2002). In some cases, anthropogenic landscape management has become fundamental to maintaining ecological integrity (Seastedt et al. 2008). Over at least the past 12,000 years, (i.e., since human settlement), fires have shaped plant and animal communities across North America (Abrams et al. 1998; Benscoter et al. 2005; Saab and Powell 2005) with particular importance in coastal wetlands in the Southeastern U.S. (Batista and Platt 1997).

Fire Suppression and Shrub Encroachment in the Southeastern U.S.

From the shore inland, these coastal wetland complexes grade from saltmarshes into brackish, intermediate marshes, and freshwater marshes. Fresh marshes then grade into mixed scrub-marsh ecotones, which give way to forested wetlands, such as seep and bottomland forests and, farthest inland, mesic forests (Battaglia et al. 2012). Closest to the sea, woody species are limited by frequent flooding and high salinities, factors which become less prevalent as distance from the shore increases; woody species expansion into intermittently flooded freshwater marshes, on the other hand, was likely limited by natural and anthropogenic landscape-level fires, caused by lightning or set to clear navigation channels and improve wildlife habitat (Nyman and Chabreck 1995). These fires likely prevented encroachment by regionally native woody species, because longer-lived species would not have had time to complete their life cycles and reproduce (Franco and Silvertown 1996) between fires, which could burn at return intervals as short as two or three years (Wade et al. 1980; Schmalzer et al. 1991). However, since the early 20th century, fire regimes along the Gulf coast have been altered considerably from historical norms (Nyman and Chabreck 1995). Coastal systems are extremely vulnerable to species invasions (Grosholz 2002) and fire suppression has played an important role in facilitating invasions by exotic woody species into Louisiana coastal prairies (Bruce et al. 1997).

Seral succession from herbaceous to woody dominance has occurred during a period of fire exclusion over the past 100 years causing marshes along the Atlantic and Gulf coasts to become replaced by scrub vegetation over vast areas; furthermore, where marshes do persist, they have become highly fragmented (Taylor 1988; Shirley and Battaglia 2006; Battaglia et al. 2007). This encroachment, presumably the result of fire suppression (Williamson et al. 1984; Uchytil 1992b; Brinson et al. 1995; Pollock and Battaglia in prep.), causes species richness declines (Warren II et al. 2007) and potentially threatens long-term persistence of the marsh. Fire suppression in coastal fresh maidencane (*Panicum hemitomon*) marshes in Florida has resulted in encroachment by woody shrub species (Huffman and Blanchard 1991).

Encroachment by Woody Species into Marshes Along the Northern Gulf Coast

Exclusion of fire from marshes along the northern Gulf of Mexico has allowed range expansions of native tree (e.g., red maple, *Acer rubrum*, slash pine, *Pinus elliottii*) and shrub (e.g., wax myrtle, *Morella cerifera*; Williamson et al. 1984; Shirley and Battaglia 2006; 2008) species. *Morella cerifera* is an avian-dispersed shrub with a broad range that stretches along the Gulf coast west to eastern Texas and north along the Atlantic coast to southern New Jersey (Van Deelen 1991). The impacts of *Morella* invasion and encroachment into coastal marshes along the northern Gulf of Mexico include increased available nitrogen, perches for avian seed dispersers (Battaglia et al. 2009), and suppression of shade-intolerant understory species (Fruchter et al. in revision). *Morella* expansion is not limited to the northern Gulf of Mexico coast; studies have examined effects of both exotic invasion into Hawaiian lava flows (Kurten et al. 2008) and native encroachment into Virginia barrier islands (Brantley and Young 2008). Given the humid, subtropical climate of the Gulf coastal region (NOAA 2012), encroachment by nitrogen-fixing shrubs likely results in increased net primary productivity, and available soil nitrogen (Hughes et al. 2006; Brantley and Young 2008, 2010; Knapp et al. 2008). Encroachment by woody species also facilitates further encroachment because avian exploitation of perches results in increased seed dispersal (Battaglia et al. 2009). Other encroaching avian-dispersed (zoochoric) woody species found in fire-suppressed coastal marshes include various hollies (*Ilex* spp.), sweetbay magnolia (*Magnolia virginiana*), and redbay (*Persea palustris*) (Drewa et al. 2002).

Fire Regime Across a Coastal Salinity Gradient at Weeks Bay, Alabama

While it is generally accepted that natural fire has played an important ecological role in coastal ecosystems (Lynch 1941; Waldrop et al. 1992; Nyman and Chabreck 1995), historical fire regimes (which include fire frequency, intensity and extent) have been highly site- and system-specific and fire regimes in wetlands along coastal elevation and salinity gradients are generally poorly described (Nyman and Chabreck 1995; Flores et al. 2011). Prevalence of woody species in estuarine wetlands increases along the elevation and salinity gradient at Weeks Bay National Estuarine Research Reserve (hereinafter, Weeks Bay NERR). Closest to the sea, woody species are excluded altogether from saltmarshes and brackish marshes. As brackish marshes grade into freshwater marshes, woody species are able to become established but have been typically reduced in abundance by fires. Farther inland, marshes grade into marsh-bottomland forest ecotones, where woody shrub species increase in abundance, and, finally, farthest inland along the gradient, are tree-dominated seep, bottomland, and mesic forests (Battaglia et al. 2012).

While primary productivity in coastal systems may be greatest in saltmarshes, taxonomic diversity is not directly related to productivity and is generally unimodally distributed along gradients (Grace 1999). Diversity along coastal gradients tends to be highest in freshwater marsh sites (Perry and Atkinson 1997; Crain et al. 2004). Due to differences in species-specific fire ecologies, suppression (and reintroduction) of fire should affect each of these communities in slightly different ways. Saltmarshes are typically dominated by just a few species, (e.g., *Spartina alterniflora*, *Phragmites australis*), which typically respond well to light and moderate surface fires (Gucker 2008a; Walkup 2011). Brackish marshes are generally slightly higher in diversity; they are also typically dominated by just a few species (e.g., *Juncus roemerianus*) that resprout vigorously following low-intensity surface fires (Uchytil 1992a). Where mesohaline marshes grade into oligohaline and freshwater marshes, diversity increases markedly and even the most dominant species (e.g., *Panicum virgatum*, *Cladium jamaicense*) occur with co-dominants (Visser et al. 1998). Due to higher diversity, oligohaline and fresh marsh species responses to fire are less general than the responses of poly- and meso-haline marsh species (Taylor et al. 1994). Nonetheless, dominant species, such as *Cladium* (Uchytil 1992b) and *Panicum* (Uchytil 1993) respond vigorously to even fairly intense surface fires occurring during the winter months. Fresh marsh-bottomland forest ecotones are characterized by having a shrub canopy (e.g., *Morella cerifera*, *Ilex vomitoria*) that grades from sparse to dense. While these shrub species are often capable of resprouting following fires, they are only moderately well-adapted and do not exhibit the pyrophilic responses of the dominant herbaceous species (Van Deelen 1991; Coladonato 1992a). Although seep forest tree species (e.g., *Magnolia virginiana*) can be killed outright by extremely intense fires, they are generally capable of resprouting after patchy fires and may establish seedlings during the first growing season (Gucker 2008b). Usually, fires do not burn intensely in bottomland forests, which are farther inland, frequently under standing water, and dominated by species that do not produce fuel litter (e.g., *Taxodium distichum*). Alterations of biogeochemistry, climate patterns, and disturbance regimes from those historically present could cause important shifts in plant community and population structure along these coastal gradients, impacting sites and having regional effects whereby species move differentially up and down the coastal gradient. This study focused on recent compositional trends occurring along the lower part of this coastal gradient.

Freshwater Marsh Communities at Weeks Bay, Alabama

Freshwater marshes at Weeks Bay are generally dominated by sawgrass *Cladium jamaicense*, a sedge species adapted to resource-poor marshes (Lorenzen et al. 2001; Goslee and Richardson 2008) that utilizes the C3 photosynthetic pathway (Bender 1971). An obligate wetland species, *Cladium* is best-known as the most abundant plant in the Florida Everglades region but is also native throughout the Gulf of Mexico and South Atlantic coasts (USDA 2011). Flooded much of the year, *Cladium* marshes tend to accumulate peat over mineral soils, such as limestone and marl (Craft and Richardson 1993).

Freshwater Marsh and Cladium *Decline*

Along the Gulf of Mexico coast, freshwater marsh seems to be declining at both the seaward and landward peripheries (Shirley 2006). Freshwater marsh species, such as *Cladium*, are relatively intolerant of salt (Ross et al. 2000; Brewer and Grace 1990) and rising sea levels could be resulting in conversion of freshwater marsh to salt- and brackish-marsh, dominated by *Spartina spp*. and *Juncus roemarianus*, at the seaward ends of fresh marshes. Additionally, even where freshwater marsh vegetation continues to dominate, community dominance shifts towards more salt-tolerant species can occur. Relative to other freshwater marsh species, *Cladium* is quite intolerant of saltwater-intrusion and rising sea levels may be driving shifts in community composition and dominance (Evers et al. 1998; Kinler and Linscombe 1998).

At the landward extent of coastal marsh range, marsh loss is occurring through wholescale conversion of community types from open, herbaceous marsh to closed-canopy, scrub-shrub thickets (Shirley and Battaglia 2006). Encroachment by woody species has driven conversion to upland vegetation (Shirley and Battaglia 2006; Shirley and Battaglia in prep. Global Change Biology). *Cladium* is highly adapted to fire (Uchytil 1992b) and longer intervals between fires in coastal marshes (Nyman and Chabreck 1995) are likely contributing to woody species encroachment.

Coastal Squeezing of Freshwater Marsh at Weeks Bay

The term “coastal squeeze” has been used to describe the process whereby saltmarshes become trapped between rising sea levels and increasing anthropogenic development and use (Doody 2004). As ecosystems are pushed farther inland and salinity and flood regimes change with climate change (Pethick 1993), similar phenomena may occur in other zones along the coastal gradient (Brinson et al. 1995). At Weeks Bay NERR in coastal Alabama, Shirley (2006) found that, between 1987 and 1996, a period of fire suppression, there was an increase in areas characterized by upland vegetation and a decrease in areas characterized by marsh vegetation. At the seaward end of the gradient, rising sea levels and more intense hurricanes (Webster et al. 2005; Pielke Jr. et al. 2006), are likely increasing salinity and may be driving areas formerly dominated by fresh marsh species to saltmarsh dominance (Rodgers III et al. 2009; Lam et al. 2011). Thus, a “squeeze” seems to be occurring in freshwater marshes at Weeks Bay, where sea levels are rising, causing the saltmarsh to move landward and, at the same time, fire suppression is allowing woody species to exploit unrealized niches down the gradient (Shirley and Battaglia 2006), squeezing fresh marshes from both ends (Pollock and Battaglia in prep.).

As sea levels rise during the 21st century, it is likely that tidal freshwater marshes will decline. As marshes disappear, the functional importance of intact tidal freshwater marshes could expand in scope to include important refugia for faunal species (Day Jr. et al. 2008). Similarly, these marshes could also serve as remnant sources of marsh propagules for future restoration projects (Zedler 2000), which may incorporate techniques still under development (e.g., assisted migration; McLachlan et al. 2007; Kalk and Battaglia in preparation).

Other Disturbances

In addition to fires, the northern Gulf of Mexico coast is subjected to periodic hurricanes (Stone et al. 1997). In the region, tropical storms occur less frequently than fires, with a relative frequency of about once every 15 – 20 years (Batista and Platt 1997; Platt et al. 2002), but their effects can be more severe (Gilliam et al. 2006). High winds and strong rainfall resulting from hurricanes can cause immediate physical damage to plants and alteration of substrates. Hurricanes can also impact ecosystems longer-term by adding salt through both storm surge and salt spray (Michener et al. 1997). Tropical storm surges also deposit wrack (beach-cast phytodetritus; Orr et al. 2005), which can physically kill or suppress plants, provide a barrier to germination (≈ 200 cm in thickness), and serve as an additional salt source (Gardner et al. 1991).

In addition to these direct effects, the interactive effects of separately occurring large-scale disturbances (e.g., hurricanes and fires) could affect communities differently from the effects of those disturbances occurring in isolation (Paine et al. 1998; Willig and Walker 1999). Fires can exacerbate the effects of tropical storms because branches weakened by fire may be less resilient to strong winds (Robertson and Platt 2001; Platt et al. 2002) and, as a result, more vulnerable to subsequent pathogens (Platt et al. 2002). Disturbance seasonality is also an important factor. South Florida slash pine (*Pinus elliottii var. densa*) post-hurricane mortality was significantly lower in wet- (natural-) season burned pine savannas but significantly higher in dry- (anthropogenic-) season burned pine savannas (Platt et al. 2002). Differential mortality due to tropical storm damage could, in turn, affect fuel loads and future fire severity (Platt et al. 2002).

As current climate change models predict that Category 4 and Category 5 Atlantic-basin hurricanes will almost double in frequency over the next century (Bender et al. 2010), combined disturbance effects may cause losses of herbaceous species (Grace and Ford 1996) and may drive state changes leading to reduced ecosystem resilience (Brinson et al. 1995; Zavaleta and Hulvey 2004).

Furthermore, storm surge and salt-spray are not the only means by which salt is introduced into the system. The area is also prone to drought (Childers et al. 1990). In times of low precipitation, onshore winds and rising Gulf of Mexico tides may cause a greater influx of saltwater through tidal creeks (Williams et al. 1999). Saltwater intrusion can cause community shifts from highly diverse freshwater assemblages (Visser et al. 1998; 2000), such as *Cladium* and *Sagittaria*, to less diverse meso- and poly-haline assemblages, and could ultimately lead to conversion of wetlands to open water (Day Jr. et al. 2000). The effects of saltwater intrusion are likely to be compounded many times over by rising sea levels.

Relative Sea Level Rise

Relative sea level rise in the eastern Gulf of Mexico region is affected by two main factors (Penland and Ramsey 1990): 1) global eustatic sea level rise, which is caused by melting of sea ice and thermal expansion of water (Munk 2003); and 2) reduced sedimentation, due to increased anthropogenic development and channelization of tidal rivers and creeks, which increase flow and reduce alluvial sediment inputs (Nordstrom 1994). In coastal Alabama, losses of alluvial inputs due to channelization and anthropogenic development have been largely offset by mitigation efforts and rates of relative sea level rise are occurring at about 0.15 cm yr^{-1}, approximately the rate of eustatic sea level rise (Penland and Ramsey 1990; Dokka 2005). Under current sea level rise projections, persistent, elevated salinity poses a major threat to coastal wetlands worldwide (Day et al. 2008).

Shrub-Encroached States as Alternate Pathways to Land Loss

The relationship between vegetation type and salinity tolerance may be a key factor in persistence of coastal wetlands. Without reintroduction of fire, woody species encroachment may continue to proceed along the gradient as far down as shrubs can tolerate salinity, potentially all the way down to intermediate or brackish marsh. Sediment accretion in *Morella*-dominated systems occurs less rapidly than in grass-dominated systems, which could potentially speed up regional relative sea level rise (Young et al. 2007). As relative sea levels continue to rise, salt stresses in areas currently within shrub species salinity tolerance may become too intense to allow scrub vegetation to persist. If shrubs occupy these areas as salinities increase, it is possible that they will provide biological filters to inward migration by salt- and brackish-marsh species (i.e., reductions in available rooting substrate, freshwater, and light), potentially driving the systems to open water. Thus, shrub-encroached coastal wetland states may not be stable, but rather serve as intermittent states occurring along an alternate, and less resistant, pathway to coastal land loss.

Prescribed Fire as an Ecological Management Tool

In systems where natural disturbance regimes have been disrupted, prescribed burning has been widely used as a means to return systems to their natural successional states. Prescribed burning is also considered an essential tool for limiting shrub expansion into shortgrass prairies (Brockway et al. 2002), tallgrass prairies (Bouressa et al. 2010) and savannas (Peterson and Reich 2001; Brockway and Lewis 1997). Fire has also been used to reduce cover density of *Morella* (Lewis and Harshbarger 1976). However, fire should not be considered a panacea and reintroduction of fire regimes should be performed in accordance with detailed planning and in order to achieve defined objectives (Hann and Bunnell 2001). *Morella* and other encroaching woody species are considered “fire endurers” or “fire survivors” because, although these shrub speces are easily top-killed by fire, their root crowns survive and often resprout following disturbances (Van Deelen 1991). The capacity of species to resprout in response to disturbances makes woody species-dominated communities more resistant to prescribed burning because infrequent fires are unlikely to have long-lasting effects if woody species can rapidly regain community dominance through resprouts (Lavorel 1999). Heisler et al. (2003) found that even annual fire could not reduce woody species abundance and cover in tallgrass prairie.

Prescribed Fire in Wetlands

Prescribed fire has been used extensively in wetlands. The National Park Service (NPS) suspended fire suppression in Everglades National Park in southern Florida in 1951 and has been prescribing burns there ever since to restore the natural disturbance regime (Kilgore 1976). Prescribed burning in brackish marshes in California resulted in greater plant community species richness, relative to null and mowing treatments (de Szalay and Resh 1997). Annual burning over a four year period in brackish and intertidal marshes in Maryland reduced litter and increased total biomass and stem density (Flores et al. 2011). It is also possible that interactions between fire and environmental factors, such as salinity and flooding, greatly impact the effects of fire (Nyman and Chabreck 1995; Flores et al. 2011).

Prescribed burns to combat shrub encroachment in wet prairies have had mixed results overall (Pendergrass et al. 1998), though repeated burns may reduce density and slow expansion (Clark and Wilson 2001). Drewa et al. (2002) found that southeastern U.S. pine savannas with fire regimes subjected to long-term shifts could not be restored simply by short-term prescribed burning.

Recent Disturbances and Fire History at Weeks Bay National Estuarine Research Reserve

Locally, disturbances have played an important role in shaping the communities present in the Weeks Bay estuary. In particular, two strong hurricanes, Ivan and Katrina, made landfall in successive years, in 2004 and 2005. Hurricane Ivan made landfall near Gulf Shores, AL (located approximately 20 km east of Weeks Bay NERR) as a Category 3 storm on 16 September 2004, with peak winds of 145 km hr^{-1} and a peak storm surge of 2.5 m. Hurricane Katrina made landfall near the Mississippi – Louisiana stateline as a category 4 storm on 29 August 2005; at Weeks Bay NERR, wind speeds peaked at 110 km hr^{-1} and storm surge peaked at 4.5 m and was sustained above 2 m over a period of five days (Lam et al. 2011). Remote sensing at Weeks Bay NERR demonstrated that, as of 26 November 2006 (approximately 15 months after Hurricane Katrina made landfall), the combined effects of these two hurricanes had resulted in a 52% decline of freshwater marsh (Lam et al. 2011). Satellite imagery also showed that estuarine emergent (tidal marsh) vegetation decreased 64% between 24 March 2005 and 28 April 2006 following Hurricane Katrina

(Rodgers III et al. 2009). Although storm surge events themselves last only a few days, soil salinities remain elevated for longer periods of time and recolonization by plants may be delayed or result in compositional shifts, particularly when wrack is deposited (Guntenspergen et al. 1995; Tate and Battaglia accepted).

In winter 2010, the Alabama State Lands Division and NOAA Weeks Bay NERR prescribed a surface fire in the wetlands along the coastal gradient at Weeks Bay for the first time since the reserve was established in order to manage the area and combat woody species encroachment into the fresh marsh. Species-level responses to these disturbances should include range expansions, contractions, and shifts. These differential responses at the species level may result in novel species assemblages that may be better equipped to maintain functional integrity (Hobbs et al. 2006; Monzón et al. 2011).

Given the historical role of fire and tropical storms in coastal wetlands (Nyman and Chabreck 1995), these disturbances may have increased salt- and brackish-marsh productivity and may have reduced species richness (Gucker 2008a; Walkup 2011). Disturbances farther up the gradient (where salinity becomes markedly reduced in the absence of tropical storm surge) likely shifted vegetation away from salt- and fire-intolerant woody species dominance and back towards herbaceous species, such as *Cladium* (Van Deelen 1991; Uchytil 1992a; 1992b; 1993; Hauser 2006; Coladonato 1992a). The mechanisms by which fire impacts this system include introducing intense heat, opening canopy, reducing biomass, and altering nutrient cycling rates, by burning plant material and removing the nitrogen-fixing *Morella cerifera*. The mechanisms by which hurricanes impact the system include strong winds, elevated soil salinities, and protracted periods of flooding.

Restoration Ecology and Threshold Dynamics in Degraded Systems

Restoration ecological theory holds that there is a theoretical “point of no return” at which restoration of the system is impractical (Palmer et al. 1997; Hobbs and Harris 2001). These critical thresholds occur where interactions between biotic and abiotic conditions at degraded sites drive feedback loops that further degrade the area (Suding et al. 2004). Overall, fresh marsh resilience to coastal squeezing depends on the capacity of communities to resist different types of changes at different ends of the gradient. At the low end, fresh marshes must resist the effects of climate change, chronic sea level rise and intensified hurricanes, which will likely cause abiotic shifts in soil salinities and hydrology (Brinson et al. 1995). At the upper end, fresh marshes must overcome biological legacies already in place due to woody species encroachment during the 20th century. The nitrogen-fixing properties and sprouting potential of encroaching woody species may drive feedback loops, thereby complicating restoration of herbaceous dominance. The role of disturbance interactions in maintaining coastal wetland resilience is unknown and it is possible that fire suppression and relative sea level rise have already driven this system past critical thresholds that may prevent restoration of resilience to further disturbances. Even assuming that the marsh can be restored, NOAA commitment to a regular prescribed burn regime may be essential to maintaining herbaceous dominance and resilience to sea level rise at Weeks Bay.

General Study Objectives

The wetlands at Weeks Bay NERR are broadly typical of estuarine wetlands throughout the northern Gulf of Mexico coast. It is virtually impossible to fully replicate landscape-scale natural disturbances and prescribed fires (Van Mantgem et al. 2001) and this series of disturbances presented the opportunity to study how sequential large-scale disturbances affected coastal wetland community composition and dominance at Weeks Bay NERR. This project sought to determine the importance of sequential disturbances in the maintenance of natural successional pathways in coastal wetland ecosystems; more specifically, the study used temporal data to investigate how two recent hurricanes, Ivan (2004) and Katrina (2005), and a prescribed fire (2010) have affected community composition and woody species abundance along the estuarine gradient at Weeks Bay NERR. As the way that species have responded to these disturbances is likely to be species-dependent, emergence of new communities or movement of pre-existing communities up or down the gradient has likely occurred. Compositional shifts in plant communities at Weeks Bay following this series of disturbances provided insight into the role of disturbance as an ecological driver in coastal plant communities. Emergent trends in woody species abundances across the gradient in 2004, 2006, and 2012 demonstrated that 21st century changes in coastal wetlands disturbance regimes could promote marsh expansion and reduce woody species encroachment.

