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# The role of coastal plant community response to climate change: implications for restoring ecosystem resiliency

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# THE ROLE OF SEED BANKS IN COASTAL PLANT COMMUNITY RESPONSE TO CLIMATE CHANGE: IMPLICATIONS FOR RESTORING ECOSYSTEM RESILIENCY

by

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B.A., Augustana College, 2007

A Thesis
Submitted in Partial Fulfillment of the Requirements for the
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THESIS APPROVAL

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# AN ABSTRACT OF THE THESIS OF

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MAJOR PROFESSOR: Dr. Loretta L. Battaglia

Accelerated sea-level rise and increased intensity of tropical storm events have challenged the conventional approaches to conservation and restoration of coastal ecosystems. In coastal communities, where survival will depend largely on the ability of species to adapt to rapidly shifting conditions or become established farther inland, historic assemblages may be lost. Seed banks may be an important component of resilience and recovery in response to altered inundation regimes, should they contain species able to adapt or migrate inland. This study assess the ability of seed banks to act as ecological buffers to storm surge disturbances and to instill ecological resilience in degraded and vulnerable coastal ecosystems. Above-ground, seed bank and propagule assemblages were surveyed from historic communities at the Grand Bay National Estuarine Research Reserve. Artificial storm surge experiments revealed that that seed banks were not well distributed throughout the coastal transition communities and that seed bank responses following storm surges are likely to vary among the different plant communities. While some relict species are expected to respond following disturbances, ruderal species are especially dominant in the upland seed bank communities and may, at least in the short term, cause shifts away from the historical assemblages. The apparent absence of seaward species in the upland seed banks may make assisted migration an important tool for the survival of communities unable to keep pace.  Community response following translocation of propagule bank application onto highly degraded buyout properties suggested that this technique may be an effective tool in introducing resilience into ecosystems already experiencing the effects of climate change. They resulted in the establishment of diverse and variable communities, containing indicator species from a number of historic communities with varying environmental tolerances. Long-term monitoring of community change and reproductive output of target species may indicate the utility of community translocation in creating resilient and future-adapted communities.

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# INTRODUCTION

***Impacts of climate change on coastal plant communities***—

Climate is one of the greatest drivers of compositional and functional change among ecosystems. Increases in atmospheric carbon dioxide and other greenhouse gases have been well documented and are intimately linked to the oceanic and atmospheric processes which shape coastal systems (Michener et al., 1997; Day et al., 2008). Current estimates by the Intergovernmental Panel on Climate Change (IPCC) project a global temperature increase of 2-5˚ C, as well as a rise in sea-level of 28-43 cm by the end of the century (Michener et al., 1997; IPCC, 2007). Many climate models are thought to be overly conservative regarding the potential rise in sea-levels because of the difficulties in measuring thermal expansion, as well as the growing uncertainties regarding the input of water from sea and glacial ice and possible feedbacks (Wolfson and Schneider, 2002; Meehl et al., 2005). Meehl et al. (2005) employed global coupled climate models to test the global commitment to sea-level rise due to thermal expansion alone. Their results indicate that even if greenhouse gases had been stabilized in the year 2000, air temperatures would not stabilize for approximately 100 years (an increase of 0.4°C and 0.6°C ) and that sea-level would continue to rise unabated for at least 4 centuries beyond 2100. In order to address some of the uncertainties inherent in physical modeling, Rahmstorf (2007) employed a semi-empirical approach to project future sea-levels. His models determined that using several IPCC emission scenarios, sea-level could rise 50 to 140 cm by 2100. He concluded that if the relationship he found between temperature and sea-level rise for the 20th century were to stay constant, or more likely, increase, the sea may rise more than 1 meter by the end of the 21st century. As a result, coastal ecosystems are on the front lines of climate change and will be markedly affected in a societally significant time-frame (Scavia et al., 2002; Day et al., 2008).

Coastal ecosystems evolved under a regime of sea-level rise and fall (Conner et al., 1989; Greening et al,. 2006; Paerl et al., 2006). The coastal marshes currently persisting along the Gulf of Mexico were formed during a period of high sea-level in the late Holocene and, in periods of climate-induced thermal expansion in the oceans, sea-levels have fluctuated up to 100 meters (Michener et al., 1997). Coastal plant communities typically maintain marsh elevations through the vertical accretion of organic and trapped inorganic sediments (Morris et al., 2002; Day et al., 2008). This allows the vegetation to adapt to periodic fluctuations in sea-level and the associated plant species to shift gradually according to changes in ocean conditions (Brinson et al., 1995; Mitsch and Gosselink, 2007). Unmodified coastal systems have adapted to survive fluctuations in sea-level, however anthropogenic activities which have modified the sediment delivery cycles and increased erosion throughout the coastal plains globally, have introduced uncertainties regarding the survival of vulnerable communities, including estuaries and mangroves (Michener et al., 1997). For example, the construction of levees, river diversions and flood control structures restrict the input of fresh water and nutrient-rich sediments into coastal floodplains and estuarine systems (Pont et al., 2002; Snedden et al., 2007). These modifications are a primary cause of wetland loss in the Mississippi River Delta because they interfere with the wetland's ability to maintain surface elevations approximate to sea-level rise and can result in the conversion of coastal marsh to open water (Morris et al., 2002; Snedden et al., 2007). As the rate of sea-level rise accelerates, heavily modified plant communities, such as these wetlands, which may have previously been capable of adapting or migrating, may be lost or replaced by novel communities capable of persisting. Donnelly and Bertness (2001) have observed a marked landward migration of *Spartina alterniflora,* a dominant salt-marsh species, into formerly fresh marsh habitats in conjunction with increased rates of sea-level rise in marsh communities in the Eastern United States. In the Florida Keys, increased levels of soil- and groundwater salinity due to sea-level rise have been linked to the replacement of *Pinus elliottii* by halophytes in formerly pine dominated communities (Ross et al., 1994; 2009).