The study did not attempt to disentangle the effects of reintroduction of fire from this backdrop of changing climate patterns; instead, it treated the reintroduction of fire as part of complex and interacting global, regional, landscape, and local changes and seeked to determine how these interacting changes may drive community-wide changes by differentially affecting individual species. The methods and results of these analyses are detailed in Chapters 2 and 3. The coastal wetlands along the northern Gulf of Mexico have important resource, historical, and cultural heritage value and perform anthropogenically important ecosystem services, such as buffering an economically important and socially developed area from the effects of periodic tropical storms (Day Jr. et al. 2005; Costanza et al. 2006). Persistence of these wetlands is currently threatened by a changing climate, rising sea levels, and anthropogenic development. Information gleaned from this study should inform coastal wetland management.

Predictions of Ecological Responses to Disturbance

Coastal wetland plant community response to multiple disturbances along the elevation gradient

I predicted that multiple large-scale disturbances (Hurricane Ivan in 2004, Hurricane Katrina in 2005, and the prescribed fire in 2010) resulted in plant community shifts throughout the gradient; these shifts were driven by reductions in less salt-and fire-tolerant species and increased dominance by halophytic and pyrophytic species. I predicted that the strong winds that occurred as a result of Hurricane Ivan and the intense and sustained storm surge from Hurricane Katrina suppressed some species that may be poorly adapted to strong winds, salinity pulses, and sustained flooding. Some species may be more vulnerable to the effects of fire and slow-growing species may respond less rapidly to increased nutrient availability, putting them at a competitive disadvantage compared with other species. As dominance by the species most vulnerable to strong winds, sustained flooding, salinity pulses, and fire damage likely varies along the elevation gradient, I predicted that the magnitude of these community shifts would be significantly correlated with distance from the tidal creek.

The nature of shifts in plant community composition

I predicted that increased light availability stimulated growth of the dominant salt-, brackish, and intermediate marsh species (i.e., *Spartina alterniflora*, *Juncus roemerianus*, *Panicum virgatum*), allowing them to outcompete some sensitive, sub-dominant species (*sensu* Levine et al. 1998) and driving overall species richness declines in the salt, brackish, and intermediate marshes following these disturbances.

In the freshwater parts of the gradient, I predicted that the strong winds of Hurricane Ivan likely damaged, and may have top-killed, many woody individuals. I also predicted that the intense and sustained storm surge that followed Hurricane Katrina suppressed less salt- and flood-tolerant species. I predicted that the effects of storm surge were likely intensified for woody individuals that were still recovering from wind damage sustained as a result of Hurricane Ivan. I predicted that woody species reductions created canopy gaps, promoting shade-intolerant dominant marsh species (i.e., *Cladium jamaicense*). As this fire burned while the community was still recovering from the effects of previous large-scale disturbances (i.e., Hurricanes Ivan and Katrina), its effects were likely intensified and may even have resulted in regime shifts in some areas from woody species dominated to herbaceous species dominated. I predicted that, although woody species richness decreased, herbaceous species richness increased, resulting in no significant changes in total species richness at the upper end of the gradient. I predicted that these recent disturbances have allowed plant species from downslope to colonize the higher end of the gradient, driving plant communities at higher elevations to become more similar to plant communities at lower elevations.

Woody species response to multiple large scale disturbances across the gradient

I predicted that overall shrub abundance across the gradient was greatest in 2004, before the disturbances, intermediate in 2006, following Hurricanes Ivan and Katrina, and lowest in 2012, following the hurricanes and the prescribed fire. I predicted that hurricanes would have the greatest impacts inland, where species were more vulnerable to elevated salinity and that hurricanes would have smaller impacts downslope. Conversely, I predicted that the effects of fire would be greatest downslope, where herbaceous fuels were continuously arranged and the fire likely burned more intensenly. I predicted that the effects of fire would be weakest upslope in the dense ecotone, where closed canopy conditions inhibit fire behavior and suppress growth of herbaceous fuels.

Specific Hypotheses

The expected effects of disturbance on both overall composition and woody species abundance lead to the following overarching hypotheses.

1) Coastal wetland plant community composition will shift following these multiple large-scale disturbances. The nature and magnitude of changes will be relative to position along the elevation gradient. At lower elevations, these changes will be driven by eliminations of some species and shifts in the ranges

of other species. At higher elevations, compositional changes will be driven by losses of woody species and upward shifts in the ranges of herbaceous species. Thus, as the ranges of downslope species shift upwards, upslope assemblages will become more similar to assemblages farther downslope.

2) Woody species abundance will be reduced throughout the gradient following hurricane and fire disturbances. Reductions as a direct result of the hurricanes should be greatest in upslope areas, whereas reductions due to the fire should be greatest in downslope areas. The hurricanes occurred several years prior to the fire. Thus, upslope areas, where I predict that hurricane impacts were stronger than fire impacts, have had a longer duration of time to recover from severe disturbance than downslope areas, where I predict that fire impacts were stronger than hurricane impacts. Therefore, overall ecological responses to these sequential disturbances are expected to be greater in downslope areas than upslope areas, though there will be drastic reductions throughout the gradient.

Description of Thesis Structure

The following two Chapters present data that address these hypotheses in detail. Chapter 2 provides details that address the first hypothesis. Data from Chapter 2 were gathered in 2004 and 2011 and focus on the incidence of vascular plant species at 35 long-term research plots along the estuarine gradient at Weeks Bay NERR. Data from Chapter 3 were gathered in 2004, 2006, and 2012 and focus on the abundance of woody plant species along a belt transect at Weeks Bay NERR. The final Chapter is a summary of this research with respect to the original hypotheses.

CHAPTER 2

CHANGING DISTURBANCE REGIMES AND COMPOSITIONAL DYNAMICS IN COASTAL WETLANDS

Abstract

During the 21st century, many coastal wetlands will be impacted by rising sea levels and increased tropical storm activity. Coastal areas are densely populated and fire suppression and landscape fragmentation have altered fire regimes, enabling woody species encroachment into historically herbaceous-dominated wetlands. Prescribed fire has been used to restore herbaceous dominance and could promote landward expansion of herbaceous species, enabling freshwater marshes to keep pace with increasingly saline conditions. Changes in interacting disturbance patterns will undoubtedly cause compositional shifts, though the functional impacts of shifts remains unclear. This study examines a fire-suppressed wetland complex along the Northern Gulf of Mexico before and after three major, sequential, landscape-scale disturbances (Hurricanes Ivan and Katrina in 2004 and 2005, and a prescribed fire in 2010). I investigated how these disturbances differentially affected plant communities across an elevation gradient (saltmarsh to marsh-scrub ecotone) and whether disturbances favored migrations of entire assemblages or differentially affected species, resulting in novel communities. The gradient was divided into sections 10 cm in elevation (saltmarsh, low brackish marsh, high brackish marsh, intermediate marsh, fresh marsh, sparse marsh-scrub ecotone, and dense marsh-scrub ecotone); five 100 m^2 plots were established in each zone (n=35) and sampled for vascular plant species incidence.

Following the disturbances, overall saltmarsh species richness and understory woody species richness declined significantly. NMDS ordination and ANOSIM testing revealed that significant compositional shifts occurred in the saltmarsh, brackish marshes, and the sparse and woody ecotones. Vector-fitting and indicator species analyses suggested that shifts between years were not driven by unidirectional movements of whole assemblages up or down the gradient but rather by the disappearance of species that were present in 2004, the appearance of new species in 2011, and species-specific range expansions, contractions, and migrations. Compositional shifts in intermediate and fresh marsh areas were not significant. These findings suggest that changes in disturbance patterns during the 21st century may maintain herbaceous-dominated oligohaline wetland ecosystems while simultaneously driving successional pathways towards *de novo* species assemblages (i.e., assemblages of species whose ranges do not currently overlap) at the upper end of the coastal gradient and species-poor saltmarsh assemblages. Further study is needed to determine whether compositional shifts are indicative of coastal wetlands able to keep pace with climate change or are concomitants of critical shifts in ecosystem function ultimately on a trajectory towards degradation.

Introduction

Ecosystem Resilience in Coastal Wetlands

Ecological resilience in coastal wetlands is declining because rising sea levels, elevated tidal salinities, and storm surges of longer durations and higher salinities place ecosystems along coastal gradients at the tipping points of state changes toward open water and/or halophyte-dominated systems (Brinson et al. 1995; Michener et al. 1997;

Shirley and Battaglia 2008). At the same time, anthropogenic use throughout the world is concentrated within coastal systems (Small and Nicholls 2003), causing them to become trapped between the effects of climate change at the seaward end and rapid conversion for anthropogenic use at the landward end (Pethick 1993). The term "coastal squeeze" has typically referred to loss of saltmarsh to urbanization and sea level rise (Doody 2004) but the concept can be applied to co-occurring threats to other wetlands along the gradient as well (Brinson et al. 1995), such as fresh marsh caught between abiotic shifts in salinity due to increased tidal intrusion and biotic shifts in community dominance towards woody species caused by fire suppression (Shirley and Battaglia 2006). Squeezing of coastal assemblages reduces landscape heterogeneity and could potentially alter ecological responses following future disturbances and climatic shifts (Harley et al. 2006; Shirley and Battaglia 2006).

Changes in disturbance regime and community dominance shifts

Modern successional theory has embraced disturbance as an important factor in succession at local, regional, and landscape levels (Clark 1991) for almost half a century (Pickett et al. 2009). In many cases, the effects of historical and current disturbance patterns (i.e., site legacies and current regimes) may be stronger drivers of vegetation physiognomy than the effects of local or regional climate (Jackson 1968; Bond et al. 2004; Gilliam et al. 2006). Deviation from historical disturbance regimes can result in shifting successional patterns. Fire suppression was an integral part of municipal, state, and federal level ecosystem management in the early part of the 20th century (Stephens and Sugihara 2006) and exclusion of fire through both direct (deliberate suppression) and indirect (e.g., landscape fragmentation) means has enabled woody species encroachment into historically herbaceous systems such as prairies (Leach and Givnish 1996) and marshes (Nyman and Chabreck 1995). Long-term fire suppression relative to historical regimes can drive fire-dependent ecosystems to alternate states (Petraitis and Latham 1999). Fire is only one type of disturbance and real-world disturbance regimes incorporate variation in disturbance type, frequency, intensity, and extent resulting not only from biotic (e.g., plant community impacts on fire regimes), abiotic (e.g., climate impacts on fire regimes), and random factors (e.g., sources of random ignitions), but also from the interactions between these factors and previous disturbances of the same and different types (e.g., climate impacts on disease vectors affecting ignition probabilities; Simenstad et al. 2006).

When large, infrequent disturbances (*sensu* Turner and Dale 1998), such as Category 4 and 5 hurricanes (Conner et al. 1989), become superimposed on systems already degraded by anthropogenic activity (e.g., fire-suppression), they may dramatically accelerate the rates of state changes and render ecosystem recovery impossible (Conner et al. 1989; Paine et al. 1998; Hobbs 1999). Once major state changes have occurred, “self-organizing” landscape vegetation patterns (Shachak et al. 2008) may make restoring ecosystems to previous states virtually impossible because they require perturbations at unrealistic scales (Suding et al. 2004). Conversely, while the underlying mechanisms by which different disturbances may affect population- and community- dynamics may differ, they may result in structurally and functionally similar communities (Laska 2001). If so, interactive effects between sequential large-scale disturbances could potentially promote long-term ecosystem stability.

The use of prescribed burning to reintroduce fire as an ecological driver of herbaceous dominance in prairies has been well-studied (Howe 1995; Brockway et al. 2002). Although historical accounts document frequent use of fire in coastal wetlands (Lynch 1941; Nyman and Chabreck 1995) and the U.S. government has burned wetlands since the National Park Service first burned sawgrass (*Cladium jamaicense*) marshes in the Everglades back in the 1950s, the effects of fire on coastal landscape dynamics remain poorly described (Nyman and Chabreck 1995; Flores et al. 2011).

Coastal wetlands are often regularly arranged in zones across elevation gradients (Eleuterius and McDaniel 1978; Odum 1988; Crain et al. 2004). At low elevations, assemblages are comprised of extremely productive flood- and salt-tolerant species (Levine et al. 1998); with increasing elevation, species less tolerant of flooding and salt stress become more abundant (Waide et al. 1999). Although the communities along these gradients are not discrete, commonly recognized treeless communities (in order of increasing elevation) include salt-, brackish-, and freshwater-marshes. Farther up the gradient, freshwater marshes grade into a primarily open canopy, sparsely wooded marsh-scrub ecotone (Battaglia et al. 2012). This sparsely wooded ecotone then grades into a densely wooded marsh-scrub ecotone, which, in turn, grades into closed canopy seep-, bottomland-, and mesic- forests (Cowardin et al. 1979; Battaglia et al. 2012).

This study examined a fire-suppressed coastal wetland complex along the Northern Gulf of Mexico and seeked to determine how the combined effects of increased tropical storm activity and the reintroduction of fire affected the communities across this elevation gradient. Fire suppression along the northern Gulf of Mexico coast has allowed woody species encroachment into the historically herbaceous-dominated communities at the low end of the gradient (Shirley and Battaglia 2006; Shirley and Battaglia in preparation). Rising sea levels and increasingly frequent intense climatic disturbances (e.g., tropical storms, droughts) are also being superimposed on this legacy of fire suppression and ecotone expansion. Intense hurricanes have already begun to increase in frequency in the Pacific basin (Webster et al. 2005) and are projected to increase in frequency in the Atlantic basin as well (Bender et al. 2010). I did not attempt to disentangle the effects of reintroduction of fire from the backdrop of changing climate patterns; instead, I considered the reintroduction of fire as part of complex global, regional, landscape, and local changes and seeked to determine how these changes may drive community changes.

Recent changes in interacting disturbance patterns may have already driven compositional shifts. This study examined the effects of three major, sequential, landscape-scale disturbances (Hurricanes Ivan and Katrina in 2004 and 2005, and a prescribed fire in 2010) along a coastal elevation gradient. I hypothesized that I would find significant compositional shifts throughout the gradient. If ecological responses to disturbances differed at the community, rather than the species, level, then disturbances favored migrations of entire intact assemblages. However, I expected species responses to disturbances to be idiosyncratic. Thus, I predicted that disturbances would drive species range shifts and give rise to assemblages comprising species whose ranges did not previously overlap.

I also hypothesized that compositional shifts in the lower part of the gradient would be driven by losses of species based on the prediction that dominant, highly productive salt- and brackish marsh plants (e.g., *Spartina alterniflora*, *Juncus roemerianus*) would be stimulated by the fire and increase in abundance, allowing them to outcompete other, less productive species. I also expected that disturbances would reduce woody species richness in the marsh-scrub ecotone and these losses of woody species would drive compositional shifts. Woody species richness tends to be greatest in the upslope areas. Thus, I hypothesized that losses of woody species from upslope parts of the gradient would drive compositional convergence in the marsh-ecotone zone.

Methods

Site Description

The study was conducted at the Weeks Bay National Oceanic and Atmospheric Administration (NOAA) National Estuarine Research Reserve (hereinafter, Weeks Bay NERR). Weeks Bay NERR is a small estuarine system nested within the much larger Mobile Bay estuary on its eastern shore and geographically located approximately 35 km southeast of Mobile, AL and across Mobile Bay at approximately 30.41° N, 87.83° W. The preserve covers approximately 2650 ha, 25% of which are occupied by terrestrial and wetland ecosystems. That Weeks Bay estuary is nested within Mobile Bay somewhat buffers the site from tidal influences and tidal variance at Weeks Bay NERR is just 0.3 to 0.5 m (Lam et al. 2011). Local landform may also reduce the frequency of short-duration storm surges, though it does not reduce the intensity or duration of surges following more intense storms (Huang 2009). Site-specific geographic characteristics (i.e., freshwater inputs and protection from tidal influences) have important compositional effects because they suppress downslope salinities and may affect where ecological zones occur relative to eustatic sea level (Rodgers III et al. 2009; Lam et al. 2011; Battaglia et al. 2012). In broader ecological contexts, however, the communities found at Weeks Bay are similar to those found throughout much of the northern Gulf of Mexico region (Lot 2004). This study focused on the salt, brackish, and freshwater marsh and freshwater marsh-scrub ecotone zones. In June 2004, two transects were established across the elevation gradient at Weeks Bay NERR. Along the first transect, established at a low-lying spit and accessible by boat only, five 100 m^2 long-term community composition survey plots were established at elevations -10 cm and 0 cm above mean high tide (hereinafter “sea level”). Along the second transect (main transect), five 100 m^2 long-term community composition survey plots were established at elevations of 10 cm, 20 cm, 30 cm, 40 cm, and 50 cm above sea level. Thus, there were 35 plots across seven elevation zones. The elevation zones were roughly associated with vegetation zones; halophytic species were dominant at -10 cm, fresh marsh species were dominant at 30 cm, and tree and shrub species were dominant at 50 cm (Figure 2.1). Communities along the gradient between these zones were mixtures of these assemblages.

Figure 2.1: Transects and plots superimposed onto Google Earth™ satellite imagery. The image was captured 31 Jan. 2008, following the hurricanes but prior to the fire. Plots are shown as squares. Plots in -10 and 0 cm elevation classes were established perpendicular to the spit transect and plots in 10, 20, 30, 40, and 50 cm elevation classes were established perpendicular to the main transect.

Weeks Bay NERR has been subjected to numerous large-scale disturbances since 1985 (Figure 2.2). Prior to 2004, Weeks Bay had not been affected by tropical storms since Hurricanes Danny and Georges made landfall in 1997 and 1998, respectively. Hurricane Danny made landfall in nearby Mullet Point, Alabama as a Category 1 storm on the Saffir-Simpson scale, with wind speeds at Weeks Bay NERR estimated at 112 km hr^{-1}. Hurricane Georges made landfall near Biloxi, Mississippi as a Category 2 storm on the Saffir-Simpson scale, with wind speeds at Weeks Bay NERR estimated at 72 km hr^{-1} (Rodgers III et al. 2006). Two strong hurricanes, Ivan and Katrina, made landfall in successive years, in 2004 and 2005. Hurricane Ivan made landfall near Gulf Shores, AL (located approximately 20 km east of Weeks Bay NERR) as a Category 3 storm on the Saffir-Simpson scale on 16 September 2004, with peak winds of 145 km hr^{-1} and a peak storm surge of 2.5 m. Less than a year later, Hurricane Katrina made landfall near the Mississippi – Louisiana state line as a category 4 storm on 29 August 2005; at Weeks Bay NERR, wind speeds peaked at 110 km hr^{-1} and storm surge peaked at 4.5 m and was sustained above 2 m over a period of five days (Lam et al. 2011). In February 2010, the Alabama Department of Conservation and Natural Resources State Lands Division, in cooperation with the NOAA Weeks Bay NERR, prescribed surface fires in these wetlands for the first time since the reserve was established in 1986 (Miller-Way et al. 1996) to promote marsh productivity and combat woody species encroachment into the fresh marsh and marsh-scrub ecotone. The fire burned most intensely in herbaceous-dominated areas and burned only sporadically in the closed-canopy dense ecotone (Scott Phipps personal communication). Fully replicating studies incorporating unpredictable landscape-scale natural disturbances is not feasible (Van Mantgem et al. 2001); thus, this study used a time-series design (Before *vs*. After) to determine how coastal wetland plant communities along this elevation gradient changed following these three large-scale disturbances.

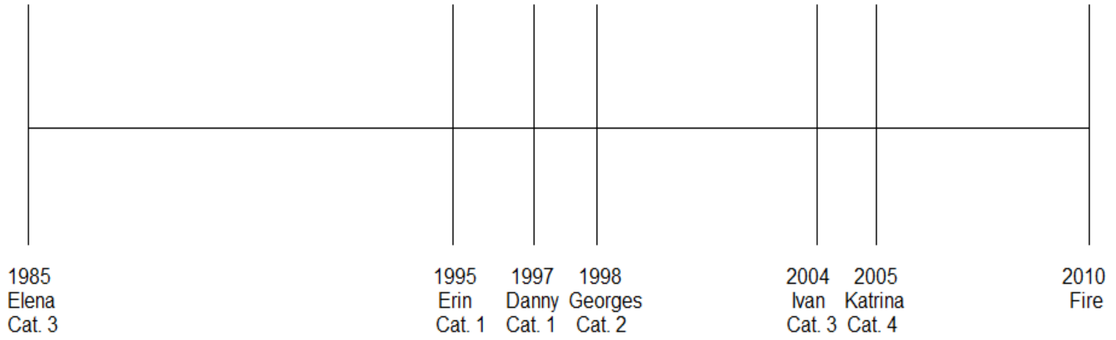

Figure 2.2: Timeline of major disturbances at Weeks Bay NERR since 1985. Hurricane categories are given according to the Saffir-Simpson scale.

Species Composition Surveys

To determine the effects of these large-scale disturbances on woody species encroachment and plant community composition in each of the vegetation zones, all composition plots were surveyed for species incidence in June 2004 and October 2011. When field identification was not possible, voucher specimens were collected and identified to species using dichotomous keys. When voucher specimens were unavailable, species were differentiated into unique morphospecies.

Statistical Methods

Mixed effects models were performed using SAS v. 9.2 (PROC MIXED; SAS Institute 2007), quadratic regression analyses were performed using SigmaPlot v.11.0 (Systat Software Inc. 2008), and all other univariate statistical testing was performed using R v. 2.12.1 (Team RDC 2010). Multivariate community ordination and statistical testing was performed using the R vegan package (Oksanen et al. 2005) and the DECODA package (Minchin 1989). Indicator species analyses were performed using the R indicspecies package (De Cáceres and Jansen 2012). The Bray-Curtis dissimilarity index was used to estimate ecological distance of plots from one another (Faith et al. 1987).