In addition to the long-term impacts of accelerated sea-level rise, increases in tropical storm activities may have immediate effects on coastal vegetation. Coastal systems are intimately linked with local storm activity, which directly alters the physical environment through wind and wave action. These events can also provide a major proportion of the annual precipitation and regulate the delivery of sediments, nutrients (Paerl et al., 2006; Craft et al., 2009) and propagules (Chang et al., 2007). Due to the integral role of sea surface temperatures in the formation of tropical cyclones, climate theory and modeling suggests that a warming climate will increase the intensity of future storm activities (Schneider et al., 2002; Bender et al., 2010). Attribution of increased hurricane frequency and intensity to increasing sea surface temperatures has been very difficult and is an issue of frequent debate. Webster et al. (2005) compiled tropical cyclone statistics for the period of 1970-2004 and determined the presence of a global trend (in various ocean basins) of increasing number, duration and intensity of tropical cyclones. While increases in the duration of cyclones were found only in the North Atlantic basin, a consistent trend has emerged in intensity distribution, with an increase in the number and proportion of the more intense hurricanes (Categories 4 and 5) throughout global ocean basins. While maximum intensity of hurricanes has not changed over time, the proportion of the most intense hurricanes has increased. In the northern Gulf of Mexico, a region considered highly vulnerable to the long-term effects of sea-level rise and erosion (Thieler and Hammar-Klose, 2000), a number of other studies also support the suggestion that tropical cyclone activities have increased in their strength over the last 30 years (Hoyos et al., 2006; Elsner et al., 2008; Bender et al., 2010). Despite the inherent difficulties in predicting the complex interactions of altered sea surface temperatures, wind shear, specific humidity, ocean circulation patterns and precipitation on tropical storm behavior, mounting evidence supports the connection between greenhouse-gas induced warming and increased cyclonic activity (Emanuel, 2005; Elsner et al., 2008; Knutson and Tuleya, 2001; Hoyos et al., 2006; IPCC, 2007). Knutson and Tuleya (2004) have shown that only a 2.2 °C increase in sea-surface temperatures has the potential to significantly increase wind strength 5-10%. Scavia et al. (2002) postulate wind damage by wave action and storm surge could increase up to 25%. With increasingly intense hurricane activity and rising sea-levels predicted for this region, the effects of storm surges on the structure and function of coastal plant communities are likely to extend further inland (Michener et al., 1997; Donnelly and Bertness, 2001; Day et al., 2008).

Hurricanes are one of the most influential natural disturbances in the coastal communities in the Northern Gulf of Mexico. They are capable of directly and indirectly impacting plant communities through increased precipitation, wind and wave action and storm surge (Chabreck and Palmisano, 1973; Riggs and Ames, 2003). Wind damage resulting from storm activity typically has a greater effect on forested coastal zones and can stimulate community change by opening tree canopies and increasing light availability (Hook et al., 1991; Putz and Sharitz 1991; Battaglia et al., 1999). Wave action associated with increased wind can differentially affect coastal systems depending on their degree of human modification and land loss can rapidly occur (Hilbert, 2006; Snedden et al., 2007). Storm surge events periodically inundate and expose the coastal communities to submergence and acute, high salinity pulses which can persist in the soil for more than a year following disturbance (Chabreck and Palmisano, 1973; L. Battaglia and W. Platt, unpublished data). This inundation stress alters community structure by causing mortality of salt and flood-intolerant species and allowing for both the colonization of newly available sites and the directional replacement by more stress-tolerant species (Baldwin et al., 2001; Conner and Inabinette, 2003; Platt and Connell, 2003). Due to differential responses of plant species to these stressors, storm surge from hurricanes can act to slow and possibly alter the successional direction of coastal plant communities (Gibson et al., 1995). Ross et al. (2009) have linked the retreat and dieback of coastal forests and freshwater wetlands, and their subsequent replacement by mangrove forests, in the low-lying islands of the Florida Keys to interactions with storm surge pulses. Because inundation gradients have a pronounced effect on community structure, the timing and intensity of storm surge events, which are associated with what are predicted to be increasingly intense tropical storms, are expected to continue to alter the composition of coastal communities in the future (Hook et al., 1991; Brinson et al., 1995; Najjar et al., 2000; Donnelly and Bertness, 2001; Crain et al., 2008).

***The role of seed banks and storm surge on coastal plant communities***—

Seed banks, the germinable portion of deposited seeds available for recruitment into a community, have been widely studied in most major ecosystems and vary compositionally due to complex life history characteristics and disturbance tolerances of the above-ground vegetative community (Johnson, 1975; Leck and Simpson, 1987; Henderson et al., 1988; Haukos and Smith, 1993). Seed banks have both persistent and transient components and contain perennial and annual species with varying intraspecific viabilities, dormancy states and germination requirements (Thompson and Grime, 1979; Hutchings and Russell, 1989; Leck, 1989). The composition of a seed bank is regulated by the presence of current and historical seed sources and by species-specific dispersal mechanisms (seed rain, hydrochory, herbivory); it can vary seasonally due to climactic variability and disturbance regimes and legacies (Hopfensperger, 2007). Transient components of the seed bank remain viable in the seed bank for only one growing season and may be seasonally recruited into the above-ground plant community (Hutchings and Russell, 1989; Leck, 1989). Seeds within the persistent portion of the seed banks are capable of remaining dormant but viable for an extended period of time (>1 year) until environmental cues, such as air temperature, pH, soil chemistry and moisture availability, signal conditions appropriate for germination. Thus, the emergence of seeds from the seed bank is intricately linked to variation in climate (Csontos, 2007). Additionally, the recruitment of seedlings into a community is governed by both the physiological constraints on the seedlings themselves and the competitive interactions with other biota which may limit or facilitate their survival. The above- ground vegetation is, therefore, not necessarily representative of the total pool of species available for recruitment.

Hopfensperger's (2007) assessment of 282 studies evaluating patterns of floristic similarity between plant communities and the associated seed banks across broad ecosystem types (forest, grassland, wetland) indicates that seed banks are of varying importance in shaping plant communities. In disturbed areas, for example, seed banks can play a large role in the development of the early successional community. Looney and Gibson (1995) reported low similarity (Jaccard's Index = .36, ~ 37%) between the above-ground vegetation and the seed bank of a coastal barrier island off the coast of western Florida. Their investigation into the patterns of seed bank development on a landscape level, however, indicated that seed bank composition can be a good indicator of the dominant above-ground vegetation, the successional stage of an ecosystem type and the level of disturbance experienced. In cases of dispersal limitation or high rates of granivory, it has also been shown that seed availability can be the limiting factor in community composition (Yorks et al., 2000; Battaglia et al., 2007; Morzaria-Luna and Zedler, 2007).

Seed banks have been recognized as powerful tools for predicting community change in coastal systems and are essential variables in understanding the regulation of community succession, post-disturbance dynamics and recovery in coastal landscapes (Leck and Simpson, 1987; Leck, 2003). Due to the high environmental variability between sites along a hydrological or elevational transition, only a handful of studies have assessed seed bank composition and distribution on a landscape scale or across ecosystem transitions (Brinson et al., 1995; Peterson and Baldwin, 2004; Liu et al., 2006; Crain et al., 2008). Seed rain and hydrochory may result in well-mixed seed banks containing components from a variety of plant communities along the elevational transition (van der

Valk, 1981; Egan and Ungar, 2000). Despite the distribution of species present in the seed bank, plant communities along the coasts are often compositionally aligned in zones parallel to the sea due to salinity and hydrologic gradients (Shumway and Bertness,1992; Pennings et al., 2005). This is especially pronounced in salt marsh plant communities, in which successively competitive species occupy the higher marsh locations and the less competitive but more salt-tolerant species persist along the marine edges (Bertness and Ellison, 1987; Pennings et al., 2005; Engels and Jensen, 2010). In the Gulf Coastal Plain along the Northern Gulf of Mexico, the vegetation typically transitions from salt marsh, consisting of halophytic plant communities capable of tolerating frequent inundation with seawater, into pine-wiregrass dominated upland communities that experience occasional pulses of seawater but are primarily regulated by precipitation and availability of light (Hilbert, 2006; Shirley and Battaglia, 2006)

*Seed bank dynamics in coastal marshes*—

Wetland seed banks vary a great deal due to differing hydrologic and chemical characteristics and, as a result, seed bank similarity and dynamics are also quite variable (van der Valk, 1981; Leck and Simpson 1987; Leck, 1989). Seeds are usually not evenly distributed throughout the landscape due to different dispersal mechanism and this can result in heterogenous and patchy patterns of seeds. Some wetland plants have low seed viability or produce large seeds that are not often obtained by traditional sampling methods. Additionally, the presence or absence of transient species in the soil is determined by the timing of seed bank sampling. As a result of the complexities of patch dynamics and seasonal variation in seed availability, seed bank studies have been found to overestimate and also underestimate species throughout the landscape (Shumway and Bertness, 1992; Egan and Ungar, 2000; Morzaria-Luna and Zedler, 2007).

In coastal marsh communities, fundamental differences exist in the seed bank along a gradient of salinity. These differences, which include the proportion of transient and persistent seeds, species of available seeds and density of seeds, are also reflected in community development and in the expression of the above-ground vegetation. This salinity gradient, or range of salinity concentrations as one moves away from the sea, is commonly the feature used in categorizing different marsh communities. For the purpose of this study, what is commonly referred to as the “low” or “hypersaline” marshes will be called salt marshes (soil salinity~28 ppt); the “mesohaline” marshes will be referred to as brackish (soil salinity ~10–20 ppt); and the “high” or “oligohaline” marshes will be referred to as fresh marshes (soil salinity ~0–5 ppt) (Baldwin and Mendelssohn, 1998; Crain et al., 2008).

Experiencing extreme and usually daily inundation by the tides, salt marsh communities and seed banks are shaped by the extreme environments in which they persist. Salt marsh communities tend to be compositionally simple and stable from one growing season to the next, consisting of one or two dominant perennial tuft-forming halophytic species arranged predictably in zones based on salinity tolerances (Bertness and Ellison, 1987; Crain et al. 2008). Hutchings and Russell’s (1989) study on the seed regeneration dynamics of a salt marsh in Sussex, U.K. yielded an estimated total seed output, entirely transient, ranging from 11,000 seeds/m$^2$, to 20,000 seeds/ m$^2$ and the viability of seeds collected ranged from 22.5% to 95%. They also found substantial similarity between the seed bank and vegetation, likely due to high germination rates of species with high seed-production rates. In the saline coastal marshes off the coast of Perdido Key in Florida, Looney and Gibson (1995) evaluated seedling density to be 9,702 seeds/m$^2$, 75% of which were perennial and 56% of which were deemed to be indicators of the above-ground vegetation type. Additionally, clonal reproduction tends to be a more dominant pathway for regeneration in salt marshes (Shumway and Bertness, 1992) and therefore seed bank species richness and density are often far less developed than in less saline marshes (Crain et al., 2008).

The effects of water level and salinity on salt marsh vegetation have been widely investigated (McKee and Mendelssohn, 1989; Broome et al., 1995; Baldwin and Mendelssohn 1998, Howard and Mendelssohn 1999). These factors, alone and in combination, have also been widely shown to suppress germination and recruitment from wetland seed banks (Webb and Mendelssohn, 1996; Baldwin et al., 2001; Willis and Hester, 2004). Bare patches tend to develop vegetation very slowly due to the suppression of germination by elevated salinity levels. Flushing salt marsh seed banks with fresh water has been shown to alleviate salt suppression and to promote seedling establishment in both saline and fresh marsh habitats (Shumway and Bertness, 1992; Flynn et al., 1995).