Spatial and Temporal Trends in Species Richness

Two-way linear mixed effects model (PROC MIXED) Analysis of Variance (ANOVA) tests were used to test whether there were differences between years and elevation classes in species richness using fixed effects of elevation and year and a random effect of plot nested within elevation class. Two-way mixed effects model ANOVA tests were also used to determine the effects of year and elevation class on woody species richness in the understory. When interactions between elevation and year were significant, *post-hoc* comparisons of interaction means (Tukey tests for multiple comparisons) were used to determine whether differences across years within elevation classes were significant. The Tukey-Kramer method of correction was used to adjust p-values (Hayter 1984). Mean species richness was plotted against elevation class to demonstrate trends in species richness across the elevation gradient.

Compositional trends across the gradient

Non-metric multidimensional scaling (NMDS) ordination was used to explore trends in plant community composition across the elevation gradient in each year and across both years (Minchin 1987). Spearman (non-parametric) correlation tests were used to determine whether position along the one-dimensional NMDS axis was significantly correlated with elevation within and across years (Van Eck and Waltman 2009). Analysis of similarity (ANOSIM) permutation testing was used to statistically test whether community composition differed across elevations within each year and across years along the entire gradient (Clarke 1993). Pairwise ANOSIM tests were used to statistically determine the significance of community differences between elevation classes within each year and the significance of differences between years within each elevation class. The p-values for pairwise ANOSIM tests were not adjusted.

Compositional Trends Within Elevation Class Groupings

NMDS ordination was also used to explore trends in plant community composition across years. Preliminary ordinations indicated that the effects of year were obscured in one-dimensional ordination due to strong trends across elevation classes. At the same time, due to extreme β-diversity across the gradient, preliminary two-dimensional ordinations were distorted (the arch effect; Brehm and Fiedler 2004). Thus, to explore compositional trends following the disturbances, the gradient was separated into three sections, each spanning three elevation classes (-10 cm to 10 cm, 10 cm to 30 cm, 30 cm to 50 cm). Sectioning the gradient reduced two-dimensional distortion, allowing temporal trends to emerge. Vector-fitting of explanatory variables, a method of multiple linear regression that determines the direction of maximum correlation between a fitted variable and community composition (Kantvilas and Minchin 1989) was used to determine the significance and strengths of correlations between community location in ordination space and elevation and year. Indicator species analyses, which take both the constancy of a species in a particular site or treatment and the fidelity of that species to that specific site or treatment into account (Dufrêne and Legendre 1997), were performed by year to determine which species were significantly more common prior to or following disturbances. Multi-levels indicator species analyses, which group site classes together to determine the group of site classes that maximizes the indicator value for each species (De Cáceres et al. 2010), were also performed by elevation class for 2004 and 2011 data to determine which species occupied different parts of the gradient before *vs.* after disturbances. The Bray-Curtis dissimilarity index was also used to estimate the magnitude of compositional divergence following the disturbances. To determine the significance of the relationship between elevation and the magnitude of compositional shifts before and after the disturbances, quadratic regression was used, with 2004 – 2011 Bray-Curtis dissimilarity as the response variable and elevation as the predictor variable.

Results

The Effects of Year and Elevation on Species Richness

There was a significant interaction effect of year and elevation on species richness (F = 6.45, df = 28, p = 0.0002; Figure 2.3). Within elevation classes, *post-hoc* comparisons of richness means within each elevation – year showed that species richness declines were significant in the -10 cm elevation class (t = 6.67, p < 0.0001). The effects of year on species richness were not significant in the 0 cm (t = 3.03, p = 0.2027), 10 cm (t = 0.76, p = 0.999), 20 cm (t = 0.57, p = 1.000), 30 cm (t = 1.89, p = 0.0654), 40 cm (t = 3.60, p = 1.000) and 50 cm (t = 1.89, p = 0.8267) elevation classes (Figure 2.4).

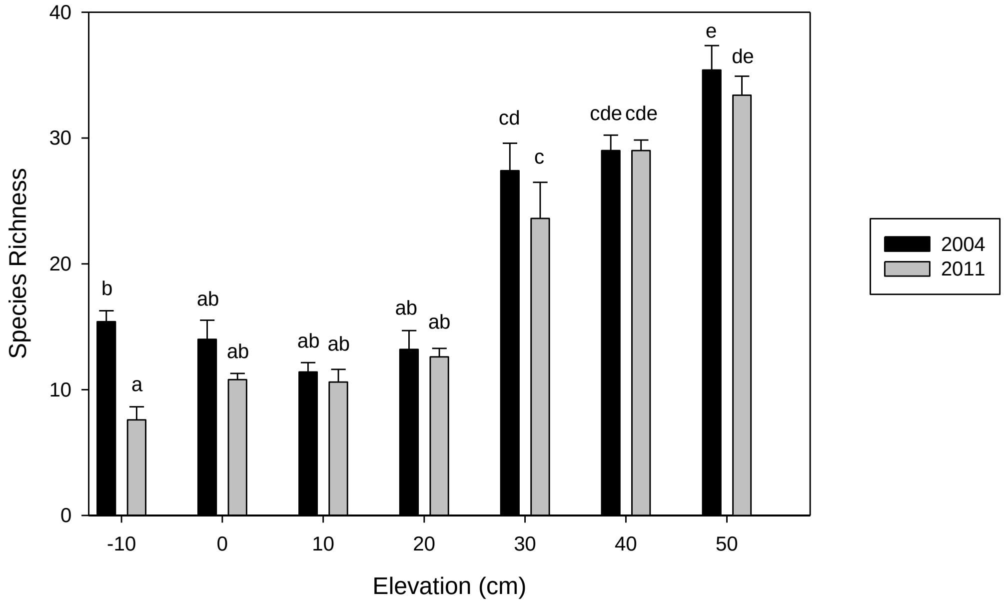

Figure 2.3: Species richness (mean ± SE) with respect to elevation class and year. The elevation classes are given across the independent axis. Solid black bars indicate species richness within each elevation class in 2004 and solid gray bars indicate species richness within each elevation class in 2011.

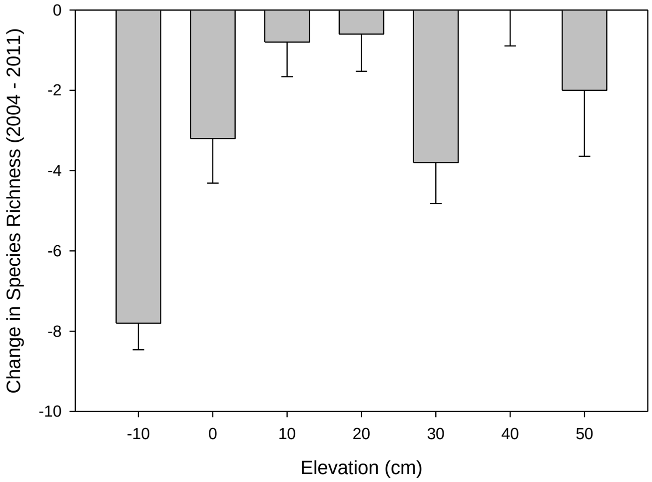

Figure 2.4: Changes in species richness between 2004 and 2012 for each elevation class. Error bars indicate standard error. Changes in the -10 cm elevation zone were significant. Changes in other elevation zones were not statistically significant.

There was a significant interaction effect between year and elevation on understory woody species richness in 100 m^2 plots ($F = 18.24$, $df = 6$, $p < 0.0001$; Figure 2.5). The effects of elevation on understory woody species richness were significant ($F = 62.31$, $df = 6$, $p < 0.0001$) and the overall effects of year were also significant ($F = 60.76$, $df = 1$, $p < 0.0001$).

Within elevation classes, *post-hoc* comparisons of woody species richness means within each elevation – year showed that woody species richness did not decline significantly in the 30 cm zone ($t = 2.08$, $p = 0.3587$), but did decline significantly in the 40 cm ($t = 4.41$, $p < 0.0085$) and 50 cm ($t = 7.01$, $p = 0.0002$) zones (Figure 2.6).

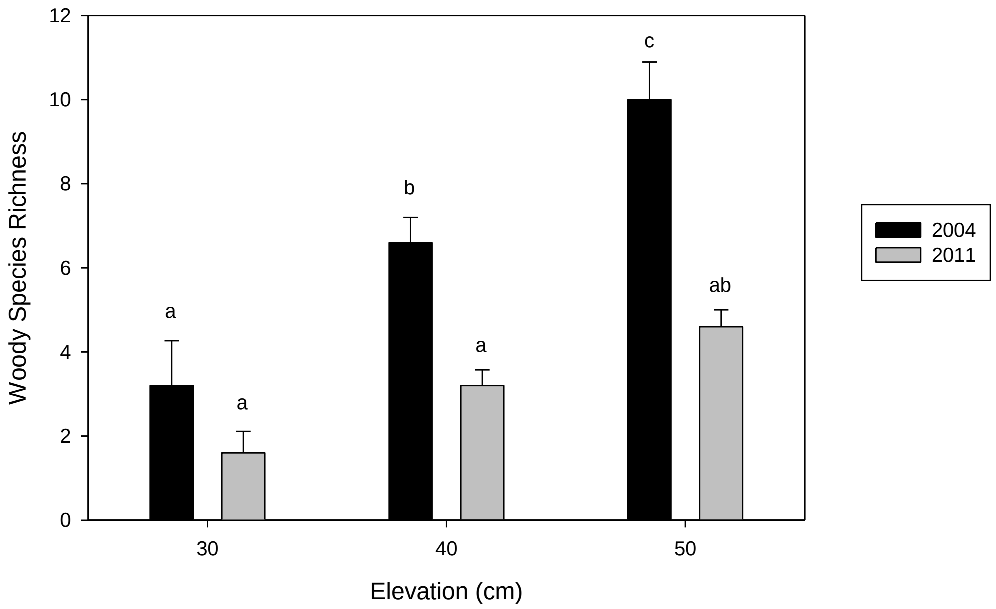

Figure 2.5: Woody species richness (mean ± SE) with respect to elevation class and year. The elevation classes are given across the independent axis. Solid black bars indicate woody species richness within each elevation class in 2004 and solid gray bars indicate woody species richness within each elevation class in 2011. There were no woody species present in the understory of the -10, 0, 10, or 20 cm elevation classes.

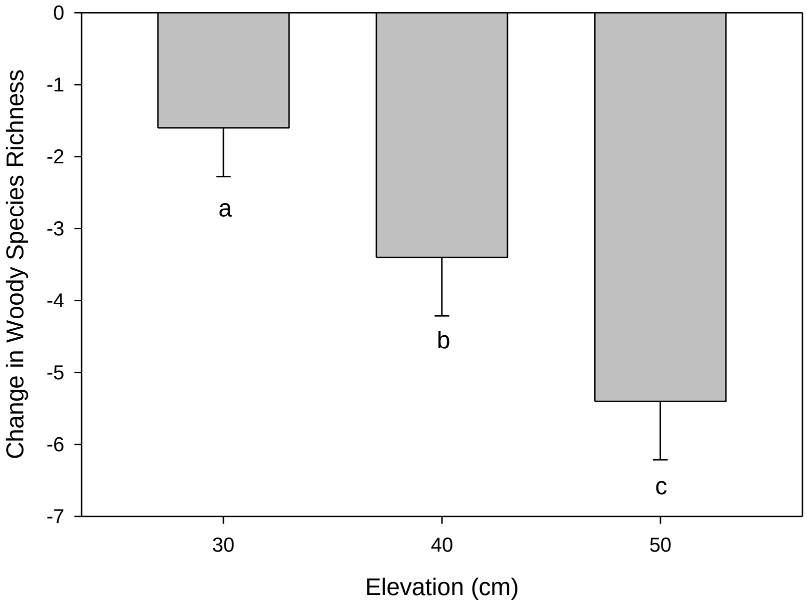

Figure 2.6: Changes in mean woody species richness between 2004 and 2012 for each elevation class. Error bars indicate standard error. Changes in the 40 cm and 50 cm elevation zones were significant. Changes in the 30 cm elevation zone were not significant.

Trends in Community Composition Across the Gradient

One dimensional NMDS ordination was sufficient to describe trends in community composition across the gradient and both years (stress = 0.1320; Figure 2.7). Spearman rank correlation tests indicated that position along the one dimensional NMDS axis was significantly correlated with elevation in 2004 ($\rho = 0.9363$; $p < 0.0001$), 2011 ($\rho = 0.9632$; $p < 0.0001$), and across both years ($\rho = 0.9364$; $p < 0.0001$). Results of ANOSIM tests indicated that community composition across the gradient did not differ significantly between years (R = 0.0189, p = 0.1442).

ANOSIM testing confirmed that differences in community composition along the elevation gradient were significant in 2004 (R = 0.8953, p < 0.0001), 2011 (R = 0.9110, p < 0.0001), and across both years (R = 0.8719, p < 0.0001). Pairwise ANOSIM tests indicated that community composition in each elevation class differed significantly from community composition in each other elevation class across both years and within each year (Appendix 2A).

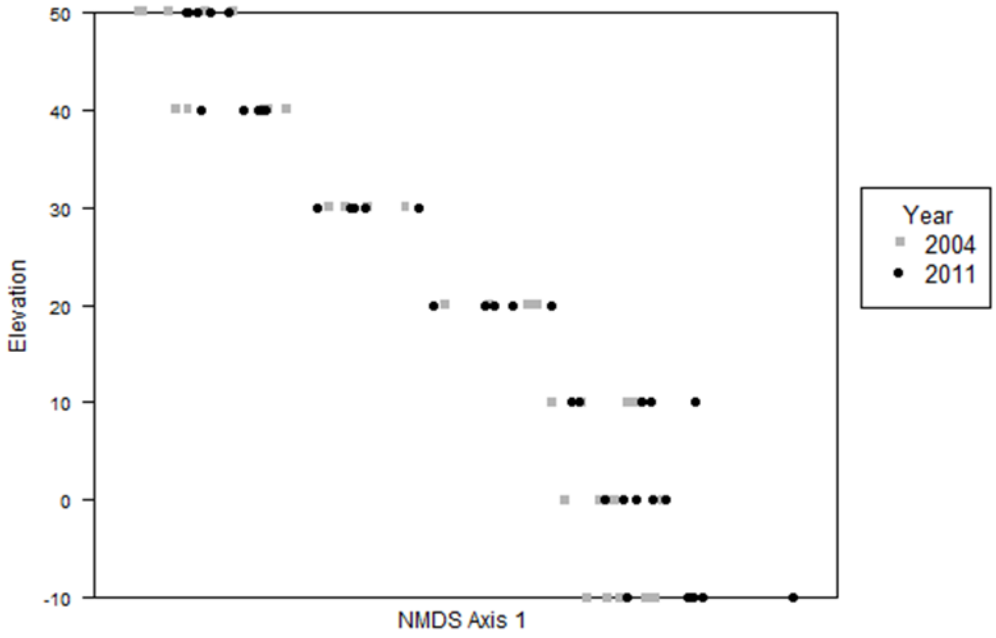

Figure 2.7: One dimensional NMDS ordination of all plots along the gradient in both years. Ordination scores are plotted on the x-axis and elevation is plotted on the y-axis.

Trends in Community Composition Within Elevation Classes

ANOSIM testing indicated that community composition differed significantly between years in elevation classes in the upper and lower parts of the gradient but not in the intermediate portion (Table 2.1), with significant shifts occurring in the -10 cm, 0 cm, 10 cm, 40 cm, and 50 cm elevation classes. ANOSIM testing indicated that community composition did not differ significantly between 2004 and 2011 in the 20 cm and 30 cm elevation classes. However, there was no significant effect of elevation on the magnitude of floral community dissimilarity from 2004 to 2011 (quadratic regression: F = 1.02, df = 34, p = 0.3201; Figure 2.8).

Table 2.1: Results of ANOSIM tests comparing community composition within each elevation class in 2004 to community composition within the same class in 2011.

Elevation Class	Results of ANOSIM testing	Significance
-10	R = 0.8360	$p < 0.0001$
0	R = 0.5580	$p < 0.0001$
10	R = 0.2520	p = 0.0395
20	R = 0.0780	p = 0.2751
30	R = 0.0704	p = 0.0704
40	R = 0.7260	$p < 0.0001$
50	R = 0.4700	p = 0.0082

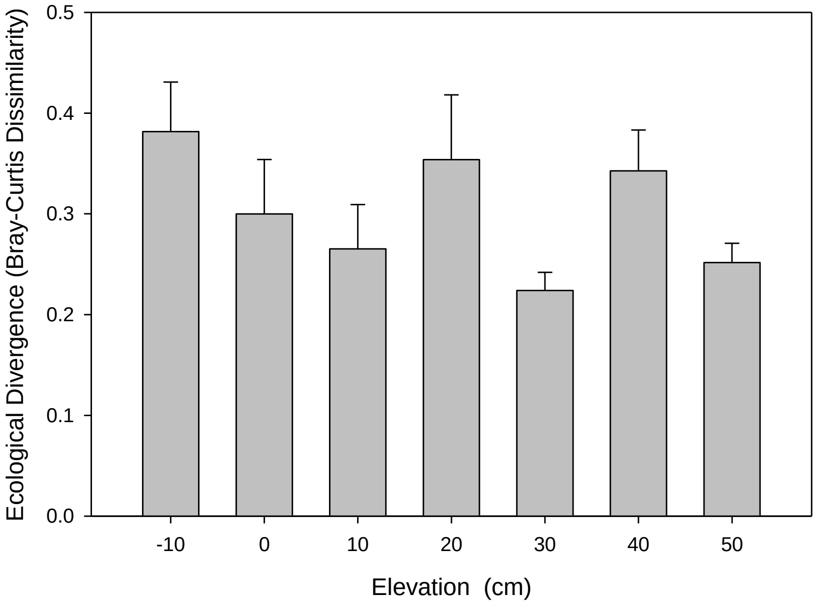

Figure 2.8: Barplot of the magnitude of ecological distance (as estimated by Bray-Curtis dissimilarity) between each community in 2004 and the same community in 2011 separated out by elevation class. There was no significant relationship between elevation and compositional divergence.

Trends in Community Composition Across Years and Elevations

Two dimensional NMDS ordination was sufficient to describe trends in community composition across years in elevation class groupings -10 cm, 0 cm, and 10 cm (salt and brackish marsh; Figure 2.9a), 10 cm, 20 cm, and 30 cm (intermediate and fresh marsh; Figure 2.9b), and 30 cm, 40 cm, and 50 cm (marsh-scrub ecotone; Figure 2.9c). Vector-fitting showed that both year ($r = 0.5256$, $p = 0.002$) and elevation ($r = 0.4166$, $p = 0.003$) were highly significant explanatory variables for the salt and brackish marsh. In the intermediate and fresh marsh, elevation ($r = 0.8858$, $p < 0.001$) was a highly significant explanatory variable but the relationship between year and community position in ordination space was not significant. Both year (r = 0.6592, p < 0.001) and elevation (r = 0.8323, p < 0.001) were highly significant explanatory variables in the marsh-scrub ecotone.

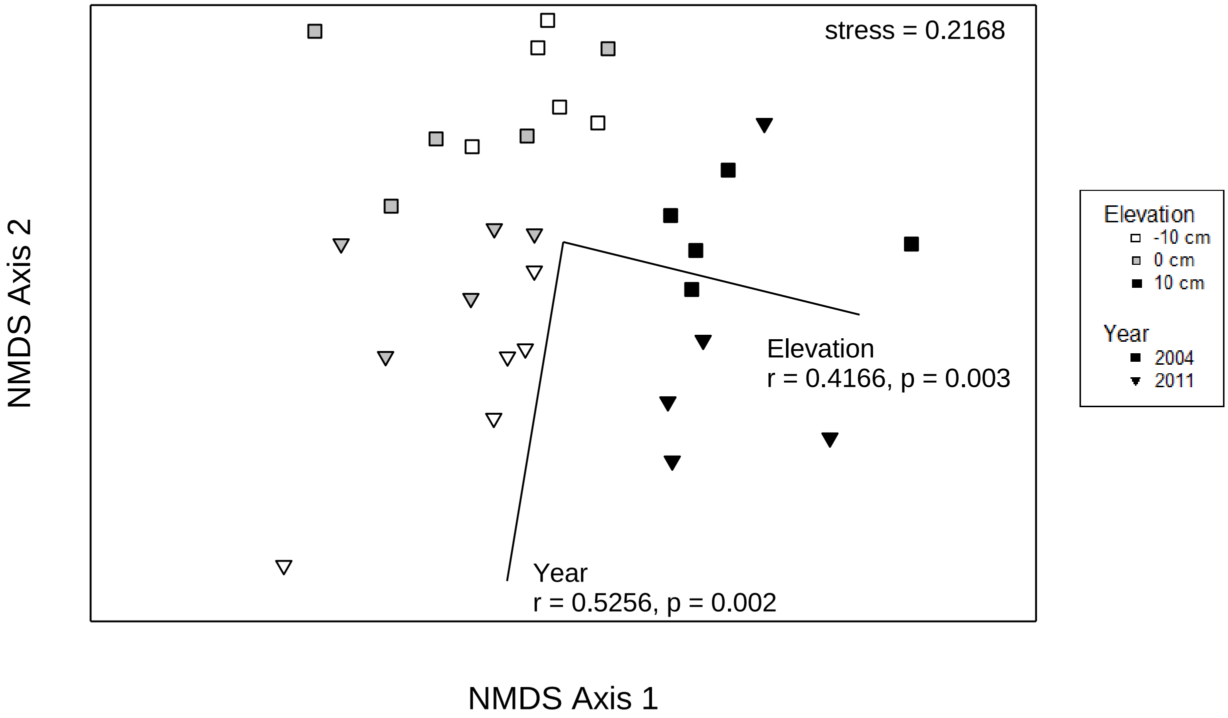

Figure 2.9a: Two-dimensional NMDS ordination (stress = 0.2168) showing plots from elevation classes -10 cm, 0 cm, and 10 cm in 2004 and 2011. Vectors for elevation and year are superimposed on the ordination.