Seed banks in freshwater to brackish tidal marshes have a stronger annual species component and are generally more representative of the aboveground vegetation than more saline marshes (Leck and Simpson, 1987; Leck, 1989). Because of the more important role of annuals, in some cases up to 90% of the vegetation (Leck and Simpson, 1995), community response is much more difficult to predict.  In part, this is because the importance of annual recruitment from the seed bank varies among species and species richness also varies between different life history stages (*i.e.* seeds, seedlings, mature plants). In their ten year assessment of seed bank and vegetation dynamics in a freshwater tidal marsh in New Jersey, Leck and Simpson (1995) found that species diversity fluctuates annually and that no correlation could be found between the seed bank, seedling and vegetation dynamics. Crain et al.’s (2008) landscape-scale study of secondary succession mechanisms along an estuarine system indicates that the freshwater wetland had a species pool 24 times greater and higher seed production than either the brackish or salt marsh. Recovery of bare patches was also reportedly much quicker due to higher overall seed availability, favorable conditions for germination and the combination of seedling colonization and vegetative reproduction. Although inundation and salinity stress negatively affect recruitment from fresh and brackish wetland seed banks as with salt marsh seed banks, there can be twice as many seedlings and five times as many species germinating from non-flooded seed banks (Baldwin et al., 2001).

*Seed bank dynamics in longleaf pine savannas*—

Longleaf pine savannas are a major conservation concern because of intense anthropogenic disturbance, fire dependent-community dynamics, as well as the biodiversity and high number of rare and endemic taxa present (1630 taxa) (Sorrie and Weakley, 2006). The longleaf pine savanna ecosystem was dominant in the Atlantic and Gulf Coastal Plains of the Southeastern United States prior to European settlement but is now only <3% of its prior coverage (Franks and Platt,2006). Dominated in the overstory by Longleaf pine (*Pinus palustris*), these upland savannas, also referred to as pine flatwoods and pine-wiregrass savannas, are highly regulated by gap dynamics involving fire and hurricane activity, and in undisturbed systems experiencing natural fire regimes , are capable of containing a highly diverse herbaceous understory (Beckage et al., 2006; Hinman and Brewer, 2007). Fire-dependent systems contain species dependent on fire disturbance for the stimulation of flowering, recruitment and dispersal. In many of these systems, fire suppression, logging and grazing have significantly altered the disturbance regimes necessary to naturally maintain these systems (Ruth et al., 2008).

Seed bank dynamics in the longleaf pine dominated savannas characteristic of the Coastal Plain in the Northern Gulf of Mexico have begun to be assessed for their importance in restoration. While some seed bank research indicates that frequently disturbed communities tend towards the production of large, persistent seed banks, scale and predictability of a disturbance may determine the importance of the seed bank in the recovery of a system (Pickett and McDonnell, 1989; Thompson 1992). Cohen et al. (2004) verified the presence of a persistent seed bank component in various *Pinus palustris* communities throughout coastal North Carolina, however, most of the taxa represented “weedy” or “fugitive” species. Andreu et al. (2009) evaluated seed bank composition at disturbed and undisturbed longleaf pine-wiregrass sites and similarly determined the presence of both relict/indicator and non-native species in the seed banks. In contrast, Coffey and Kirkman’s (2006) evaluation found only transient/short-term persistent seeds indicative of the historical *Pinus palustris* communities. Hopfensperger (2007) reviewed patterns in seed bank studies across ecosystem types (forests, grasslands, wetlands) and determined that seed banks of forested ecosystems are the least similar to their standing vegetation, averaging similarity values less than 60%. This discrepancy between vegetation and seed bank composition is thought to be the result of a number of characteristics of forested systems, including the low germination of large, persistent seeds forming the canopy layer, the clonal nature of shrub vegetation, the higher predation on larger seeds by birds and small mammals and the technical difficulties involved in obtaining large seeds for seed bank and greenhouse studies (Cohen et al., 2004; Hopfensperger, 2007). Beckage et al. (2006) hypothesized that in the pine dominated systems of the southeast, increases in atmospheric CO2 and altered fire and hurricane disturbances may result in increased canopy cover and further reduction in the herbaceous understory. Ruth et al. (2007, 2008) attributed the low seed bank viability found in their study of pine-scrub seed banks to this increase in canopy cover and decrease in gap availability.

### *Storm surge and seed bank dynamics*—

The contribution of seed banks to community dynamics in systems undergoing climate change is poorly understood. As climate change begins to alter the stage upon which communities develop and recover (Thompson and Grime, 1979; van der Valk, 1981; Parker and Leck, 1985), as well as potentially increase acute and chronic inundations by the sea (Najjar et al., 2000), the threat of further loss and degradation of coastal systems makes it essential to assess the possible effects of these inundations on seed bank availability and regeneration.

Due to the unpredictable nature of tropical storms (e.g. timing and intensity), inferences about storm surge impact on seed bank communities are typically based on the known effects of inundation and salinity stress on germination and seedling dynamics. The conditions following the recession of storm surge can vary but high levels of salinity and inundation have been shown to both reduce and suppress germination rates of several dominant coastal species (Baldwin and Mendelssohn, 1998; Baldwin et al., 2001). Storm surges have been shown to influence long-distance patterns of propagule dispersal and retention in tidal communities and are capable of altering microsite characteristics for more than a year following recession (Chang, 2007).

Studies are beginning to emerge which assess patterns of recruitment and recovery of coastal systems following the retreat of natural storm surges (Middleton, 2009 a,b; Miller et al., 2010). While the initial recovery and regeneration following recession of storm surge are driven by surviving individuals and response of the potential flora already residing in the soil seed bank, patterns of recovery vary among ecosystems. In coastal forests, saltwater influx from the storm surges can result in high mortality of many tree species but also increased seedling regeneration due to the higher light availability (Conner and Inabinette, 2003; Middleton, 2009a). Middleton (2009b) evaluated seedling regeneration in the coastal marshes following storm surges of Hurricanes Katrina and Rita and found significantly higher seedling regeneration with increasing distance from the sea in both field and seed bank studies. Additionally, the application of salinity and flooding treatments indicated that higher sea-levels and increased inundation by storm surge would probably result in lower germination and recruitment from marsh seed banks. In coastal barrier island and sand dune communities, which are frequently disturbed by storm events, the spatial structure of their plant and seed bank communities has also been shown to be related to their distance from the shoreline and/or frequency of disturbance by surge events (Looney and Gibson, 1995; Miller et al., 2010). Very little information exists from which to determine the potential for recovery and reassembly of inland communities which are not ordinarily exposed to storm surge. Therefore, predictions of coastal community response to increased storm surge will require an improved understanding of the presence and composition of seed banks which act as a source for regeneration, as well as their ability to withstand and recover from increased storm surge stress.