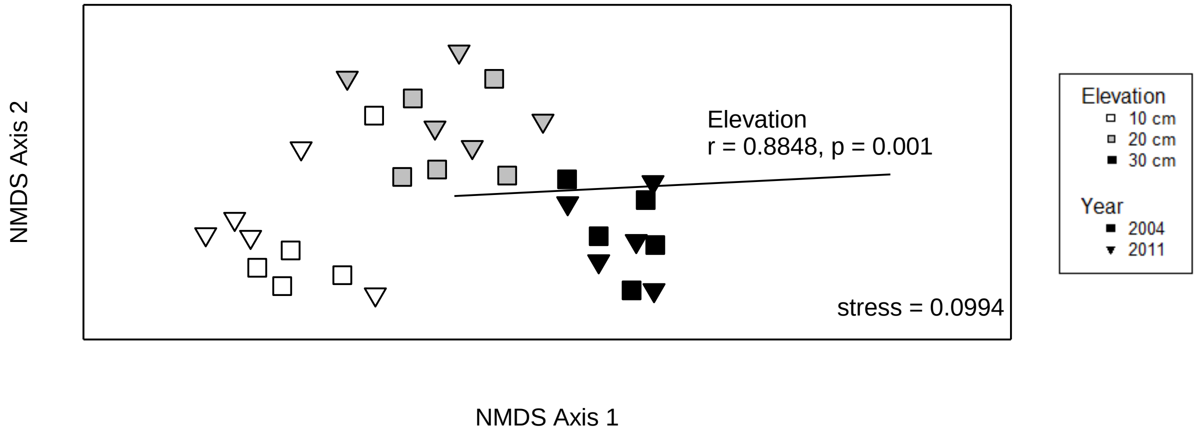

Figure 2.9b: Two-dimensional NMDS ordination (stress = 0.0994) showing plots from elevation classes 10 cm, 20 cm, and 30 cm in 2004 and 2011. A vector for elevation is superimposed on the ordination. Vector-fitting permutation tests suggest that year was not significantly correlated with composition.

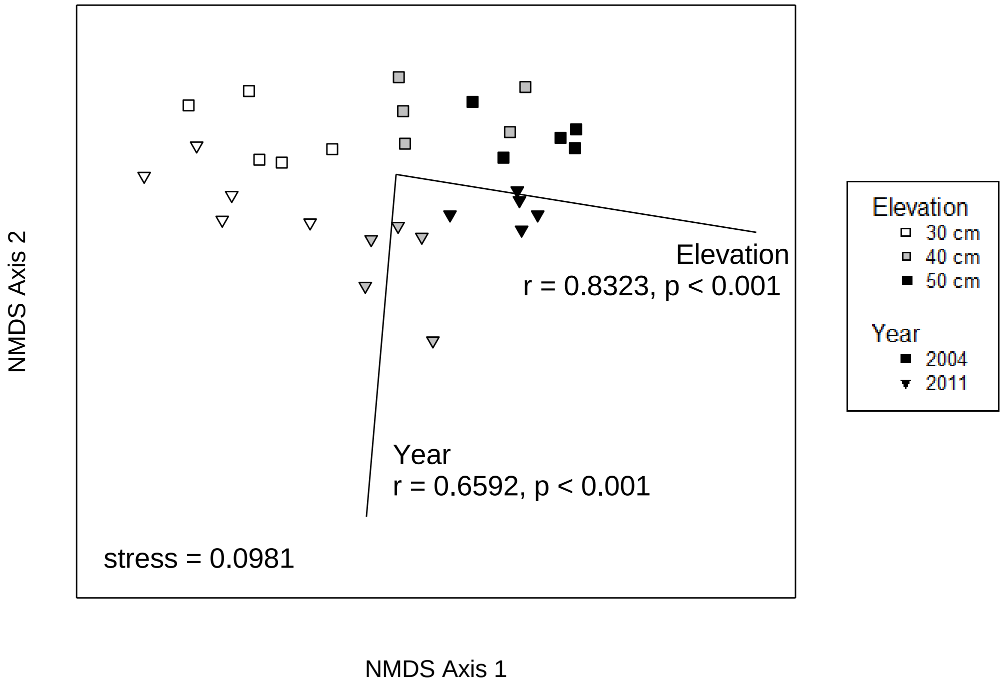

Figure 2.9c: Two-dimensional NMDS ordination (stress = 0.0981) showing plots from elevation classes 30 cm, 40 cm, and 50 cm in 2004 and 2011. Vectors for elevation and year are superimposed on the ordination.

Indicator Species Analyses

There were four taxa that were significant indicators of the 2004 community and three taxa that were significant indicators of the 2011 community (Table 2.2). Species that were significant indicators in 2004 were: *Nyssa biflora*, *Polygonum amphibium*, *Saururus cernuus*, and *Scirpus robustus*. In 2004, *N. biflora*, a woody species, and *S. cernuus*, an herbaceous species, were both significant indicators of the 40 cm and 50 cm zones. *P. amphibium* and *S. robustus*, on the other hand, were found at the low end of the gradient. *S. robustus*, a significant indicator of the -10 cm zone in 2004 was found farther up the gradient in 2011, whereas *P. amphibium*, an indicator of the -10 cm, 0 cm, and 10 cm zones in 2004, was not located in 2011 at all. Taxa that were significant indicators of the 2011 community were: *Amaranthus spinosus*, *Cyperus strigosus*, and *Spartina alterniflora*. In 2011, *A. spinosus* and *C. strigosus* were both significant indicators of communities in the upper portion of the gradient, with *A. spinosus* an indicator of the 40 cm zone and *C. strigosus* a significant indicator of the 30 cm, 40 cm, and 50 cm zones. Although *S. alterniflora*, a dominant saltmarsh species, was found in 2004, it was much more prevalent in 2011.

Table 2.2: Taxa that were significant indicators of year, the years for which they were significant indicators, and their growth habits. Indicator values are based on constancy and fidelity and are calculated as per Dufrêne and Legendre (1997).

Species	2004	2011	Growth Habit
Nyssa biflora	IV = 0.4140, p = 0.026		Tree
Polygonum amphibium	IV = 0.4780, p = 0.007		Forb
Saururus cernuus	IV = 0.5071, p = 0.004		Forb
Scirpus robustus	IV = 0.4587, p = 0.05		Graminoid (Sedge)
Amaranthus spinosus		IV = 0.4781, p = 0.009	Forb
Cyperus strigosus		IV = 0.5855, p = 0.001	Graminoid (Sedge)
Spartina alterniflora		IV = 0.6126, p = 0.008	Graminoid (Grass)

Many species that were significant indicators of elevation classes in 2004 remained significant indicators of the same elevation classes in 2011, while other species expanded, contracted, or migrated up or down the gradient (Table 2.3). Some species that were significant indicators of the communities at an elevation class in 2004 were not located at all (e.g., *Polygonum amphibium*) or were located but not significant indicators (e.g., *Scirpus robustus*) in 2011. In some cases, range contractions resulted in some species, such as *Aster tenuifolius*, losing their indicator status in some elevation classes but maintaining it in others, and expansions resulted in some species (e.g., *Cladium jamaicense*) becoming significant indicators of communities in elevation classes where they had not been in 2011.

Table 2.3: Species that were significant indicators of elevation class, separated out by year. Elevation classes for which species were significant indicators for 2004 are shown with a solid line, elevation classes for which species were significant indicators for 2011 are shown with a dashed line. * denotes that the species was present in the corresponding year but was not a significant indicator of any elevation class. ** denotes that the species was not located in the study during the corresponding year. For species that were significant indicators of year, the year for which they were significant indicators is in parentheses.

Species	-10	0	10	20	30	40	50
Spartina alterniflora (2011)	— - - -	- - -	- - -				
morphospecies (1)	— **						

Table 2.3, Continued

morphospecies (2)	—— **						
Scirpus robustus (2004)	—— *						
morphospecies (3)	—— ----	—— ----					
morphospecies (4)		—— *					
Lythrum lineare	—— ----	—— ----	—— ----				
Lilaeopsis chinensis	—— ----	—— ----	—— ----				
Spartina cynosuroides	—— ----	——	——				
Aster tenulifolius	——	—— ----	—— ----				
Polygonum amphibium (2004)	——	—— **	——				
Spartina patens	—— ----	----	—— ----	—— ----	—— ----		
Juncus roemerianus	—— ----	—— ----	—— ----	—— ----	—— ----		

Table 2.3, Continued

Distichlis spicata	—— - - -	—— - - -	—— - - -	—— - - -	—— - - -		
Sagittaria lancifolia	——			—— - - -	—— - - -	—— - - -	
morphospecies (5)		** - - -					
Ipomoea sagittata		—— - - -	- - -	—— - - -	—— - - -	—— - - -	- - -
Fimbristylis castanea			——	—— - - -	—— - - -	—— - - -	
Hibiscus moscheutos	——			—— - - -	—— - - -		
Pluchea odorata			—— - - -				
morphospecies (6)			** - - -				
Lobelia cardinalis				—— - - -			
morphospecies (7)				** - - -			
Sagittaria subulata				* - - -			
Kosteletzkya virginica	——			—— - - -	—— - - -		
Pluchea rosea				* - - -	- - -		
Panicum virgatum				—— - - -	—— - - -		——
Ampelopsis arborea					* - - -		

Table 2.3, Continued

Hydrocotyle verticellata					— - - -	- - -	
Andropogon glomeratus					— - - -		
Amaranthus spinosus (2011)						** - - -	
Boltonia asteroides						* - - -	
Eupatorium serotinum				- - -	— - - -	— - - -	- - -
Morella cerifera					— - - -	— - - -	— - - -
Cladium jamaicense				- - -	— - - -	— - - -	— - - -
Osmunda regalis					— - - -	— - - -	— - - -
Pinus elliottii					—	—	— - - -
Ilex vomitoria					— - - -	— - - -	— - - -
Mikania scandens					— - - -	— - - -	— - - -
Scutellaria integrifolia					—	— - - -	— - - -
Acer rubrum					— - - -	— - - -	— - - -
Centella asiatica					—	—	— - - -
Toxicodendron radicans					— - - -	— - - -	— - - -

Table 2.3, Continued

Hypericum nitidum					——	—— - - -	—— - - -
Eleocharis baldwinii					—— - - -	—— - - -	—— - - -
Cyperus strigosus (2011)					- - -	** - - -	- - -
Baccharis halimifolia						* - - -	- - -
Smilax laurifolia						—— - - -	—— - - -
Persea palustris						—— - - -	—— - - -
Hydrocotyle umbellata					- - -	—— - - -	—— - - -
Ilex cassine						—— - - -	—— - - -
Magnolia virginiana						—— - - -	—— - - -
Rubus betulifolius						—— - - -	—— - - -
Pinus taeda						——	—— - - -
Boehmeria cylindrica						——	—— - - -
Saururus cernuus (2004)						—— **	——
Vitis rotundifolia						——	—— - - -

Table 2.3, Continued

Nyssa biflora (2004)						——— **	———
Quercus nigra						———	——— - - -
Hymenocallis sp.							——— - - -
Peltandra sagittifolia							——— - - -
Coreopsis tripteris						- - -	——— - - -
Dichanthelium chamaelonche							——— - - -
Triadica sebifera							——— *
Gelsemium rankinii							——— **
Juniperus virginiana							——— - - -
Parthenocissus quinquefolia							——— **

Table 2.3, Continued

Polygonum hydropiperoides						- - -	— - - -
Rhynchospora gracilenta							— - - -
Osmunda cinnamomea							— - - -

Discussion

Trends in Diversity Between Years

As expected, position along the elevation gradient had a strong effect on species richness. Although I expected to find that species diversity was unimodally distributed along the gradient, with its maximum in the fresh marsh (*sensu* Grace 1999), species richness actually continued to increase through the 50 cm elevation class, as far up the gradient as this study examined. It is likely that the co-occurrence of both woody and herbaceous species in this dense ecotone promoted greater species richness, compared with the fresh marsh zone, which was dominated by herbaceous species only. Had this study examined seep and bottomland forests farther up the gradient, I may have found decreases in species richness at the highest elevations (Grace 1999; Sharpe and Baldwin 2009; Watson and Byrne 2009).

Between 2004 and 2011, significant changes in community composition occurred within elevation classes throughout the gradient. This trend was most notable with overall species richness declines in the -10 cm elevation class. Although α-diversity (as estimated by per plot species richness) declined only slightly overall following these disturbances, these declines occurred mainly in the -10 cm elevation class, the only elevation zone in which losses were significant (15.4 ± 0.872 to 7.6 ± 1.030; means ± SE). Shifts in richness likely had little effect on overall saltmarsh productivity (Waide et al. 1999). Nonetheless, rare saltmarsh species can perform important functions (Odum 1988; Keer and Zedler 2002), As rarer species become displaced, some of these functions, such as suppressing competition and promoting accretion (Zedler et al. 2001), could be lost or reduced in performance. Given that coastal wetlands will need to keep pace with chronic sea level rise (Brinson et al. 1995), accretion could be a particularly important saltmarsh function. Although significant declines in overall species richness did not occur at other elevations, there were significant losses of woody species richness at the upper end of the gradient.

Woody species can greatly affect ecosystem properties (Shachak et al. 2008) and losses of woody species could drive reductions in overall biomass (Fruchter et al. in revision). On the other hand, if woody species are reduced in abundance, increased light availability could promote herbaceous productivity. Emergent halophytes replaced woody species during a period of sea level rise in coastal Florida (Williams et al. 1999). Coastal wetland dominance shifts towards herbaceous flora could enhance marsh accretion (Young et al. 2007). The observed loss in overall species diversity (from 93 species to 86 species) occurred mainly as losses of herbaceous species from the low end of the gradient and losses of woody species at the high end of the gradient. Losses of species from the high end of the gradient may be ephemeral. Given time free from major disturbances, species whose ranges contracted up the gradient and out of the study area into seep and bottomland forest areas could potentially recolonize the study site (Freckleton and Watkinson 2002). Conversely, species losses from the low end of the gradient may be more permanent. Halophytes are poor competitors (Davy 2002) and it is unlikely that species characteristic of the -10 cm zone retreated up the gradient past the 50 cm zone, though it is possible that these species moved laterally out of the study plots but persisted in the -10 cm zone, in which case there is still potential for recolonization. While it is also possible that these species persisted in the seedbank but were not present in vegetative states, extended exposure to high salinity can reduce germination potential (Qu et al. 2008) and seedbanks may be of low importance in saltmarshes (Hartman 1988).

Compositional Trends

Losses of overall saltmarsh richness and woody richness in the marsh-scrub ecotone helped drive the compositional shifts in the upper and lower parts of the gradient. These shifts did not occur following disturbances in the intermediate and fresh marsh, possibly signifying that intermediate and fresh marsh are more resilient to hurricane and fire effects. However, analyses at the plot, rather than elevation class, level indicated that elevation did not significantly affect compositional divergence following disturbances. These results are not counter to one another; rather, they simply mean that compositional shifts in the intermediate marsh may have been just as strong as shifts at other elevations but did not occur unidirectionally. That no regular pattern existed could be construed as evidence that disturbances drive random ecological drift (Hubbell 2006) in intermediate and fresh marsh. The oligohaline zone is likely a “crossroads” between the dual ecological drivers of fire and salinity (Nyman and Chabreck 1995) and disturbances could potentially affect the species there in similar ways. If so, it makes sense that small-scale heterogeneity would be evident, as opposed to uniform changes throughout the vegetation zone (Levin 1992). Compared with trends in saltmarsh and ecotone indicator species, trends in intermediate marsh indicator species were generally weak. Stronger species-level trends in the lower and upper parts of the gradient were ultimately responsible for the broader scale patterns observed there.

Many species at the low end of the gradient (e.g., *Juncus roemerianus* and *Spartina alterniflora*) are well-adapted to frequent disturbances. I expected to find unidirectional shifts at the low end of the gradient because I expected that the disturbances would favor the species most tolerant of salinity and fire. Saltmarsh indicator species whose ranges contracted up the gradient (e.g., *Aster tenuifolius, Sagittaria lancifolia, Kosteletzkya virginica*) may have been responding to the storm surge effects of Hurricane Katrina (Chabreck and Palmisano 1973; Howard and Mendelssohn 1999).

Other saltmarsh indicator species suffered range contractions down the gradient, possibly because the more productive species were able to take advantage of increased light availability following the fire (Levine et al. 1998). Although this study did not attempt to quantify changes in abundance, losses of saltmarsh indicator species may have occurred due to competition with *S. alterniflora* and *J. roemerianus* (Brewer et al. 1997). Seasonality of the disturbances and plant-specific phenology could also play a strong role in community response (Lavorel and Garnier 2002); *Spartina cynosuroides*, a C-4 grass (Beale and Long 1997), may have been outcompeted throughout much of its previous range by the dominant C-3 species (*Spartina* *alterniflora* and *Juncus roemerianus*), which would be able to take advantage of immediate post-fire conditions following the winter fire (Schmalzer et al. 1991). If so, it is also possible that reintroduction of fire during the growing season could promote C-4 plants at the expense of C-3 plants (Keeley and Rundel 2005). Shifts in dominant plant functions could potentially occur at the upper end of the gradient as well.

Consistent with my hypotheses, disturbances did not result in migrations of intact assemblages but rather seemed to differentially favor two types of species: (1) strongly competitive, pyrophilic species (e.g., *Eupatorium serotinum* and *Coreopsis tripteris*; Carter et al. 2004; Suding and Goldberg 2001); and (2) flood- and salt-tolerant species (e.g., *Baccharis halimifolia*, *Polygonum hydropiperoides*; Stalter and Baden 1994). Some early-successional taxa (e.g., *Amaranthus spinosus* and *Cyperus strigosus*) colonized the study area as well, presumably the result of post-disturbance anemochory, hydrochory, or emergence from the seedbank (Neff and Baldwin 2005).

Also consistent with our hypotheses were drastic reductions in woody species, which were forced up gradient (e.g., *Pinus elliottii*) or eliminated from the survey plots entirely (e.g., *Nyssa biflora*). Contrary to our hypotheses, however, losses of woody species did not result in compositional convergence in upslope assemblages. Shifts in the upper part of the gradient were driven not only by losses of woody species but also by colonization and migration of species from up- and downslope. Even in the dense ecotone, herbaceous species richness far outweighs woody species richness and it is likely that compositional convergence as a result of shifts in woody species composition was obscured by compositional trends in herbaceous species. Areas farther up the gradient may have served as refugia for woody species poorly equipped to deal with hurricanes and fires (White 1979). Greater densities of woody species can help “break” hurricane winds, preventing physical damage as a result of the storm (Foster 1988), and reduced light availability in closed-canopy areas may result in less continuously distributed fuels and microclimatic conditions that reduce fire intensity (Nowacki and Abrams 2008). In a separate but related study quantifying woody abundance, I found that woody species abundance actually increased in the 50 cm zone following fire (Fruchter et al. in prep).

Considered together, differential shifts in individual plant species ranges suggest strong compositional changes following these disturbances, which seem to be distinctly correlated with position along the gradient. Strong storm surge following Hurricane Katrina may have negatively impacted species in the lower part of the gradient with more intermediate levels of tolerance (e.g., *Hibiscus moscheutos* and *Sagittaria lancifolia*) and the 2010 fire may have increased the effects of competition (Levine et al. 1998). Species at the high end of the gradient were likely vulnerable to storm surge as well and higher aspect woody species were likely strongly impacted by strong winds (Foster 1988) during Hurricane Ivan and the 2010 fire (Armentano et al. 1995; Nyman and Chabreck 1995).

Overall, these results support our hypotheses that significant compositional shifts would occur in the upper and lower parts of the gradient following tropical storms. As expected, shifts in the saltmarsh were driven mainly by losses of species richness, shifts in the marsh and marsh-scrub ecotone were driven, at least in part, by losses of woody species, and compositional changes throughout the gradient were driven by species-level responses rather than community-level responses. Unexpectedly, however, these losses did not result in overall compositional convergence, perhaps because woody species comprise only a fraction of coastal wetland plant diversity, even in the closed-canopy ecotone (Odum 1988). Upslope migrations of woody species may also have obscured any trends towards compositional convergence, though trends in ordination space suggest changes following the disturbances were not correlated with differences across the gradient. Also unexpectedly, I did not find significant shifts in the intermediate and fresh marsh zones, indicating that these areas may be strongly resilient to projected disturbance regime shifts (Suding et al. 2004).

Conclusions

Compositional shifts in ecosystems serve as ecological indicators of the Earth's capacity to respond to change (France and Duffy 2006). Over the next century, changing climate patterns will likely further alter landscape-level disturbance patterns relative to historical norms. Estuarine systems are at the forefront of rising sea levels and increasingly frequent intense hurricanes and have been heavily altered for anthropogenic development since human settlement (Shirley and Battaglia 2006). Trapped between the effects of salinization due to rising sea levels and encroachment by forest species as a result of years of fire suppression, coastal marshes are in jeopardy of becoming squeezed out and threatened with broadscale regime shifts towards saltmarsh or scrub woodland (Brinson et al. 1995; Michener et al. 1997; Pollock and Battaglia in preparation). Superimposed on this backdrop of changing climate and altered disturbance regimes is a renewed movement towards the use of fire as a management tool to promote ecological restoration to ecosystems similar to historical norms (Nyman and Chabreck 1995; Flores et al. 2011). Changes in these interacting disturbance regimes will likely favor expansion of some species at the expense of other species, resulting in the emergence of novel assemblages, which may be functionally similar or dissimilar to historical analogs (Hobbs et al. 2006).

Here, I studied ecological divergence in estuarine wetlands in response to two hurricanes and a prescribed fire. Although species diversity is often positively correlated with disturbances, the intermediate disturbance hypothesis predicts that intensities, frequencies, and scales of disturbance greater than historical background rates may actually reduce ecosystem diversity (Wilkinson 1999), a pattern that seems to have emerged at Weeks Bay following three, sequential, large-scale disturbances between 2004 and 2011. Compositional trends at Weeks Bay were driven by individual species range expansions, contractions, and shifts, as well as emergence and disappearance of species. Our results indicate that compositional shifts following these disturbances do not result in community convergence at the upper end of the gradient but instead result in novel species assemblages. As the communities at Weeks Bay NERR are structurally, compositionally, and functionally similar to wetland complexes across the Northern Gulf of Mexico (Eleuterius 1972; Withers 2002; Lot 2004), projected changes in disturbance regimes will likely elicit similar ecological responses throughout the region. Over the next century, persistent abiotic changes at the low end of the gradient (e.g., increasing salinities due to rising sea levels) may drive permanent compositional shifts. Conversely, compositional shifts at the upper end of the gradient may be more ephemeral; given time free from disturbances, woody species may recolonize these upslope areas.

CHAPTER 3

DO SEQUENTIAL LARGE-SCALE DISTURBANCES REDUCE WOODY SPECIES ABUNDANCE IN COASTAL WETLANDS?

Abstract

Coastal vegetation communities have been impacted by climatic changes and resultant natural disturbance regime shifts since the pre–settlement era. Since settlement, coastal areas have been affected by anthropogenic disturbance and land-use. During the 20th century, fire suppression throughout wetlands along the Northern Gulf of Mexico coast enabled woody species to colonize marshes historically dominated by herbaceous plants. Climatologists project that 21st century climate change will cause sea levels to rise and tropical storm activity to increase; resultant changes in wetland salinity could reduce cover of salt-intolerant fresh marsh species. Together, the dual effects of conversion to shrubland upslope and conversion to brackish marsh downslope could “squeeze” fresh marsh species, reducing cover and potentially threatening marsh persistence. To mimic historical disturbance regimes and combat woody species encroachment, ecosystem managers have begun to prescribe fire and use of prescribed burning could gain further popularity during the 21st century. Shifts in fire and hurricane regimes may cause community-level changes in woody species abundance and composition. I hypothesized that two recent hurricanes, Ivan and Katrina in 2004 and 2005, respectively, and a prescribed fire in 2010, would differentially affect woody species abundance along an estuarine gradient at Weeks Bay, Alabama and drive overall reductions in woody species abundance. Specifically, I hypothesized that hurricane effects would be greatest upslope and fire effects would be greatest downslope. Beginning at a tidal creek, I divided a 210 m estuarine gradient perpendicular to that creek into 10 m increments and surveyed all tree and shrub species along the gradient in 2004 (before the hurricanes), in 2006 (following the hurricanes), and 2012 (following the hurricanes and fire). Quadratic modeling and nonparametric two-way ANOVA tests showed reductions in abundance of woody species following each set of disturbances. Although direct gradient and indicator species analyses indicated some different hurricane and fire effects at the species level, in general, most species' ranges shifted upslope following the disturbances. Following the hurricanes, overall woody species abundance decreased in the upper portion of the gradient following the hurricanes but effects were not as strong closer downslope. Following the fire, reductions in woody species abundance were greatest in the marsh. Upslope ecotonal areas may not have burned at all and woody species revegetation of the marsh-scrub ecotone had begun to occur by 2012. Given these findings, reintegration of fire and 21st century shifts in tropical storm regimes could prevent woody species encroachment and reduce woody species density throughout the marsh-scrub ecotone, providing tidal freshwater marshes throughout the northern Gulf of Mexico coast relief from coastal squeezing.

Introduction

Disturbance Regime Shifts in the pre- and Post-Settlement Eras

Landscape-level disturbance (e.g., fire) predates human settlement as an important factor in determining community physiognomy and composition (Naveh 1967) by maintaining landscapes as mosaics of communities dominated by early-, mid-, and late-successional species. The period of initial human settlement of North America coincided with dramatic climatic shifts (i.e., Pleistocene-Holocene deglaciation), megafaunal extinctions, and increasing fire frequencies, giving rise to novel plant assemblages (Gill et al. 2009). Isolating the relative ecological importance of each of these shifts (e.g., decreased herbivory as a result of megafaunal extinctions) from the effects of the others (e.g., changing climate and increasing fire frequency) is not practicable because these shifts did not occur in isolation of one another and the interactions between these changing regimes may have been as important as the shifts themselves (Gill et al. 2009). Conversely, emergence of certain species could imply some causal mechanisms for compositional shifts across the landscape (e.g., emergence of salt-tolerant species following tropical storm surge could imply that changes were driven by increases in salinity; Brinson et al. 1995).

European settlement also coincided with dramatic climate shifts (i.e., “Little Ice Age”) and increasing fire frequencies, patterns that also drove ecological shifts towards novel species assemblages across landscapes, characterized by further increases in dominant early- and mid-successional species (McAndrews 1988; Pederson et al. 2005). During the 20th century, however, development and parceling of land led to discontinuities across the landscape (Delcourt and Delcourt 1988), reducing spatial extents of fires. More importantly, widespread management practices focusing on deliberate fire suppression dominated wildland fire policy (Stephens and Ruth 2005), resulting in fire regimes outside historical ranges of variability (*sensu* Morgan et al. 1994) often characterized by less frequent, but more severe fires (Stephens and Ruth 2005).

Ecological Responses to Fire Suppression

Over time, ecosystems may come to rely on periodic natural (Paine and Levin 1981; Platt and Connell 2003) and anthropogenic (Bugalho et al. 2011) disturbances (e.g., fires) within the historical range of variability. These disturbances help maintain historic communities by maintaining heterogeneity and periodically resetting or temporarily altering physiognomy (McCook 1994; Gilliam et al. 2006; Pickett et al. 2009). This 20th century period of fire suppression relative to recent and historical regimes coincided with encroachment by woody species into areas historically dominated by herbaceous species (Archer et al. 1995). This initial phase of woody species encroachment is relatively short in duration but important in ecological scope, causing intense, and often unpredictably system-specific, shifts in vital and functional ecosystem attributes such as productivity, water usage, and nutrient availability (Hughes et al. 2006; Knapp et al. 2008). Following initial woody species colonization, these changes can occur quite abruptly because establishment of woody species can facilitate further encroachment by providing bird perches or increasing nutrient availability (Battaglia et al. 2009). Once woody species become dominant, they can cause intense landscape-level changes by altering shade, water, and litter regimes (Shachak et al. 2008). In coastal systems with maritime climates, woody species encroachment often coincides with increased water usage, nutrient availability, and overall aboveground productivity, creating closed canopy conditions, which inhibit herbaceous growth (Knapp et al. 2008; Battaglia et al. 2009). As shifts from herbaceous to woody vegetation occur, productivity shifts from belowground root biomass to aboveground stem and leaf biomass (Brown 1997). These reductions in root:shoot ratio could reduce soil accretion in coastal marshes (Young et al. 2007; Darby and Turner 2008).

Fire Suppression in Coastal Wetlands

In a general sense, the potential effects of suppression are greatest where anthropogenic development has displaced fire-dependent ecosystems (Guyette et al. 2002). Human populations and anthropogenic impacts tend to be concentrated within coastal areas (Small and Nichols 2003) and natural and anthropogenic fire has been an important ecological driver in many coastal ecosystems since before human settlement (Stanturf et al. 2002), so fire-dependent coastal ecosystems may be extremely vulnerable to the effects of fire suppression.

Natural systems in coastal areas are arranged along distinct elevation and salinity gradients (Ray 1991; Battaglia et al. 2012); they range from extremely productive saltmarshes dominated by shade-intolerant halophytes in tidally and semi-permanently flooded areas, to mesic areas at the interior, dominated by woody species less tolerant of salt, flooding, and fire, but more tolerant of shade (Simpson et al. 1983). It has been hypothesized (Nyman and Chabreck 1995) that tidal flooding, tropical storm, and fire regimes are interacting ecological drivers of dominant coastal wetland vegetation type, with the relative importance of each regime varying based on both regional factors (e.g., climate) and local factors (e.g., proximity to the shoreline). Inland species are often unable to become established downslope because they may be intolerant of elevated salinities and semi-permanent flooding. Farther inland, tidal influences become less prevalent, enabling freshwater species to become dominant.

Where flooding is infrequent and salinities are low, fires may be necessary to prevent woody species encroachment from upslope (Williamson et al. 1984; Shirley and Battaglia 2006)

Development and fire suppression along the Northern Gulf of Mexico coast have resulted in woody species encroachment by dominant tree and shrub species (e.g., wax myrtle *Morella cerifera*) down coastal gradients into fresh marsh areas formerly dominated by pyrophilic herbaceous species (e.g., *Cladium jamaicense*; Shirley and Battaglia 2006; Pollock and Battaglia in prep.). Woody species encroachment into coastal marshes may cause important shifts in function, including: reduced light availability (Battaglia et al. 2009); altered productivity, decomposition, and biomass accumulation rates (Fruchter et al. in revision); and hindered marsh accretion rates (Young et al. 2007). Complicating matters further, coastal ecosystems will also need to respond to rapidly changing climate over the next century.

Coastal Wetlands and Climate Change

Superimposed on the legacy of fire suppression in coastal wetlands will be changing climate patterns during the 21st century. Current climate projections suggest that eustatic sea level will rise and tropical storm activity will increase over the next 100 years throughout the Atlantic basin (Bender et al. 2010). Globally, coastal areas are population centers and the importance of coastal wetlands as tropical storm “buffers” will only increase as storms intensify (Day Jr. et al. 2007). Coastal wetlands, which by definition, occupy the marine-terrestrial transition zone, have served and will continue to serve as the first onshore responders to elevated salinities due to rising sea levels and intensified storms (Shirley and Battaglia 2008; Lam et al. 2011). As sea levels rise and intense storms increase in frequency, species and assemblages at the upper limits of their salt tolerance may be “pushed” back up the gradient (Brinson et al. 1995). In some cases, however, woody species encroachment downslope may inhibit successful migration and establishment of herbaceous species upslope, essentially “squeezing” the fresh marsh between increasingly saline conditions due to chronic sea level rise and intensified storms and woody species encroachment resulting from fire suppression. These dual forces can prevent freshwater tidal marshes from being able to keep pace with rising sea levels (Brinson et al. 1995; Michener et al. 1997; Pollock and Battaglia in preparation).

Reintroduction of Fire to Release Marshes from Coastal Squeezing

In recognition of the negative impacts of fire suppression policies (Leopold et al. 1963), fire policies were updated throughout the 20th century, eventually leading to abandonment of suppression and embracing of fire prescription (Stephens and Ruth 2005). Prescribed fire has long been used as a management tool in southeastern U.S. forests and wetlands (Shea 1940), with the first federally prescribed fire implemented at Osceola National Forest in coastal Florida in 1943 (Bickford and Newcomb 1946). Prescribed burning continued to gain traction as a coastal wetland management tool, with the National Park Service burning at Everglades National Park in 1958 (National Park Service 2012) and resource managers throughout the Northern Gulf of Mexico have been attempting to reintroduce fire across coastal landscapes (Stanturf 2002; Scott Phipps, personal communication).

Interactions Between Changing Disturbance Regimes

In spite of widespread acceptance of fire as an important ecological process and resultant attitudes of ecosystem managers towards prescribed burning, the effects of reintroducing fire into coastal wetlands have not been thoroughly described. Furthermore, interacting large-scale disturbances can drive ecosystem regime shifts (Paine et al. 1998). How coastal wetlands already subjected to a legacy of fire suppression and woody species encroachment will respond to these changing disturbance patterns is unknown, though it is hypothesized that intensification of tropical storms could potentially alter the effects of fire. As hurricanes make landfall, they produce regionally extensive storm surges, which introduce salt into coastal ecosystems and cause "salt burn" damage to inland, freshwater species as far as 240 km from the hurricane's path (Fritz et al. 2007). Hurricanes that make landfall locally not only salinize soils but also introduce strong winds, which may uproot or cause limb breakage to high aspect vegetation (e.g., shrub and tree species) (Armentano et al. 1995). Previous research suggests that there are interactive effects between hurricanes and fires (Myers and van Lear 1998; Robertson and Platt 2001); individuals weakened by wind damage and storm surge may be more susceptible to the effects of subsequent fires (Platt et al. 2002).

This study examined the effects of three sequential large-scale disturbances (Hurricane Ivan in 2004, Hurricane Katrina in 2005, and a prescribed surface fire in 2010) on woody species abundance in a coastal wetland complex at Weeks Bay, Alabama, U.S.A. This series of disturbances afforded the opportunity to study the effects of these disturbances on coastal wetlands at Weeks Bay National Estuarine

Research Reserve (Weeks Bay NERR), and these impacts may serve as a model for ecological responses to projected disturbance regime shifts throughout the Northern Gulf of Mexico because Weeks Bay NERR had been free from tropical storm effects since 1998, when Hurricane Georges made landfall near Biloxi, Mississippi (Rodgers III et al. 2006). Fully replicating studies that incorporate unpredictable landscape-scale natural disturbances is not feasible (Van Mantgem et al. 2001); thus, this study used a time-series design to determine how these three large-scale disturbances impacted woody species encroachment at Weeks Bay NERR.

I expected that salinity tolerances of species would be a driving factor of woody species composition across the gradient, with downslope species more salt-tolerant than upslope species. I hypothesized that salt-tolerant species would increase and salt intolerant species would decrease with increasing salinity. I used the distance from a tidal creek as a proxy for salinity concentration. I expected disturbances to differentially affect species and reduce overall woody species abundance. Thus, I hypothesized that there would be strong interactions between changes in overall woody species abundance and time (hurricane and fire disturbances) and between changes in individual species abundance and time. Since I assumed inland woody species would be most sensitive to salt stresses (Ewe et al. 2007), I hypothesized inland species would decrease in abundance more than seaward species following hurricanes. Herbaceous biomass is more abundant downslope (Fruchter personal observations), and therefore I expected that the fire may have burned more intensely closer to the tidal creek. Thus, I predicted that fairly low-intensity surface fire would have more severe effects on woody abundance in the marshy areas.

Specifically, I expected woody species further from the tidal creek to decrease in abundance following hurricanes. I expected woody species closer to the tidal creek to decrease following fire. As the fire occurred more recently, downslope areas have had a shorter time to revegetate following severe disturbance. Thus, I expected overall responses to the combined effects of the hurricanes and fire to be strongest in downslope areas.

Methods

Site Description

The study was conducted at the Weeks Bay National Oceanic and Atmospheric Administration (NOAA) National Estuarine Research Reserve (hereinafter, Weeks Bay NERR). Weeks Bay is a small estuarine system nested within the much larger Mobile Bay estuary, approximately 35 km southeast of Mobile, AL at approximately 30.41° N, 87.83° W. The preserve covers 2650 ha, approximately 25% of which are occupied by terrestrial and wetland ecosystems and 75% of which are aquatic and marine, a ratio typical of the Alabama coastal area (Miller-Way et al. 1996). That Weeks Bay estuary is nested within Mobile Bay somewhat buffers the site from tidal influences and tidal variance at Weeks Bay NERR is just 0.3 to 0.5 m (Lam et al. 2011). Similarly, this nesting may reduce the frequency of short-duration storm surges, though it does not seem to mitigate the effects of less frequent, more intense storms (Huang 2009).

Recent Disturbances Affecting Weeks Bay NERR

Following several years free of tropical storm effects (Figure 3.1), two strong hurricanes, Ivan and Katrina, made landfall in 2004 and 2005, respectively. Hurricane

Ivan made landfall near Gulf Shores, AL (located approximately 20 km east of Weeks Bay NERR) as a Category 3 storm on the Saffir-Simpson scale on 16 September 2004, with peak winds of 145 km/hr and a peak storm surge of 2.5 m. Less than a year later, Hurricane Katrina made landfall near the Mississippi – Louisiana state line as a category 4 storm on 29 August 2005; at Weeks Bay NERR approximately 100 km from the MS-LA stateline, wind speeds peaked at 110 km/hr and storm surge peaked at 4.5 m; a storm surge above 2 m was sustained for five days (Lam et al. 2011). In winter 2010, the Alabama Department of Conservation and Natural Resources State Lands Division prescribed surface fires in these wetlands for the first time since the reserve was established in 1986 (Miller-Way et al. 1996) with the aim of reducing woody species abundance in the marsh-scrub ecotone. The fire burned intensely in herbaceous-dominated areas but only weakly in the closed-canopy dense ecotone where sparse ground cover was apparently unable to carry fire (Scott Phipps personal communication).

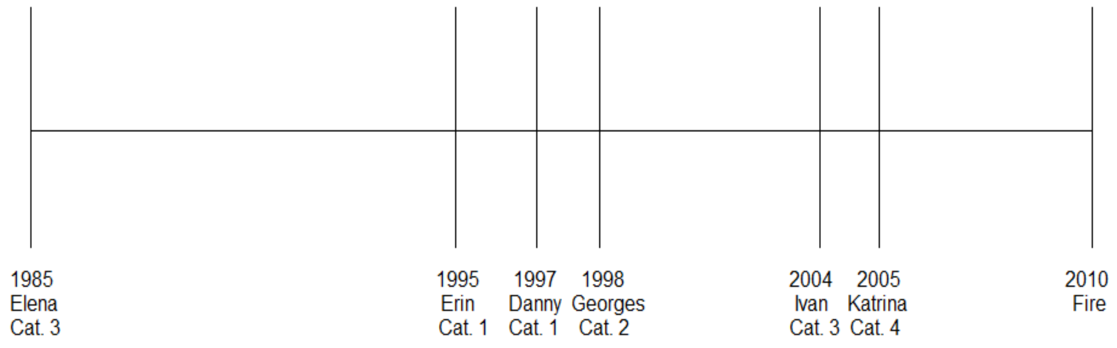

Figure 3.1: Timeline of major disturbances at Weeks Bay since 1985. Hurricane categories are given according to the Saffir-Simpson scale.

Study Area

This study focused on the freshwater marsh and marsh-scrub ecotone zones and quantified woody species abundance as a descriptor of encroachment and dominance of woody species in these zones. In 2004, prior to these disturbances, a transect was established perpendicular to a tidally flooded creek on a 330° bearing (Figure 3.2). Halophytic vegetation dominated at the creekside with the influence of salt decreasing with distance along the transect. When the transect was established, the fresh marsh zone, dominated by Jamaica sawgrass (*C. jamaicense*), began approximately 70 m from the creek and graded into a marsh-scrub ecotone, dominated by wax myrtle (*Morella cerifera*), red maple (*Acer rubrum*), and Carolina St. Johnswort (*Hypericum nitidum*) at approximately 110 m. Anecdotally, woody species density within the ecotone was roughly, though not perfectly, associated with distance along the transect and woody species began to occur between 70 and 80 m (Loretta Battaglia personal observations). Thus, areas between the tidal creek and 70 m were not analyzed. Other shrub and tree species occupying the ecotone included yaupon (*Ilex vomitoria*), redbay (*Persea palustris*), sweetbay (*Magnolia virginiana*), and slash pine (*Pinus elliottii*) (Miller-Way et al. 1996).

Figure 3.2: Belt transect superimposed on Google Earth™ image. The image was captured in January 2012, following the hurricanes and fire and shortly after the final survey.

Sampling Methods

The transect was divided into ten-meter increments, beginning at the tidal creek and ending in a closed canopy marsh-scrub ecotone. A belt transect sampling method was employed; all living shrub and tree individuals at least 1.5 m in height and less than 10 m from the transect were sampled for species and diameter at breast height (DBH); thus there were a total of 21 plots, each 20 m x 10 m (Figure 3.3). When shrubs or trees had more than one stem, the largest stem was measured. Total and species-specific basal area was estimated from DBH. The transect was surveyed three times:

the first survey, recorded in July 2004, provided a baseline estimate of woody species abundance before these three disturbances; the second survey, recorded in July 2006, provided insight into the impacts of two sequential hurricanes, Ivan and Katrina; and the final survey, recorded in January 2012, provided insight into the combined and (potentially) interactive effects of the hurricanes and the prescribed fire.

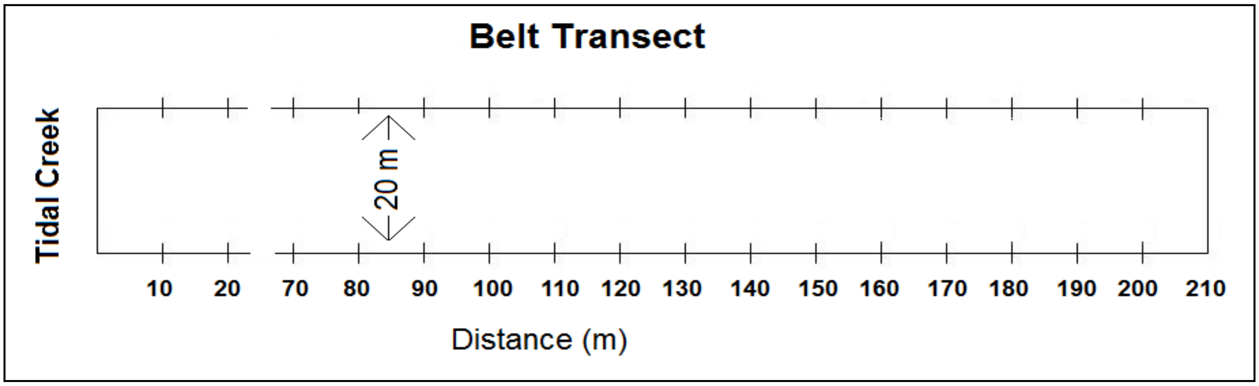

Figure 3.3: Representation of the belt transect running 210 m perpendicular to the tidal creek. The belt was 20 m in width and the transect was divided into sections 10 m in length. All woody species > 1.5 m in height were sampled. In 2004 and 2006, woody species began to occur between 70 and 80 m from the tidal creek. In 2012, woody species began to occur between 90 and 100 m from the tidal creek.

Statistical Methods

Quadratic regression modeling was performed using Sigmaplot v. 11.0 (Systat Software Inc. 2008) and all other univariate statistical testing was performed using R v. 2.12.1 (Team RDC 2010). To determine the relationship between woody species stem density and gradient position at each timestep, quadratic regression modeling was used, with separate models to fit woody species stem densities before the hurricanes (2004), after the hurricanes (2006), and after the hurricanes and fire (2012) to gradient position. To determine if there was a significant interaction between the effects of the disturbances and the effects of distance from the tidal creek, two-factor linear model ANCOVA testing was used to model stem density based on the fixed effects of gradient position, time interval, and the interaction between gradient position and time interval. If the interaction between gradient position and time interval was significant, then effects of the disturbances were significantly different across the gradient. To determine which pairwise interactions between gradient position and time were significant, separate pairwise ANCOVA models were used. To illustrate the relative magnitudes of the effects of the disturbances with respect to transect position, the relative changes in woody species stem densities in each survey were plotted against transect position. Spearman nonparametric tests for correlation were used to determine the significance of the relationship between distance from the tidal creek and relative changes in stem density between timesteps. The relative changes in stem densities were calculated as:

$RC_D = ((D_f – D_i) / D_i) * 100$, where:

RC_D = relative change in stem density, expressed as a percentage

D_t = stem density at time t

D_i = stem density at time i

To demonstrate the effects of time on the relationship between woody species basal area and transect position, basal areas in 2004, 2006, and 2012 were plotted against gradient position on one set of axes. To illustrate the relative magnitudes of the effects of the disturbances with respect to transect position, the relative changes in woody species basal areas in each survey were plotted against transect position.