***Restoration targets and the utility of donor propagule banks in coastal plant communities***—

As climate change alters the ecological template on which plant communities develop, new approaches to restoration will be essential for the survival of vulnerable ecosystems and species. Conventional restoration approaches rely on a baseline historical condition as a target, but shifting environmental conditions necessitate an approach which considers the potential future communities that a site may support (Harris et al., 2006; Hobbs et al., 2009). In recognition of the need for a definition of ecological restoration not solely focused on historical recovery, the Society for Restoration International (SERI) recently changed its definition of "ecological restoration" to the more open-ended "process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SERI 2004). Saxon et al. (2005) used mapping techniques to predict which ecosystems were most at risk due to climate change impacts and determined that over half of the land in the United States would experience altered moisture, soil and temperature conditions so significant that historic ecosystem features could no longer be supported. Mitsch and Gosselink (2007) estimate that with a 1 m rise in sea-level, 26-66% of coastal wetlands will be lost to the sea, making the question of appropriate restoration targets for the coasts a major priority both ecologically and economically. Although major uncertainties remain, restorations that do not consider predicted sea-level, precipitation and air temperature conditions may be both unsuitable and unproductive (Choi et al., 2008). For example, reforested coastal sites may be inundated by the ocean before the woody species planted even reach maturity.

A common theme in discussion of the appropriate targets for "futuristic" restorations is the importance not only of maintaining ecosystem function but actually creating habitat that will act to protect future assemblages given different climactic conditions (Harris et al., 2006). Given knowledge of an assemblage's historical range and known climate, species-specific tolerances for temperature and precipitation and our knowledge of how and when migration occurs, it may be possible to evaluate a site and estimate its potential to support a variety of different community types (Davis, 1994; Berry et al., 2002; Harris et al., 2006). If restoration ecologists were able to build resilience into a system and accommodate the likely pathways plant communities might take as climate changes the environment, they may be able to conserve valuable ecosystems and encourage their survival (Lavendel, 2003; Choi et al., 2008). In fragmented landscapes or protected areas, this resilience might involve creating or expanding corridors to aid in dispersal (Hannah, 2008). It has also been suggested that using plant materials from both local and non-local sources may increase genetic variability and adaptability in restorations likely to experience rapid abiotic changes (Harris et al., 2006). Should climate change result in a rapid reduction in the available habitat or a major geographic shift in the bioclimatic envelope in which a species can exist, however, many species may not be able to persist in the range they previously occupied (e.g., montane, desert or island species) (Vitt et al., 2010 ).

Although it is an issue of considerable debate among conservationists and ecologists, assisted migration of a species or assemblage has been considered as a mechanism for aiding the survival of species with a low likelihood of survival in future climate scenarios (McLachlan, 2007; Hoegh-Guldberg et al., 2010; Sandler 2010). The movement of rare or vulnerable species outside of their known range presents serious concerns about invasion but may be the only mechanism for those species unable to migrate or disperse quickly enough to keep up with the pace of climate change.

The donor propagule bank, which is also referred to as the soil seed bank, the diaspore bank, a community translocation, a top soil translocation, a propagule amendment, a soil stockpile and as mulch) has shown potential for providing disturbed or degraded systems with this resilience by providing a variety of propagules and allowing the environment to determine which assemblages it is capable of supporting. The process involves the removal and transfer of topsoil containing both seed and vegetative propagules from a donor site onto a recipient site and is often performed to aid in mitigation for civil engineering projects in which the donor site will no longer be appropriate habitat (i.e., excavation, road building, filling of wetlands, etc.) (Bullock, 1998). If effective, restorations which employ propagule banks for revegetation are efficient and low-impact; these projects introduce diverse plant species capable of hindering the establishment of non-target species, such as invasives (Brown and Bedford, 1997; McKnight, 1992), and the locally adapted microbial community necessary for the proper functioning of the given system (Harris, 2009; Zedler and Kercher, 2005). When propagule sources are not widely available, due to dispersal limitation or site degradation, passive revegetation from the seed bank may not be successful in meeting restoration targets. Propagule limitation has been shown to be a limiting factor in the natural regeneration and restoration of some coastal plant communities (Middleton, 2009a; Morzaria-Luna and Zedler, 1992; Ruth et al., 2008). Donor propagule banks have been used with some success in the restoration or community enhancement of a variety of plant communities, including non-tidal, freshwater wetlands (McKnight, 1992; Brown and Bedford, 1997; Stauffer and Brooks, 1997; Anderson and Cowell, 2004;), lakeshore vegetation (Nishihiro et al., 2006), rich fens (Cobbaert et al., 2004), abandoned sand mines (Vivian-Smith and Handel, 1996), meadows and grasslands (Bragg, 1986; Stiegman and Ovenden, 1986; Vecrin and Muller, 2003) and roadway buffers (Nordbakken et al., 2009).

Limited data are available, however, about the potential of donor seed banks for conserving coastal systems and there do not appear to be any previous studies documenting community level effects of applying donor banks along the coasts. Salt marsh restoration studies tend to focus on the importance of clonal reproduction and hydrochory as mechanisms for seed dispersal and revegetation (McKnight, 1992; Thompson, 1992; Morzaria-Luna and Zedler, 2007). Leck's (2003) investigation of seed bank and vegetative response in a tidal marsh in New Jersey illustrated that regional and local dispersal sources were adequate for natural regeneration and that stockpiled donor material, as is often used on created wetlands, would be unnecessary. In longleaf pine savannas, replanting of *Pinus palustris* can be done quite successfully, however the fire-maintained herbaceous ground cover can be more difficult to restore if lost (Cohen et al., 2004). Mixed results have been found about the presence of persistent seed banks in longleaf pine systems; in some cases, seed banks appear to lack a sufficiently viable and diverse persistent component (Coffey and Kirkman, 2006; Rush et al., 2008). Cohen et al. (2004), however, found a viable and persistent seed bank for both weedy and rare species indicative of longleaf pine communities throughout several disturbed and undisturbed former longleaf pine savannas in North Carolina. The loss of the diverse herbaceous component in the seed bank is recognized widely and restoration efforts in these systems appear to require some form of seed reintroduction as a necessary component (Coffey and Kirkman, 2006; Iacona et al. 2010).