Spearman nonparametric tests for correlation were used to determine the significance of the relationship between transect position and relative changes in basal area between timesteps. The relative changes in basal areas were calculated as:

$RC_A = ((A_f - A_i) * A_i^{-1}) * 100$, where:

RC_A = relative change in basal area, expressed as a percentage

A_t = basal area at time t

A_i = basal area at time i

As woody species basal area data were not normally distributed, Quade's testing, a nonparametric analog to two-way ANOVA, was used to determine the significance of the effects of time and gradient position on woody species basal area (Conover and Iman 1982).

Direct Gradient Analyses

Direct gradient analyses allow us to study patterns of species abundances with respect to an underlying environmental gradient (Whittaker 1967). To visually show the distributions of species prior to disturbances, following hurricanes, and following hurricanes and fire, direct gradient analyses was performed with 2004, 2006, and 2012 data, respectively. Species with fewer than 10 individuals were omitted from these direct gradient analyses. Direct gradient analyses were also performed for selected species to assess how their ranges shifted over time. Three types of species were selected for direct gradient analysis: (1) species that appeared to respond to the disturbances differently from many of the other species (*Hypericum nitidum*, *Acer* *rubrum*, *Pinus elliottii*, and *Baccharis halimifolia*); (2) species with different distributional patterns (*Ilex vomitoria*, *Magnolia virginiana*, and *Persea palustris*); and (3) *Morella cerifera*, the most abundant species observed.

Indicator Species Analyses

To determine whether differential species responses observed in direct gradient analyses were significant, indicator species analyses were performed. Indicator species analyses take both the constancy of a species in a particular community and the fidelity of that species to that specific community into account (Dufrêne and Legendre 1997). Use of both constancy and fidelity allows us to isolate species-level trends from community-level trends. Indicator species analyses were performed across time to identify the significance of species-level trends following disturbances, relative to its initial abundance and trends in other species. Multi-levels indicator species analyses, which group site classes together to allow species to be indicators of more than one site class (De Cáceres et al. 2010), were performed using the multipatt function in the R indicspecies package (De Cáceres and Jansen 2012).

Nonmetric Multidimensional Scaling Ordination and Vector-Fitting

Multivariate community ordination and vector fitting were performed using the DECODA package (Minchin 1989). Nonmetric multidimensional scaling (NMDS) ordination was used to explore trends in community composition (Minchin 1987). Species abundance data were standardized by species maxima and the Bray-Curtis dissimilarity index was used to estimate ecological distances between plot plant assemblages (Faith et al. 1987). Vector-fitting, a form of multiple linear regression, was used to determine the significance of the effects of distance from the tidal creek and time on community composition (Kantvilas and Minchin 1989).

Results

Woody Species Stem Density

Stem density (the number of stems per hectare) was positively correlated with distance from the tidal creek in 2004, prior to the disturbances ($y = (-24431 \pm 8454) + (406 \pm 133)x + (1.1 \pm 0.5)x^2$; $R^2 = 0.7568$, $F = 21.227$, $df = 13$, $p = 0.0002$). In 2006, after Hurricanes Ivan and Katrina had occurred, stem density was unimodally correlated with distance from the tidal creek ($y = (-20205 \pm 4882) + (306 \pm 77)x + (-1.2 \pm 0.3)x^2$); $R^2 = 0.6695$, $F = 14.1666$, $df = 13$, $p = 0.0009$) . In 2012, after the hurricanes and the 2010 prescribed fire, stem density was positively correlated with distance from the tidal creek ($y = (3998 \pm 2278) + (-82 \pm 36)x + (0.42 \pm 0.13)x^2$; $R^2 = 0.8044$, $F = 27.738$, $df = 13$, $p < 0.0001$; Figure 3.4). Linear model ANCOVA testing showed that the interaction between treatment and time was highly significant ($F = 8.082$, $df = 12$, $p = 0.00126$). Pairwise ANCOVA tests to determine the significance of the differences in slopes between time periods demonstrated that the relationship between woody species stem density and gradient position was significantly different between 2004 and 2006 ($F = 8.697$, $df = 6$, $p = 0.007$) and 2004 and 2012 ($F = 12.47$, $p = 0.002$), but not between 2006 and 2012 ($F = 0.005$, $df = 2$, $p = 0.942$). Spearman nonparametric tests confirmed a significant relationship between transect position and relative changes in stem density between 2004 and 2006 ($\rho = -0.604$, $p = 0.025$), 2006 and 2012 ($\rho = 0.9417$, $p < 0.0001$), and 2004 and 2012 ($\rho = 0.906$, $p < 0.0001$; Figure 3.5).

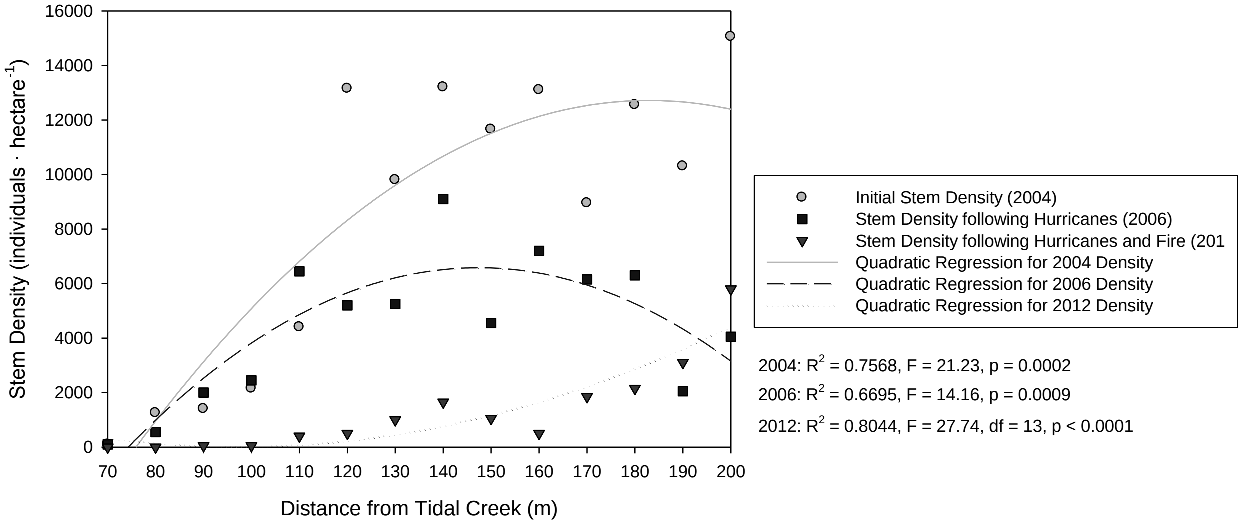

Figure 3.4: Distribution of woody species stem densities relative to distance from the tidal creek. Lines are modeled relationships for each group.

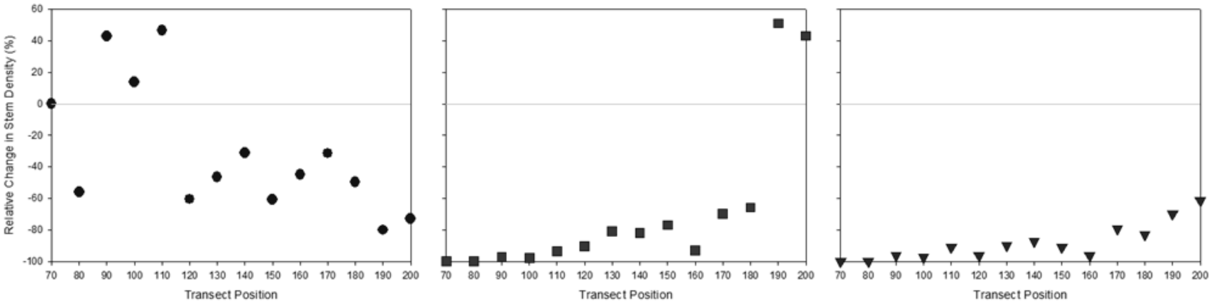

Figure 3.5: Distribution of the relative changes in stem densities between each set of disturbances with respect to distance from the tidal creek. The first pane depicts relative changes between 2004 and 2006, the second pane depicts relative changes between 2006 and 2012, and the third pane depicts relative changes between 2004 and 2012. The gray line represents zero change.

Trends in Woody Species Basal Area

In each survey, maximum woody species basal area was found between 140 m and 150 m (Figure 3.6). The results of Quade's tests showed that the effects of time (F = 21.9005, df = 2, $p < 0.0001$) and gradient position (F = 6.9327, df = 13, $p < 0.0001$) were significant; basal area increased with distance from the tidal creek and decreased with time. Spearman nonparametric tests confirmed a significant relationship between transect position and relative changes in basal area between 2004 and 2006 ($\rho = -0.5736$, $p = 0.035$), 2006 and 2012 ($\rho = 0.8757$, $p < 0.001$), and 2004 and 2012 ($\rho = 0.7393$, $p = 0.003$; Figure 3.7). The magnitudes of relative changes increased with distance from the tidal creek between 2004 and 2006 and decreased with distance from the tidal creek between 2006 and 2012. The magnitudes of relative changes throughout the study period (2004 through 2012) decreased with distance from the tidal creek.

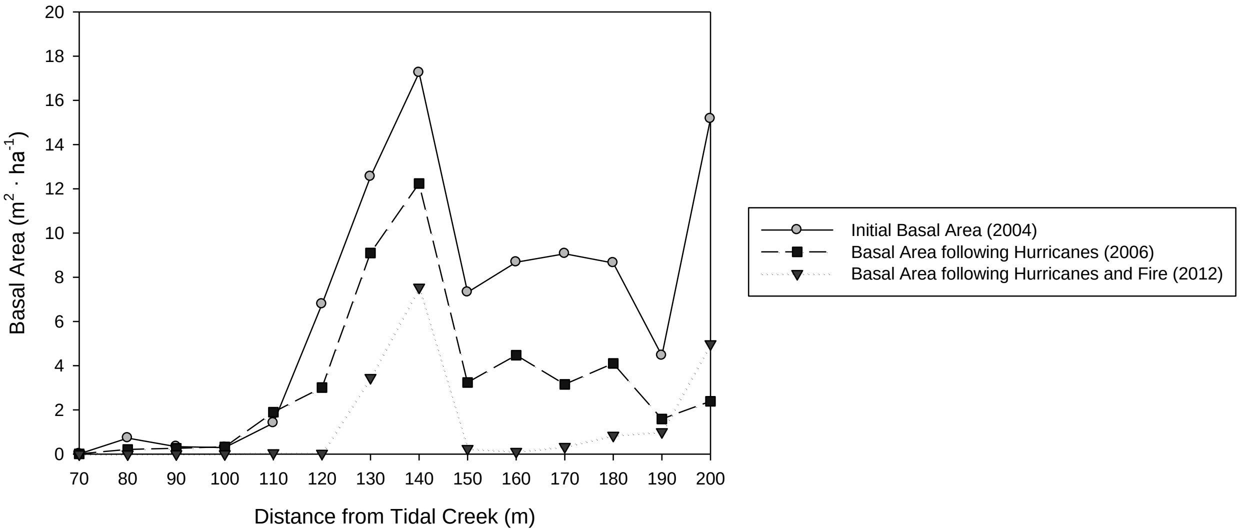

Figure 3.6: Distribution of woody species basal areas relative to distance from the tidal creek. Lines are drawn between points to aid visual clarity.

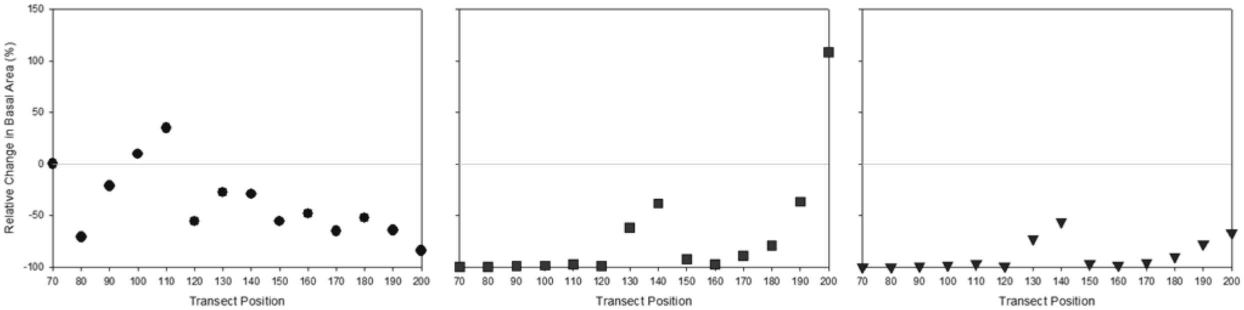

Figure 3.7: Distribution of the relative changes in basal areas between each set of disturbances with respect to distance from the tidal creek. The first pane depicts relative changes between 2004 and 2006, the second pane depicts relative changes between 2006 and 2012, and the third pane depicts relative changes between 2004 and 2012. The gray line represents zero change.

Direct gradient analyses of initial abundances showed similar species relationships across the gradient, with increasing abundance across the gradient (Appendix 3A). Notable exceptions to these general relationships did occur. Prior to the disturbances, *Hypericum nitidum* and *Magnolia virginiana* were quite dense in downslope areas but were almost completely eliminated following the hurricanes. Direct gradient analyses by species also showed similar species trends across the gradient and time, again, with a few notable exceptions (Appendix 3B): even in downslope areas where overall hurricane effects were weakest, *Hypericum nitidum* was almost completely eliminated following the hurricanes and *Morella cerifera*, *Ilex* *vomitoria* and *Baccharis halimifolia* emerged in upslope areas following the hurricanes and fire.

Trends Within Species

Indicator species analyses were performed by year to determine the significance of shifts in species abundance over time relative to one another (Table 3.1). There was one species that was a significant indicator of the pre-disturbance (2004) communities only: *Hypericum nitidum* (IV = 0.788, p = 0.002). Two species were significant indicators of the two pre-fire communities (2004 and 2006): *Acer rubrum* (IV = 0.936, p < 0.001) and *Pinus elliottii* (IV = 0.864, p < 0.001). *Baccharis halimifolia* (IV = 0.655, p = 0.003) was the only species that was a significant indicator of the post-fire (2012) community.

Table 3.1: List of species that were significant indicators of year and the years for which they were significant indicators. Species growth form is indicated. Black bars indicate years for which each species was a significant indicator.

Species	Growth Habit	2004 Pre-disturbance	2006 Post-hurricanes	2012 Post-hurricanes and fire
Hypericum nitidum	Shrub	▬		
Acer rubrum	Subcanopy tree	▬	▬	

Pinus elliottii	Canopy tree	—	—	
Baccharis halimifolia	Shrub			—

Community Trends

ANOSIM testing demonstrated that there were significant differences between communities (R = 0.2344, $p < 0.001$). Pairwise ANOSIM tests showed significant differences between pre-disturbance and post-Katrina (R = 0.1172, p = 0.001), pre-disturbance and post-fire (R = 0.3149, $p < 0.001$), and post-Katrina and post-fire communities (R = 0.2843, $p < 0.001$). Two dimensional NMDS ordination was sufficient to display trends in woody species communities across the gradient and time (stress = 0.1670). Vector-fitting permutation tests showed that both time (r = 0.6752, $p < 0.001$) and distance from the tidal creek (r = 0.5546, p = 0.001; Figure 3.8) were significantly correlated with compositional trends.

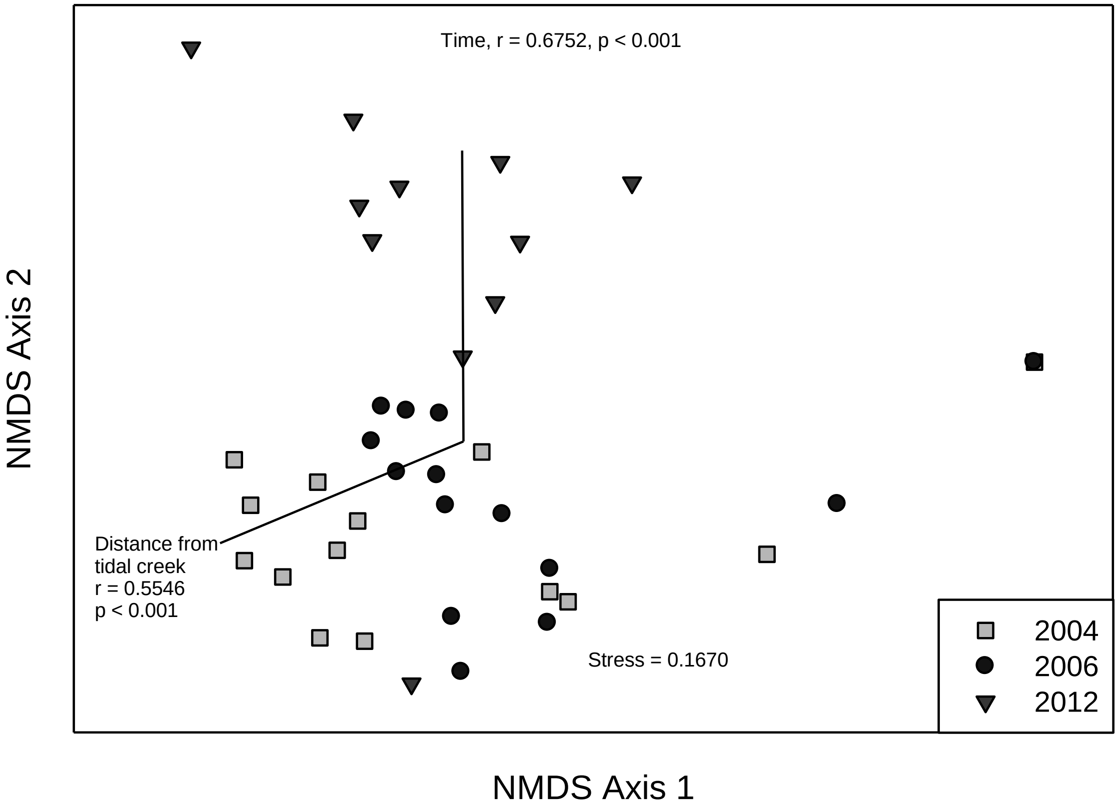

Figure 3.8: Two-dimensional NMDS ordination demonstrating trends in woody species composition. Fitted vectors for distance from the tidal creek and time are superimposed on the ordination and represent significant patterns across the gradient and time, with vector lengths proportional to correlations.

Discussion

Initial Woody Species Abundance and Composition

Consistent with my predictions, quadratic regression and Quade's testing indicated that initial woody species abundance was strongly correlated with distance from the tidal creek and NMDS ordination and vector-fitting suggested that distance from the tidal creek was significantly correlated with woody species composition. While it is unlikely that distance from the creek is an intrinsic compositional driver, it can be a determinant of other strong community drivers, such as flood and salinity regimes (Battaglia et al. 2012). Direct gradient analysis of 2004 data showed that species-level relationships across the gradientwere generally weak. Together, these results suggest that the initial differences in composition relative to the tidal creek were likely due to differences in total woody species abundances rather than differences in relative species composition. I did not expect to find that observed species-level trends were weak given that previous research has shown that woody species in tidal freshwater wetlands tend to be discretely zoned (Schneider and Sharitz 1986; Peterson and Baldwin 2004). It is possible that the extent of this study was too fine (i.e., all of the sampled positions were within the same general zone) or the grain of the study was too coarse (i.e., each of the sampled positions incorporated many zones) to observe this heterogeneity.

Temporal Trends in Overall Woody Species Dominance

As expected, woody species abundance (as estimated from stem density and basal area) increased along the transect and decreased over time, presumably the result of mortality due to Hurricanes Ivan and Katrina in 2004 and 2005 and the prescribed fire in 2010. The 2006 survey showed that the magnitudes of the effects of Hurricanes Ivan and Katrina were positively correlated with distance from the tidal creek. These hurricanes resulted in storm surges, introducing salt throughout the gradient (Lam et al. 2011). Strong onshore winds make tidal influences more common downslope and it is likely that the species farther upslope were more vulnerable to novel salt stresses (Brinson et al. 1995). However, the direct gradient analysis of the 2004 community did not suggest strong species-level relationships across the gradient at this scale. Localized differences in landform and hydrology may have exacerbated the effects of storm surge at higher elevations and these intensified storm surge effects impacted the species present in similar ways. Freshwater tidal flooding and groundwater inputs in areas nearer to the tidal creek may have diluted soil salinities following tropical storm surges (Fritz et al. 2007). As more inland areas are not tidally flooded and very little precipitation occurred during the months following Hurricane Katrina, soil salinities may have remained elevated throughout the 2006 growing season (Rodgers et al. 2009).

Although it is impossible to separate the effects of the disturbances from the effects of time and the effects of the fire from the interactive effects of the fire and the hurricanes, an interesting trend emerged. Hurricanes had stronger effects upslope. I attributed this effect to longer-lasting effects on salinity in upslope areas and more ephermeral effects on salinity in freshwater marsh. The fire had greater effects downslope. Trends in herbaceous dominance may be responsible for differential fire effects across the study area. To continue burning in wetlands, where the ground may be saturated or under standing water, fires need fuels to be continuous, readily available, and dry (Martin and Kirkman 2009). Areas near the tidal creek are dominated by dense stands of vertically arranged fuels, such as Jamaica sawgrass (*Cladium jamaicense*), a pyrophilic herbaceous species that dries quickly and burns hot (Lynch 1941). Abundance of the shade-intolerant *Cladium* (Conway 1942) becomes greatly reduced in the closed canopy ecotone area (approximately 190 m – 210 m; Fruchter personal observations) and reductions in herbaceous fuel loads and cooler, more humid microhabitats reduced the severity of a subsequent fire in the dense ecotone (Battaglia personal observations).

Temporal Trends in Indicator Species

Indicator species analyses across years revealed species-level responses to these disturbances. Species that were significant indicators in 2004 but not 2006 or 2012 may be vulnerable to tropical storm damage because they were indicators of the pre-hurricane communities but not in the post-hurricane assemblages. I cannot disentangle the direct effects of the fire from the interactive effects of these sequential disturbances; thus, I cannot determine whether species indicative of 2004 and 2006 communities but not 2012 communities responded directly to fire or to the interactive effects of fire and previous hurricane impacts. Species that were not significant indicators in 2004 but which arose in 2006 or 2012 could potentially depend on frequent disturbances to persist and may increase in abundance under disturbance regime shifts projected to occur with climate change.

Indicator species analyses across times showed that *Hypericum nitidum* was a significant indicator of the 2004 (pre-disturbance) communities. *H. nitidum* is a small shrub with flexible branches so it is unlikely that it was impacted by the strong winds during Hurricane Ivan; thus, it is more likely that dieback occurred in response to the sequential storm surges resulting from Hurricanes Ivan and Katrina. Although *H. nitidum* was the only species sufficiently frequent in 2004 to be considered a significant indicator, several other species were observed in 2004 but not in 2006 (e.g., *Itea virginica*, *Liquidambar styraciflua*, *Nyssa sylvatica*, *Triadica sebifera*). With the exception of *Triadica sebifera*, an exotic species, these species were more common farther inland in 2004 (Battaglia unpublished data) and are likely poorly adapted for persistence farther downslope (Kozlowski 1997). Although infrequent, tropical storm surges do impact wetlands on the northern Gulf Coast at return intervals between 15 and 20 years (Batista and Platt 1997) and other indicators of the pre-disturbance communities were also indicators of the post-hurricane, possibly signifying that they are at least somewhat resilient to the effects of tropical storms (Conner et al. 1989; Kozlowski 1997).

Indicator species analyses also showed that *Acer rubrum* and *Pinus elliottii* were significant indicators of the pre-fire (2004 and 2006) communities. Fire is one factor that may limit the spread of *A. rubrum*, a generalist species tolerant of a wide range of climates, soil types, and hydrologies (Walters and Yawney 1990), though *A. rubrum* is capable of resprouting (Walters and Yawney 1990). Some resprouts from top-killed trees at Weeks Bay were 2 m tall in 2012 (Fruchter personal observations). I did not expect that *P. elliottii*, a tree species whose resistance to fire damage is well-documented (McCune 1988), would be an indicator of the pre-fire communities. Multiple disturbances can result in heightened mortality of *P. elliottii* (Platt et al. 2002), and it is likely that the interactive effects of sequential disturbances played an important role at Weeks Bay NERR as well because trees already weakened by storm surge may have been more vulnerable to fire effects. Population age and size demographics may also have played a role in these results because larger *P. elliottii* individuals are more tolerant of fire but less tolerant of storm surge than smaller individuals (Sah et al. 2010). At Weeks Bay NERR, mean *P. elliottii* DBH was reduced following the hurricanes, though these reductions were not statistically significant. Nonetheless, it is possible that the surge caused mortality in larger individuals, leaving smaller trees that were vulnerable to the 2010 fire. The only indicator of the 2012 (post-fire) community was *Baccharis halimifolia*, a fast-growing ruderal shrub (Aber Krischik and Denno 1990), which likely responded quickly to increased light and nutrient availability following the 2010 fire (Van Auken and Bush 1990).

Overall, the results were generally consistent with my predictions. As expected, relative reductions in woody species abundance following the hurricanes increased in magnitude with distance from the tidal creek. I expected to find that reductions in woody species would be greatest upslope based on the underlying assumption that upslope species would be more sensitive to salinity stresses (Conner et al. 1998; Middleton 2009); however, within-species trends across this part of the gradient were weak. The few individuals of species dominant in and characteristic of mesic forest communities upslope of the study site (e.g., *Liquidambar styraciflua*, *Nyssa sylvatica*) were eliminated following the storms but these species were not sufficiently abundant to drive overall community trends. Still, tolerance of extreme salinity is a rare trait in woody species (Kozlowski 1997) and, with the possible exception of *B. halimifolia*, all of the species observed at Weeks Bay were quite vulnerable to the effects of the storms.

As expected, the effects of fire seemed to be strongest in the downslope areas and weakest in the upslope areas. Farthest from the creek, the scrub becomes quite dense, reducing light availability to herbaceous plants and preventing the drying of litter and saturated soils (Fruchter personal observations), factors that can greatly inhibit fire behavior (Nowacki and Abrams 2008). In the primarily herbaceous-dominated marsh and sparse marsh-scrub ecotone areas, abundance of woody species was greatly reduced following the fire. However, the fire seemed to “fizzle” out in areas where woody species were dominant, likely because fuels were not available and microclimatic conditions did not support active fire behavior. It is impossible to isolate the effects of the fire from the effects of time and shrub encroachment would be expected to be concentrated at the landward end of the gradient. Thus, it is likely that revegetation of woody species in upslope areas was not the result of the fire but rather the result of several years free from major disturbances following Hurricanes Ivan and Katrina.

Overall, as expected, the combined effects of these sequential disturbances did elicit similar ecological responses (drastic reductions in woody species) throughout the gradient, suggesting that intensification of hurricanes and reintroduction of fire during the 21st century could result in reduced woody species abundance in coastal wetlands throughout the northern Gulf of Mexico. However, the effects of hurricanes were comparatively weak in downslope encroachment sites and regular fire at return intervals as frequently as every two to four years may be vital to preventing encroachment (Schmalzer et al. 1991; Wade et al. 1980).

Conclusions

Natural disturbances have been important drivers of coastal wetland species composition and overall vegetation type since the pre-settlement era. Changes in disturbance type, frequency, and intensity have coincided with increasing human population density. Landscape fragmentation and the concern for property in developed coastal wetlands led to fire suppression in the 20th century. Although the importance of fire has become widely recognized (Leopold et al. 1963), a legacy of fire suppression throughout coastal landscapes along the Northern Gulf of Mexico has already allowed compositional shifts from herbaceous to woody-dominated communities. The shift from herbaceous to woody vegetation in coastal wetlands increases aboveground net productivity (Knapp et al. 2008), yet reduces belowground productivity (Brown 1997). As productivity is shunted from roots to aboveground components, soil accretion becomes markedly reduced (Young et al. 2007; Darby and Turner 2008). Over time, reduced accretion could prevent coastal wetlands from keeping pace with persistent sea level rise, potentially jeopardizing long-term marsh persistence (Brinson et al. 1995; Shirley and Battaglia 2006; Darby and Turner 2008).

Recently, there has been a renewed emphasis on the use of prescribed fire as a “natural” coastal wetland community driver. Superimposed on the return of fire are 21st century changes in climate, which will result in coastal wetland salinization through rising sea levels and increasingly intense tropical storms (Michener et al. 1997). Interacting large-scale disturbances may upset ecosystem stability, potentially causing wholescale ecosystem regime shifts (Paine et al. 1998), and the effects of shifting disturbance regimes in coastal wetlands remain unknown. Over the past eight years, Weeks Bay NERR has been affected by three sequential large-scale, landscape-level disturbances, Hurricanes Ivan and Katrina and a prescribed fire. The 20th century encroachment of shrubs at Weeks Bay (Pollock and Battaglia in prep.) and in other Northern Gulf of Mexico wetlands was attributed to fire suppression (Shirley and Battaglia 2006; 2008). This study provides direct support for the conclusion that fire suppression led to historic shrub encroachment, because woody species that previously colonized the fresh marsh at Weeks Bay NERR (Pollock and Battaglia in prep.)

decreased in abundance after fire. The combined effects of hurricanes and fire caused slight, but significant, shifts in woody species composition and statistically significant reductions in overall woody species abundance that potentially have broader ecosystem impacts, such as reducing canopy cover, stimulating herbaceous productivity, and promoting accretion (Young et al. 2007). Community-level responses to these disturbances can serve as a model to help predict how future changes in disturbance regime (i.e., intensification of hurricanes and reintroduction of prescribed burning) will impact similar shrub-encroached ecosystems. These findings may indicate that the coupling of projected shifts in tropical storm and reintegration of fire regimes could potentially restore herbaceous dominance to coastal wetlands and release inland marshes throughout the region from the effects of coastal squeezing (Shirley and Battaglia 2006, 2008; Pollock and Battaglia in prep; Fruchter et al. in prep).

CHAPTER 4

CONCLUSIONS

The general purpose of this research was to investigate the effects of natural and anthropogenic disturbances on coastal wetlands with the goal of predicting how 21^{st} century changes in disturbance regimes may drive shifts in species composition and overall community dominance by woody species. A coastal wetland complex was sampled for species composition along an estuarine gradient before and after a series of three, sequential, large-scale disturbances to determine whether compositional shifts occurred following those disturbances and whether the magnitude of each shift was correlated with position along the gradient. Woody species abundances along that gradient were compared across three times to determine whether shifts in woody species dominance occurred. Although trends were not uniform across the gradient, important shifts in both plant species composition and woody species abundance did occur.

In the Introduction, predictions of ecological response to these disturbances were made based on hypothesized mechanistic effects for each disturbance, as well as hypothesized interactions between these disturbances. Two overarching hypotheses were developed and the following passage is a synthesis of this research with respect to those hypotheses.

1) Coastal wetland plant community composition will shift following these multiple large-scale disturbances. The nature and magnitude of changes will be

relative to position along the elevation gradient. At lower elevations, these changes will be driven by eliminations of some species and shifts in the ranges of other species. At higher elevations, compositional changes will be driven by losses of woody species and upward shifts in the ranges of herbaceous species. Thus, as the ranges of downslope species shift upwards, upslope assemblages will become more similar to assemblages farther downslope.

Shifts at the low end of the gradient towards less species-rich communities were expected because the recent fire may have enabled better competitors, such as the dominant *Spartina alterniflora* and *Juncus roemerianus*, to become even more dominant, thereby excluding sub-dominant species (Levine et al. 1998). Shifts at higher elevations were expected to be driven by losses of woody species due to general trends in woody species physiology and life history and by upward shits in herbaceous species ranges due to the capacities of downslope species to colonize sites that became suitable following the disturbances (Menges and Hawkes 1998).

Nonmetric multidimensional scaling (NMDS) ordination was used to graphically display ecological distance between communities, based on both elevation and time. Vector-fitting and Analysis of Similarity (ANOSIM) tests were used to statistically determine whether elevation and time significantly affected community composition. Indicator species analyses were used to determine how shifts in individual species helped drive overall compositional patterns. These analyses indicated that shifts in the low part of the gradient occurred partially as a result of significant losses of species richness, but also in part due to emergence of species not found in 2004 and shifts in the ranges of indicator species. Richness losses in the saltmarsh (-10 cm) plots were particularly evident, as mean richness · 100 m^{-2} decreased from 15.4 ± 0.872 species in 2004 to 7.6 ± 1.030 species in 2011. Shifts in the upper portion of the gradient were due mainly to reductions of woody species richness and upward migrations of herbaceous species but also by emergences and losses of herbaceous species. ANOSIM and vector-fitting suggested that these disturbances did not result in significant compositional differences in the intermediate portion of the gradient.

Shifts at the low end of the gradient were primarily driven by species losses and emergences, rather than upward and downward migrations. Thus, in ordination space, these compositional shifts occurred perpendicular to the arrangement of compositional differences along the gradient (Kantvilas and Minchin 1989). In the upper portion of the study area, shifts that occurred following the disturbances again appeared to be perpendicular to compositional differences along the elevation gradient. Consistent with the initial hypotheses, assemblage shifts in the lower portion of the gradient occurred due to declining species richness and caused shifts in ordination space perpendicular to trends correlated with elevation. Although I cannot be certain of the cause, it is possible that the fire stimulated dominant species, allowing them to outcompete rarer ones (Levine et al. 1998).

I did not expect to find that compositional shifts in the intermediate and freshwater marsh zones were not statistically significant. It is possible that the hurricanes drove short-term shifts in the intermediate marsh. If so, species that were vulnerable to hurricane effects were able to recolonize prior to the 2011 survey. Shifts in the upper portion of the gradient were somewhat consistent with the hypotheses because shifts were driven at least in part by losses of woody species. However, contrary to predictions, ecological shifts in ordination space were perpendicular to compositional differences along the gradient, not coincident with them. These trends suggest that the disturbances did not favor compositional convergence in the upper part of the gradient but rather resulted in assemblages of species whose ranges did not previously overlap (Kantvilas and Minchin 1989). Thus, the results of these analyses did provide some support to the first overarching hypothesis but did not fully confirm it.

2) Woody species abundance will be reduced throughout the gradient following hurricane and fire disturbances. Reductions as a direct result of the hurricanes should be greatest in upslope areas, whereas reductions due to the fire should be greatest in downslope areas. The hurricanes occurred several years prior to the fire.   Thus, upslope areas, where I predict that hurricane impacts were stronger than fire impacts, have had a longer duration of time to recover from severe disturbance than downslope areas, where I predict that fire impacts were stronger than hurricane impacts. Therefore, overall ecological responses to these sequential disturbances are expected to be greater in downslope areas than upslope areas, though there will be drastic reductions throughout the gradient.

It was expected that the magnitude of the effects of the disturbances would be strongly correlated with position across the gradient. Hurricane and fire disturbances elicit ecological responses by different mechanistic processes and these processes may be highly constrained by ecosystem and community properties (Jones et al. 1997). Hurricanes affect woody individuals by strong winds, which can cause defoliation (Putz and Sharitz 1991) and physically damage inflexible woody species (Foster 1988), and by storm surges, which cause physiological salt and flood stresses (Michener et al.

1997). As defoliation provides a short-term stress but generally does not induce mortality and most of the woody species in the marsh and marsh-scrub ecotone are low aspect shrubs and sub-canopy trees with flexible limbs, it was expected that the effects of the hurricanes would be confined mainly to the effects of storm surge. Given that tidal flooding and groundwater intrusion likely introduce salt and cause flooding in the marsh zone even during periods free from intense weather events, I expected that species in the lower end of the gradient would be somewhat more tolerant of storm surge than species in areas farther from the sea (Michener et al. 1997). Fires affect woody individuals by intense heat and altering nutrient availability (Reich et al. 2001). Given that fires in wetlands need vertically-arranged, continuously distributed fuels that are readily available and dry (Smith et al. 2001), I expected that fires would burn much more intensely and with greater severity in downslope, open canopy areas, which are dominated by herbaceous species, such as the pyrophilic Jamaica sawgrass (*Cladium jamaicense*). Given that upslope areas would have longer to revegetate following effects of the hurricanes than downslope areas would have to revegetate following effects of the fire, I predicted that the combined effects of the two hurricanes and the fire would be greater in herbaceous-dominated areas closer to the tidal creek.

Quadratic modeling was used to determine the significance of the effects of distance from the tidal creek on woody species abundance and two-way ANOVA and Quade’s tests were used to determine the effects of the disturbances on woody species abundance, relative to position along the gradient. Changes in abundance over time relative to initial abundance were plotted against distance from the tidal creek to show how gradient position was correlated with disturbance effects. Direct gradient and indicator species analyses, in conjunction with NMDS ordination and vector-fitting, were used to describe temporal trends across the gradient at both species and community levels. Quadratic models showed that there was a significant relationship between woody species density and distance from the tidal creek. Two-way ANOVA and Quade's tests showed that woody species abundance significantly decreased following disturbances. NMDS ordination and vector-fitting showed that community composition was significantly correlated with both position along the gradient and disturbances. The results of direct gradient and indicator species analyses showed some trends at the species level but suggested that compositional trends were more strongly driven by overall changes in woody abundance than with species-level changes.

Consistent with the original hypothesis, woody abundance was reduced following disturbances throughout the gradient. Also consistent with the original hypothesis, hurricane effects were strongest upslope. Unexpectedly, however, species-level trends across the gradient were generally weak. Since species-level trends were weak, it is unlikely that hurricane effects were strongest farther inland because of differences in species physiological tolerance to flooding and salt stress. Instead, it seems more likely that relative differences in hurricane effects were correlated with differences in landform and hydrology (Fritz et al. 2007). Storm surges resulting from Hurricanes Ivan and Katrina brought salt into these coastal wetlands and soil salinities likely remained elevated following recession of those surges. Salinities in upslope areas may have remained elevated over a longer duration because salt may have been flushed out of soils closer to the creek by tidal freshwater flooding from the Fish and Magnolia rivers upstream. Furthermore, following Hurricane Katrina, precipitation throughout the northern Gulf of Mexico was lower than normal, which may have exacerbated salt stresses in upslope areas (Fritz et al. 2007). As expected, the effects of fire were strongest in open-canopy, herbaceous marsh and actually coincided with an increase in woody species density in the closed-canopy marsh-scrub ecotone, where the fire may have been naturally extinguished because fuels were not available and microclimatic conditions did not support active fire behavior (Gordon 1998). In the dense ecotone, very little light is available to herbaceous plants, which limits fuel availability. Canopy cover also prevents the drying of litter and saturated soils (Fruchter personal observations), which inhibits fire behavior (Nowacki and Abrams 2008). The overall results were generally consistent with the hypothesis that the combined effects of fire and hurricanes drove similar reductions in woody species abundance throughout the gradient.

The purpose of this study was to determine how the cumulative effects of three recent and sequential disturbances influenced coastal plant assemblages along an estuarine gradient at Weeks Bay, Alabama, in the northern Gulf of Mexico region. During the 20th century, coastal ecosystems throughout the region were fire-suppressed (Shea 1940), resulting in possible shifts throughout the gradient and encroachment by woody species into areas formerly dominated by freshwater herbaceous species (Shirley and Battaglia 2006). It was unknown how fire-suppressed wetlands would respond to increasing hurricane and fire activity. Compositional trends at Weeks Bay were driven by individual species range expansions, contractions, and shifts, as well as emergence and disappearance of species. Trends in woody species dominance following disturbances were driven mainly by overall reductions in woody abundance but some species-level trends were evident. These results indicated that these disturbances reduced dominance by woody species but did not result in compositional convergence. The communities at Weeks Bay NERR are regionally typical and ecological responses to disturbances observed at Weeks Bay NERR are likely to be conserved throughout the Northern Gulf of Mexico. How coastal species shift in response to rising sea levels and intensified storms during the 21st century will ultimately drive attendant shifts in dominant wetland vegetation type. Chronic sea level rise at the low end of the gradient may drive permanent compositional shifts, whereas compositional shifts at the upper end of the gradient may be more ephemeral. Given time free from disturbances, woody species may recolonize these upslope areas. Projected changes in both anthropogenic and natural disturbance regimes could potentially release estuarine wetlands from coastal squeezing.

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APPENDICES

Appendix A: Pairwise ANOSIM test results showing significant differences between elevation classes.

Pairwise ANOSIM test results for elevation classes in 2004.

	-10	0	10	20	30	40
0	R = 0.8389 p = 0.0071					
10	R = 0.7360 p < 0.0001	R = 0.6080 p = 0.0095				
20	R = 0.9960 p = 0.0074	R = 0.9780 p = 0.0070	R = 0.6680 p = 0.0166			
30	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 0.9960 p = 0.0084	R = 0.8120 p = 0.0076		
40	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 0.7660 p = 0.0083	
50	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 0.3980 p = 0.0343

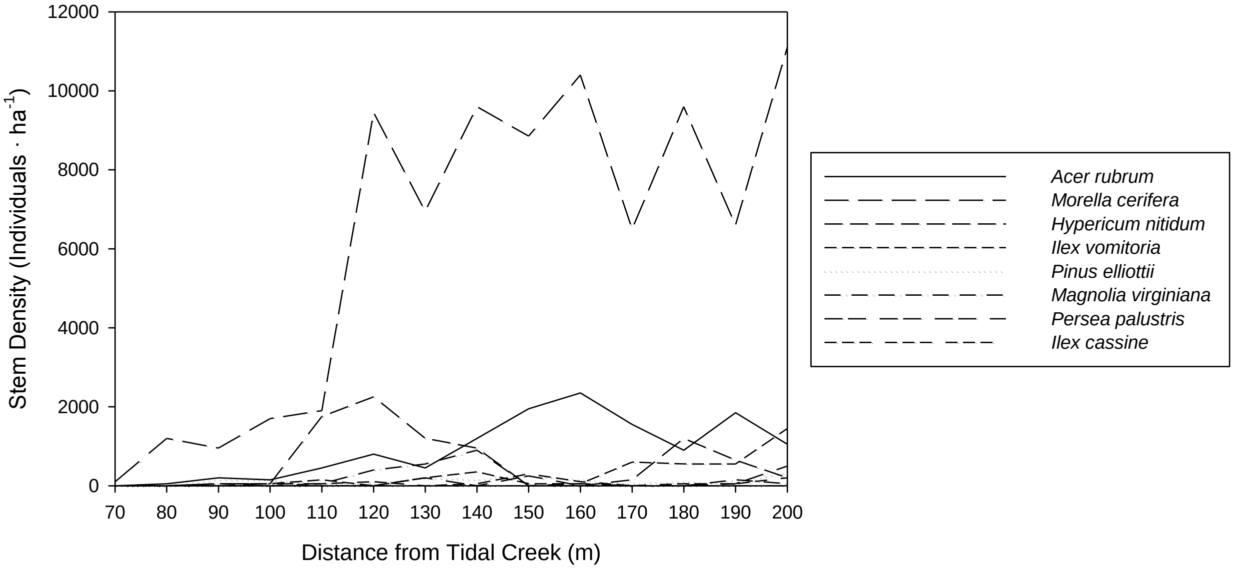
Appendix 1, Continued

Pairwise ANOSIM test results for elevation classes across in 2011.