Given the uncertainties regarding the ability of the coastal plant communities to respond to increasingly intense and further reaching storm surges, further research is needed to examine the potential for seed banks to not only aid in the recovery following disturbances but also in the possible transition to more seaward assemblages as the environment changes. If it determined that seed and propagule banks are sufficient to “buffer” coastal plant communities from acute surge events, they may also be important tools for instilling resilience into and guiding the restoration of degraded sites already experiencing the effects of climate change.

# CHAPTER 2

# SEED BANKS AS COMPONENTS OF ECOSYSTEM RESILIENCE IN COASTAL ECOSYSTEMS EXPOSED TO HURRICANE STORM SURGE

## ABSTRACT

The contribution of seed banks to community dynamics in systems experiencing climate change is poorly understood. Plant communities with seed banks containing species able to adapt or migrate inland may be able to survive the rapid environmental changes associated with the acceleration of sea-level rise and intensified storm surge. Assemblages that do not have a resilient and responsive seed bank, however, may not be capable of surviving altered inundation regimes. The objectives of this study were to evaluate the composition and species distribution of the standing vegetation and seed banks in major vegetation zones along a typical Gulf Coast transition and to assess the effects of simulated storm surge on seed banks to predict community change with altered inundation regimes. I hypothesized that seed dispersal throughout the transition results in well-mixed seed bank communities that are capable of acting as biological buffers, which provide propagules for variety of potential assemblages following acute storm surge events. In June 2009, I sampled the standing vegetation and seed bank along six dominant vegetation zones in the intact coastal transition at Grand Bay National Estuarine Research Reserve (GBNERR) in coastal Mississippi. In order to assess the likely response of the seed banks to experimental storm surge, I examined the germinable seed bank using the Seedling Emergence Method (SEM) following a three-day exposure to full-strength seawater. Analyses of the species composition of the standing vegetation and seed banks reveal a pattern of increasing plant species diversity with distance from the sea that is correlated with declining soil salinity.

Most seed banks were comprised of a subset of species present in the standing vegetation but saline marshes exhibited much higher resemblance to their seed bank communities. The upland seed banks contained some indicator and dominant species but largely contained transient and weedy species not present in the standing vegetation. Storm surge treatments reduced seedling abundance and richness across all vegetation zones. This study suggests that seed banks may of minor importance following storm surge events and further studies may show that vegetative growth may be more dominant. Evidence from this study suggests disturbances would likely result in replacement of some species present in the former vegetation but that upland seed banks are poorly equipped to act as a seed source following storm surge events. Intense storm surges which affect inland communities may facilitate invasion by exotic and weedy species and decrease species overall species richness. Future research should be aimed at the total propagule availability, including vegetative propagules, in better assessing ecosystem resilience.

## INTRODUCTION

The contribution of seed banks to community dynamics in systems experiencing climate change is poorly understood. In coastal marshes, seed bank development is affected locally by hydrochory and the salinity gradient generated by regular tidal activity but may also be affected further inland following hurricanes (Nathan et al. 2005; A.Tate and L.Battaglia, SIUC, unpublished). Initial recovery following recession of storm surge events is driven by surviving individuals and response of potential flora already residing in soil seed banks (Middleton, 2009b). These dynamics are of particular importance in the northern Gulf of Mexico, which has experienced a near doubling in the proportion of intense tropical storms (Category 4 and 5) over the last 30 years (Webster et al. 2005; Bender, 2010), and is expected to see increasingly intense storm surge events in the future (Najjar et al., 2000). To further complicate the issue, these acute disturbances are occurring in conjunction with much higher sea-levels, and climate models project a rise in sea-level of 28-43cm by the end of the century (Church and White, 2006; IPCC, 2007). Predictions of community response to intensified storm surge will require an improved understanding of seed bank composition of seaward and inland communities across the entire coastal transition, as well as their ability to withstand and recover from increased storm surge stress (Middleton, 2009a; b; Miller et al., 2010). If seed banks contain species capable of recruitment following storm surge events, or future climate conditions, they may contribute to community recovery and survival. If the seed banks, however, are as discretely zoned and contain the same suites of species as the coastal vegetation (Ungar and Riehl, 1980; Bertness and Ellison, 1987; Pennings et al., 2005), they may not contain the best suited species for responding favorably to storm surge and may not become quickly established in situ.

Seed bank composition is rarely assessed across ecosystem transitions due to the high environmental variability between sites along hydrological and elevational gradients. (Brinson et al., 1995; Liu et al. 2006). The storm surges generated by Hurricane Katrina in 2005 penetrated more than 12 km inland, inundating the interior plant communities, which are not regularly exposed to the sea, and depositing sediments and wrack in massive beds up to 12 km from the sea’s edge. Seed bank studies have traditionally focused on the complexity of local factors which drive and influence seed bank development and seedling recruitment in one type of community (van der Valk and Davis, 1976; Hutchings and Russell 1989; Baldwin et al., 2001). Studies have emerged which argue that in wetland complexes, in which seed banks are very important in recovery and propagules are widely dispersed through water, regional and landscape level processes may play a large role in seed bank regulation (Peterson and Baldwin, 2004; Liu et al., 2006; Crain et al., 2009). While the distribution of seeds in the soil is often heterogenous and patchy, with most seeds being dispersed within the vicinity of the parent plant (Chang et al., 2007; Csontos, 2007), small-scale studies may not be adequate to reveal the ecologically meaningful patterns that may result from long-distance dispersal of seawater and propagules in storm surge events.