	-10	0	10	20	30	40
0	R = 0.4780 p = 0.0227					
10	R = 0.7080 p < 0.0001	R = 0.6040 p = 0.0093				
20	R = 1.000 p < 0.0001	R = 0.9920 p = 0.0087	R = 0.8600 p < 0.0001			
30	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 0.9260 p = 0.0065		
40	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 0.8840 p < 0.0001	
50	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 1.000 p < 0.0001	R = 0.9960 p = 0.0071	R = 0.8840 p < 0.0001

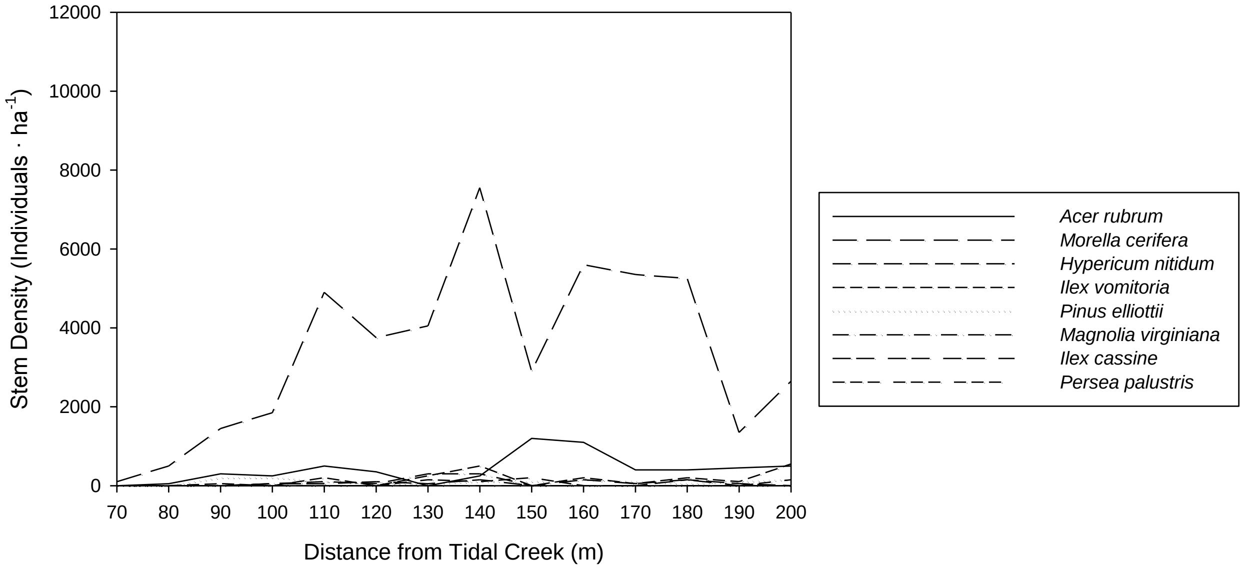
Appendix 2: Results of direct gradient analyses for 2004, 2006, and 2012. Species with fewer than ten individuals were omitted from the analysis.

I Direct gradient analysis for 2004



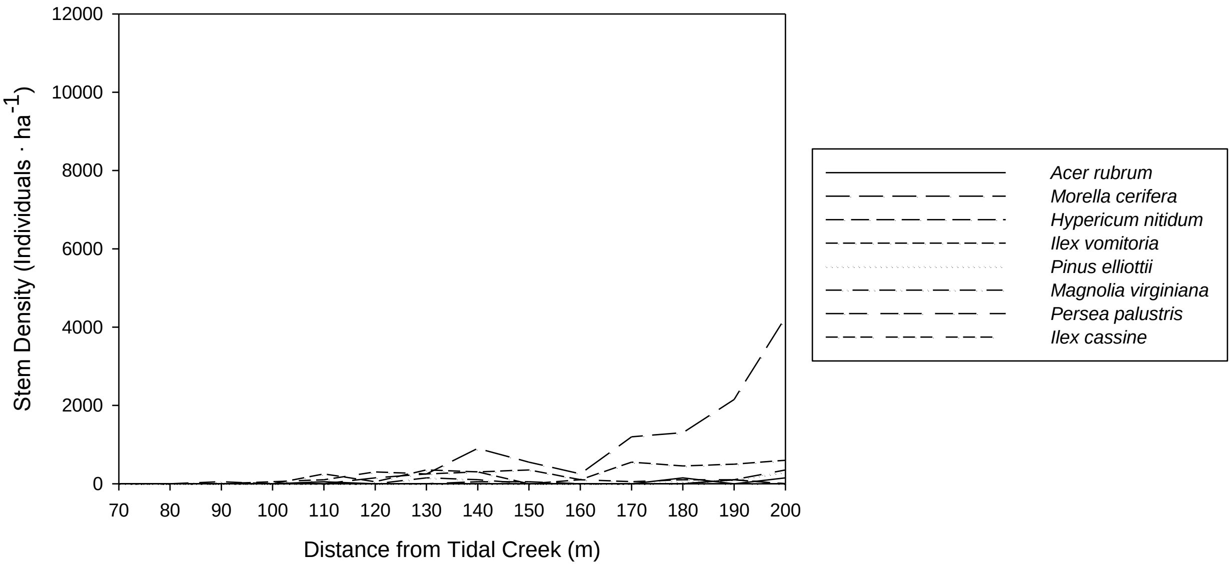
Appendix 2, Continued

II Direct gradient analysis for 2006



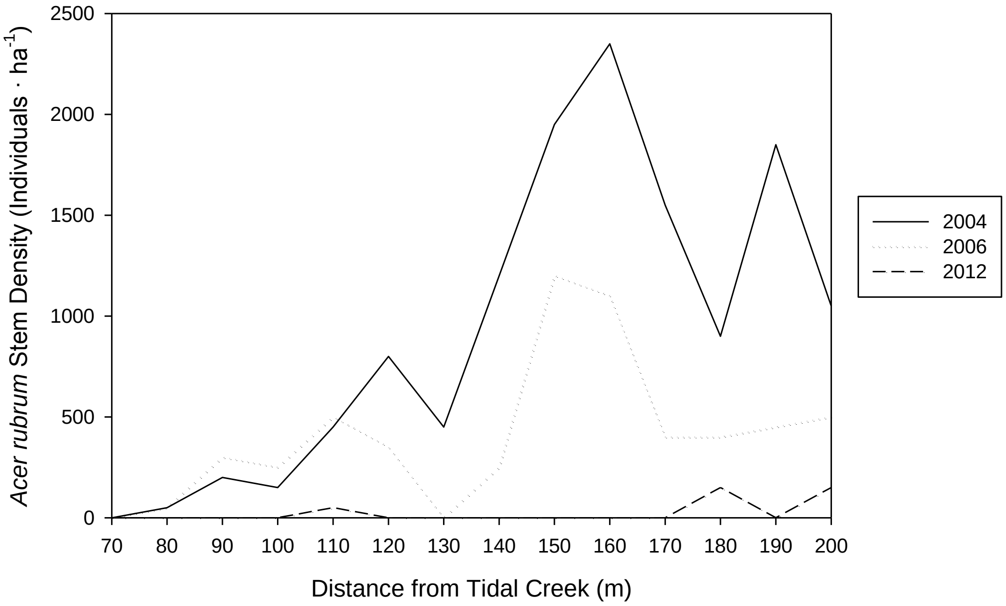
Appendix 2, continued

III Direct gradient analysis for 2012



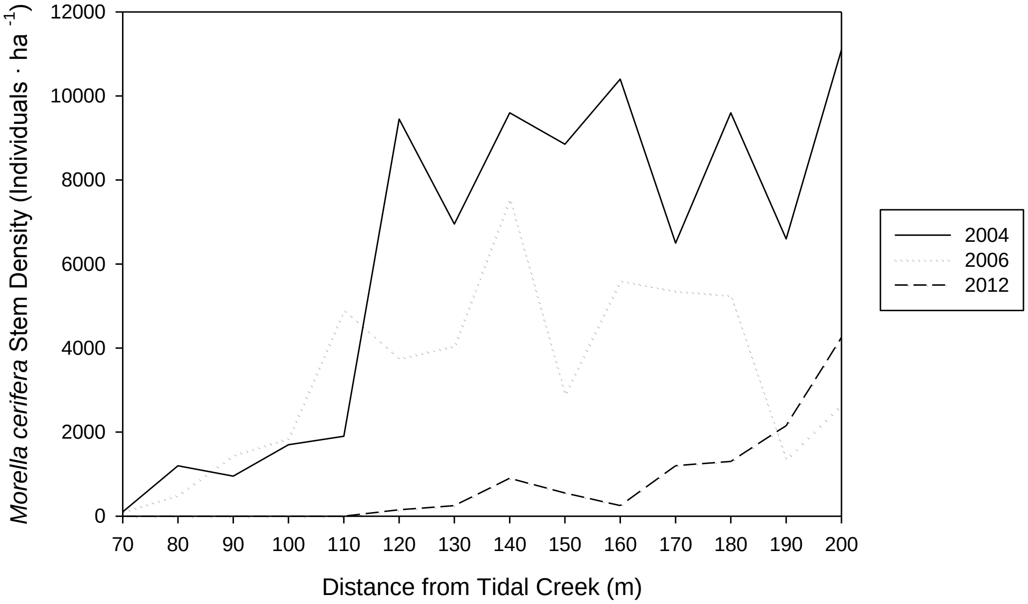
Appendix 3: Results of direct gradient analyses by species during all three time periods. Analyses show changes in species distributions across the gradient and time.

I Direct gradient analysis for *Acer rubrum*



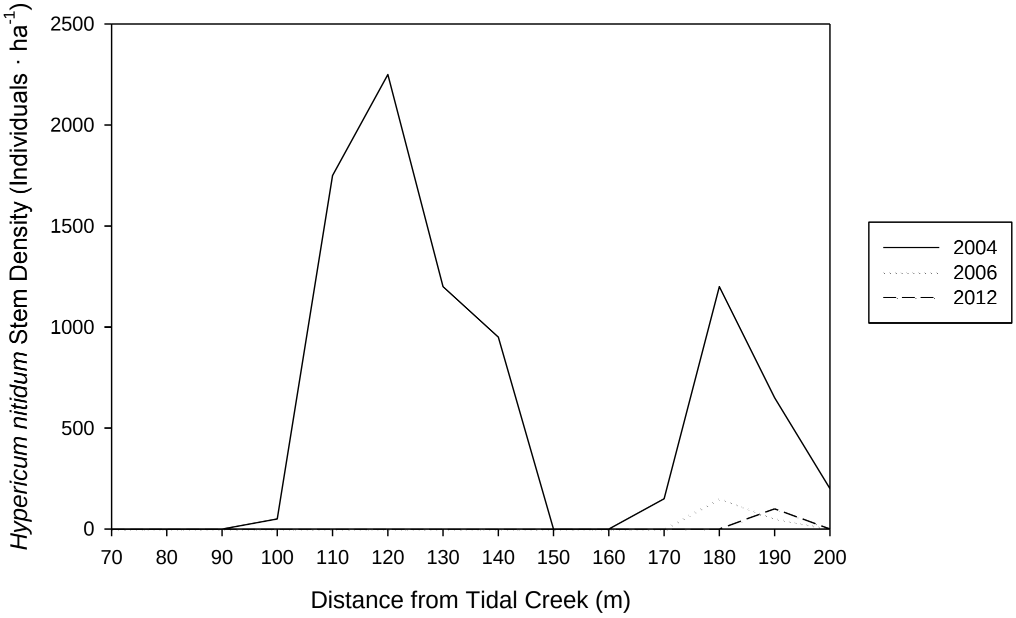
Appendix 3, Continued

II Direct gradient analysis for *Morella cerifera*



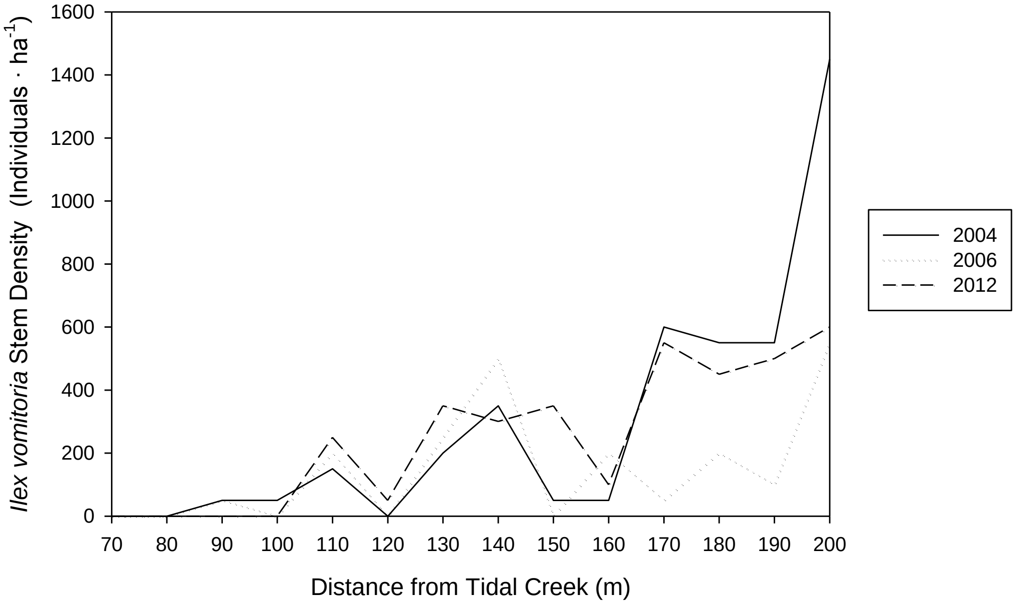
Appendix 3, Continued

III Direct gradient analysis for *Hypericum nitidum*



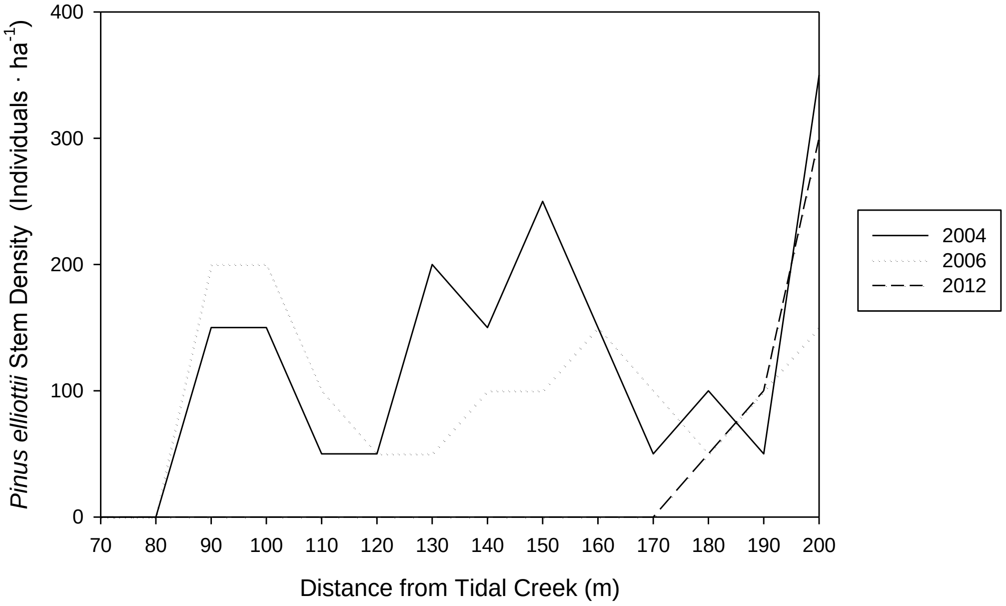
Appendix 3, Continued

IV Direct gradient analysis for *Ilex vomitoria*



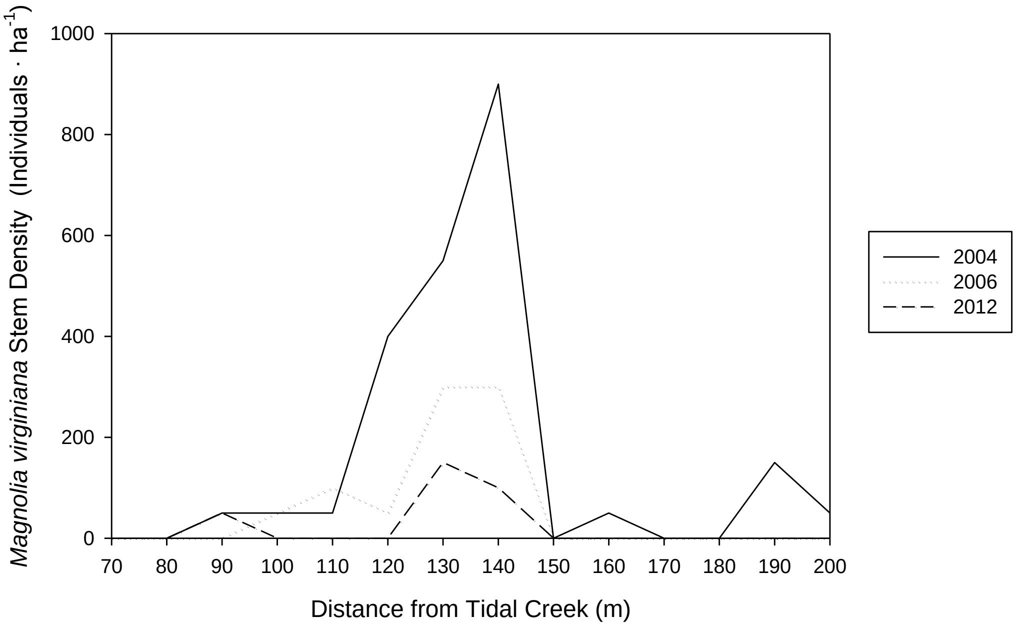
Appendix 3, Continued

V Direct gradient analysis for *Pinus elliottii*



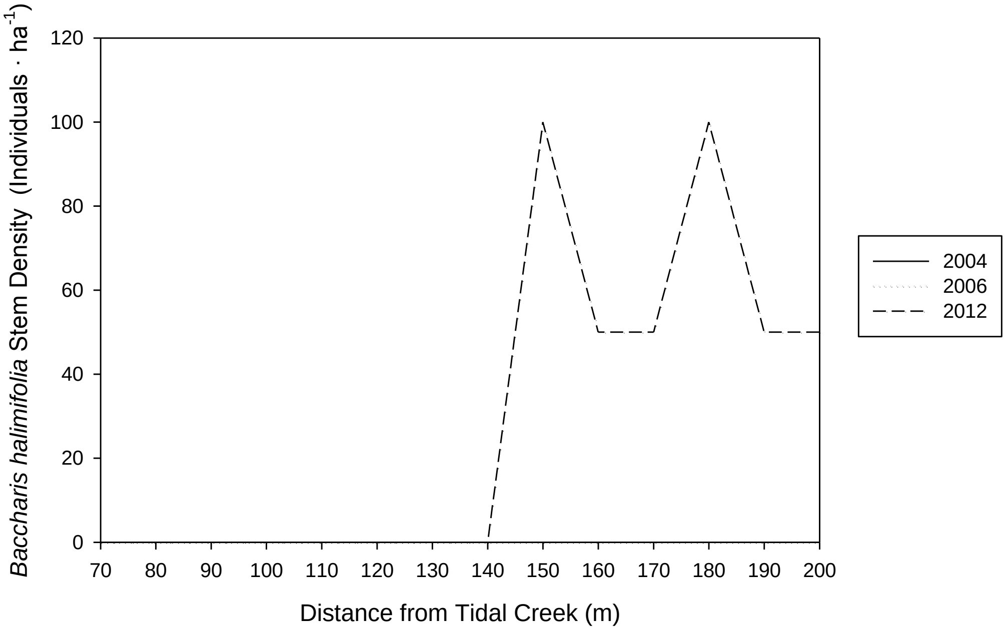
Appendix 3, Continued

VI Direct gradient analysis for *Magnolia virginiana*



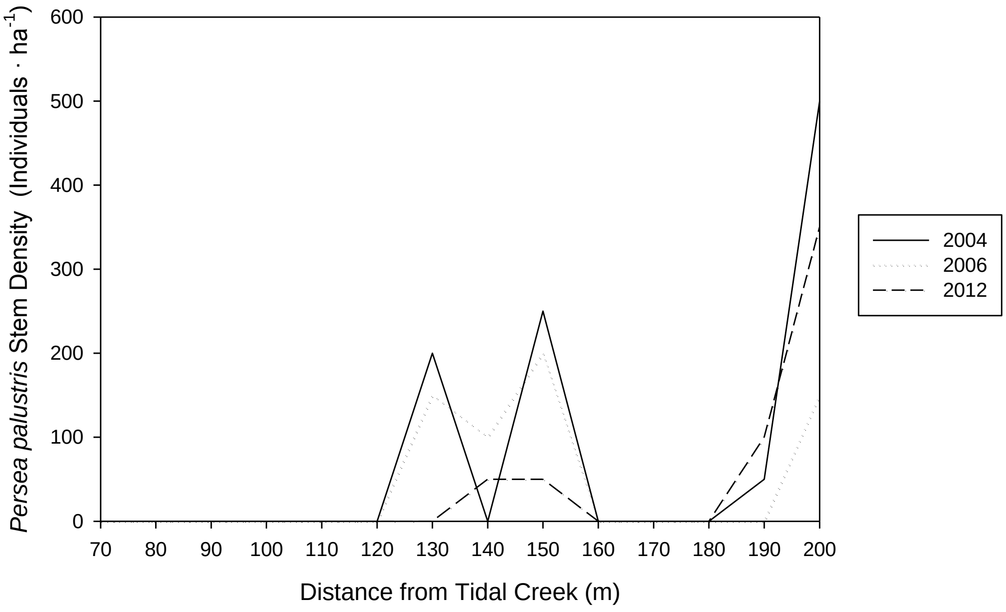
Appendix 3, Continued

VII Direct gradient analysis for *Baccharis halimifolia*



Appendix 3, Continued

VIII Direct gradient analysis for *Persea palustris*



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Fruchter, J. Accepted. Danube Delta. In: Howarth, R.W. (ed.) *Biomes and Ecosystems: An Encyclopedia.* Salem Press. Croton-on-Hudson, NY, U.S.A.

Fruchter, J., J.A. Looft, L.L. Battaglia, S. Paudel, and P.R. Minchin. In revision. Short-term changes in floating freshwater marsh communities in the Mississippi Deltaic Plain following storm surge and saltwater intrusion events. Wetlands.

Abstracts:

J. Fruchter and L.L. Battaglia. 2011. Peat balance, soil depth, and resilience in floating marshes. Oral Presentation at the 31st Annual Midwest Ecology and Evolution Conference, Carbondale, IL.

J. Fruchter and L.L. Battaglia. 2011. Do peat accumulation and loss rates vary within soil profile depths in floating marshes? Poster Presentation at the 96th Annual Ecological Society of America Meeting, Austin, TX.