Extensive research has been done on the relationships between the seed bank and associated standing vegetation in tidal marshes, which can fundamentally differ in composition along a gradient of salinity and inundation (Parker and Leck, 1985; Hutchings and Russell, 1989; Ungar and Woodell, 1993). Coastal plant communities are often compositionally aligned in zones parallel to the sea due to differential physiological tolerances to the salinity and inundation gradient (Shumway and Bertness, 1992; Pennings et al., 2005). This zonation is especially pronounced in marsh communities, in which successively competitive species occupy the higher marsh locations and the less competitive but more salt-tolerant species persist along the marine edges (Bertness and Ellison, 1987; Bertness, 1991; Pennings et al., 2005). In the Gulf Coastal Plain along the Northern Gulf of Mexico, the vegetation typically transitions from salt marsh communities, consisting of halophytic species capable of tolerating frequent inundation with seawater, into pine-wiregrass dominated upland communities that experience occasional pulses of seawater but are primarily regulated by precipitation and availability of light (Hilbert, 2006; Shirley and Battaglia, 2006).

Much less is known about seed bank composition in the pine communities that inhabit the upland end of the coastal transition. Seed bank surveys in the upland longleaf pine communities have been driven by interest in restoration and reintroduction of fire into the landscape (Platt, 1999; Ruth, 2007; 2008) but have largely found seed banks to be undeveloped and unrepresentative of the species richness found in the standing vegetation (Cohen, 2004; Coffey and Kirkman, 2006; Andreu et al., 2009). The seed banks of the maritime pine communities, which are more frequently exposed to salt spray and storm surge, are largely unstudied.

Given the potential for propagules to be moved directly by water (Huiskes et al., 1994; Chang et al., 2007),wind (Willson, 1993), sediment (Goodson et al., 2003) and wrack (Mitchinton, 2006; A. Tate and L. Battaglia, SIUC, in prep.), I am interested in determining if there is storage of seeds from the seaward communities further upland, in which species pools and abiotic conditions are quite different. While seed banks in marshes are often mixed locally, containing species representative of other marsh types along an elevational or salinity gradient (van der Valk 1981; Egan and Ungar 2000), to my knowledge, no studies have yet surveyed the potential overlap of species in seed banks across the estuarine marsh-wet pine forest transitions which formerly characterized much of the Gulf of Mexico. The objectives of this study are: 1) to characterize the species composition in the standing vegetation along a typical Gulf Coast transition, 2) to evaluate the composition and distribution of seed banks in major vegetation zones and 3) to assess the effects of simulated storm surge on emergence from seed banks to predict community change with altered inundation regimes. I hypothesized that seed dispersal occurs throughout the coastal transition, resulting in well-mixed seed bank communities that are capable of acting as diverse and viable seed sources following acute storm surge events. Specifically, it is hypothesized that species dominant in the seaward communities will be present in the upland seed banks and that salinity suppression may reduce the emergence of upland species and favor the emergence of halophytes.

## METHODS

***Site Description***—

The research site, Grand Bay National Estuarine Research Reserve (GBNERR), is a 7284-hectare complex containing one of the largest intact transitions of emergent marsh-wet pine flatwood assemblages remaining in the Gulf of Mexico (Fig. 2.1). It is located in the low-lying Gulf Coast Plain in southeastern Mississippi and is a marine protected area established in 1999 as part of the National Oceanic and Atmospheric Association's National Estuarine Research Reserve System (NERRS) (Hilbert, 2006). The GBNERR contains a variety of productive and diverse ecosystems, both marine and terrestrial, and was historically maintained by natural fire (return intervals between 1 and 10 years; Glitztenstein et al., 1995) and hurricane regimes. The transition has an elevation gradient of < 2m and even slight changes in elevation result in significant differences in the frequency and duration of inundation events (L.Battaglia and W.Platt, SIUC, unpublished data). As a result, turnover of plant species is high and compositional shifts in vegetation are pronounced along the gradient. Grand Bay is relatively unimpacted by anthropogenic disturbance (Hilbert, 2006) and serves as the primary study site for seed bank analysis.

***Data Collection***—

I have examined six of the dominant vegetation zones (salt marsh, low brackish marsh, high brackish marsh, fresh marsh, maritime pine forest, and wet pine flatwoods) of the coastal transition. These dominant vegetation zones extend from the ocean to the upland within GBNERR and are designated according to their major community type and dominant species. A band of mixed pine-hardwood was excluded from this study due to its proximity to a firing range, which has left it fire-suppressed. A permanent 12km transect and associated vegetation plots were established in GBNERR in 2007 to investigate the impacts of climate change on this coastal transition ecosystem. Relative elevation (Fig. 2.2), soil salinity (Fig. 2.3) and soil texture were measured at every 100m interval (L.Battaglia and W. Platt, SIUC, unpub,; Paudel and Battaglia, SIUC, in prep.). It is important to note that while salinity levels frequently change, these measurements act as a snapshot of soil salinity just prior to Hurricanes Gustav and Ike in 2008.

*Seed Bank Study*—

In June 2009, 10 replicate 1m$^2$ plots were established at random points within each of six of the major vegetation zones present along the Grand Bay transition. Above-ground vegetation was surveyed for species presence/absence, richness and percent canopy cover of all species rooted in the plots. Soil seed bank sampling, usually performed in the spring or autumn, is occasionally performed in the summer to measure persistent seed banks in communities that are dominated by perennials and summer annuals (Baskin and Baskin, 2001). A June seed bank sampling was performed in this study in order to determine the persistent seed bank present during the hurricane season. Soil seed banks in the top 10cm were collected from each plot using a soil core sampler (2cm in diameter x 10cm in height). Twenty cores were taken from within each plot and homogenized into one sample (volume = 628.57cm$^3$); the total area encompassed in the composite sample was approximately 0.6% of each 1m$^2$ plot. For large scale investigations of the soil seed bank, the seedling emergence method (SEM) is the approach most frequently used (Thompson and Grime, 1979; Ter Heerdt et al., 1996). Seed bank samples were returned to SIUC and stored for three days in a cold room at 4°C before being placed in a 2cm deep layer in a 30cm X 15cm plastic tray on top of a 2cm layer of sterile vermiculite/perlite mix. Trays were arranged in a random block pattern in metal bins in the SIUC greenhouse and were re-randomized every 2 weeks to reduce bench effect. Treated seed banks were flooded with 5cm of seawater (~23 ppt) collected from GBNERR for three days and then all bins had holes drilled in them to allow for the drainage of standing seawater. Seedling emergence was monitored every two days for 22 weeks and, upon identification, all emerged seedlings were identified and removed from the flats to prevent seed input from the maturing plants. Three weeks following the initial germination, the flats were flushed with distilled water and returned to the greenhouse for germination. Banks were allowed to overwinter in the cold room for 8 weeks and were returned to the greenhouse for a second year of germination in April 2010. All taxa were identified to the finest taxonomic level the material allowed, usually species. Taxonomic concepts followed Godfrey and Wooten (1979 a;b) and the USDA Plants Database (2009-2010), except for *Dichanthelium* and *Panicum,* which were consistent with Barkworth et al. (2003, 2007). Density of seedlings was scaled up to number of individuals/m$^2$ on a per area basis.

*Heat shock pilot study*—

In order to determine if seed banks contain a fire-dependent component, requiring the heat from fire to break physical dormancy, a pilot study was conducted in July 2009 to determine the most appropriate temperature and duration for encouraging germination.

Above-ground material was clipped and removed from 30 0.50m$^2$ x 0.25m$^2$ seed bank sods, which were then cut out to a depth of 5 cm. They were sampled only from the wet pine flatwoods, assumed to be the most fire-dependent system, and returned to SIUC to undergo heat shock treatments. Based on heat shock studies performed in other fire dependent ecosystems worldwide (Gashaw and Michelson, 2002; Wills and Read, 2002; Herrero et al., 2007; Paula and Pausas, 2008) and on probable soil temperatures during wildfires in the longleaf pine dominated uplands (Heyward, 1938; Garner, 2005), sods were put into an oven at a temperature of 80ºC, 110ºC or 130ºC for a duration of 5, 10, or 30 minutes. Three replicates received each treatment and three control sods remained unheated. Following the heat treatment, seed banks were allowed to germinate under grow lights for 4 months and seedlings were identified to finest taxonomic level possible, primarily to species.

*Total soil salinity/conductivity*—

Additional soil samples were taken in June 2009 to a depth of 10 cm from each plot for assessing total soil salinity. These samples were dried in an oven at 105º C for 48 hours, sieved to remove any coarse organic matter, dissolved in deionized water and tested for salinity and conductivity using a hand-held salinity meter (YSI 30).

***Statistical analysis***—

Species diversity was calculated using the Shannon-Wiener index based on vegetation surveys within each plot and mean diversity and richness were calculated within the vegetation zones. Seedling richness and abundance data were normalized using a square root transformation and a one-way analysis of variance for fixed-effects (ANOVA) was used to test for differences in species diversity and richness between vegetation zones. Two-way analysis was also employed to assess vegetation zone and storm surge effects on species diversity and richness of seed bank recruits (SAS ®9.1) (Sokal and Rohlf, 1995). Where overall differences were indicated by the ANOVA, post-hoc multiple mean comparisons were performed using Tukey's HSD test to assess significant differences among the means of each zone.

While a number of indices are used for examining the similarity of ecological datasets (Jaccard, Kulczyniski), I used the Bray-Curtis similarity values, often referred to as Sørensen's index of similarity, to compare the composition of the standing vegetation to that of the seed bank (McCune et al., 2002). These values were computed from species absence-presence data but comparisons of compositional similarity could only made for the seed banks which experienced seedling emergence. Non-metric multidimensional scaling (NMDS) was used to perform an exploratory compositional comparison of the seed bank and standing vegetation and an examination of variation within and between vegetation zones. All ordinations were performed in DECODA and NMDS was used because it is considered to be the most robust method for displaying ecological data (Kenkel and Orloci, 1986; Minchin, 1987). Due to variability in the seedling emergence data, Bray-Curtis similarity values used in the ordinations were calculated on presence/absence data (Anderson, 1971). The ordinations of the standing vegetation were calculated with both species percent-cover data, to examine the density-driven patterns, and raw presence/absence data in order to make it comparable to the seed bank ordination. Vector fitting was performed to determine the directionality and magnitude of environmental variables which significantly correlated with patterns in the ordinations. Ordinations based on raw presence-absence data from the seed bank and standing vegetation zones were overlain to examine relationships between them. A Procrustes analysis, which fits a test ordination onto a target ordination, was performed in DECODA to evaluate the goodness of fit of the two. PERMANOVA, an analysis which allows simultaneous testing for multiple variables and interactions, was employed to evaluate the effects and possible interactions of the vegetation zone and storm surge treatments on species composition of the emergents from the seed banks (Anderson, 2001). An indicator species analysis was run to identify any species which act as reliable indicators of vegetation zones (Dufrêne and Legendre, 1997*)*. The presence of these indicator species in seed banks throughout the research area in which they are not present in the standing vegetation may suggest their dispersal and migration potential across the landscape.

## RESULTS

***Standing Vegetation Assessment***—

Vegetation surveys of permanent plots indicated the presence of 69 species, from 27 different families. Based on the above-ground vegetation survey (Table 2.1), the marsh areas were dominated at their seaward edge by *Spartina alterniflora* Loisel. and grade into homogenous stands of *Juncus roemerianus* Scheele. Several thin bands of freshwater marsh, dominated primarily by *Cladium mariscus* (L.) Pohl ssp. *jamaicense* (Crantz) Kük and *Baccharis halimifolia* L., persisted in low-lying swales surrounding islands of maritime pine assemblages. The canopy of these islands were dominated by *Pinus elliottii* Engelm. and the understory was a relatively rich assemblage of shrubs (*Morella cerifera* (L.) Small, *Ilex vomitoria* Aiton , *Ilex glabra* (L.) A. Gray, *B. halimifolia)* and graminoids *(J.roemerianus, Spartina patens* (Aiton) Muhl., *Setaria parviflora* (Poir.) Kerguélen*)*. The wet-pine flatwoods assemblage, the most upland site along this transition, was dominated in the canopy by sparse stands of *Pinus elliottii* and *Pinus palustris* Mill. but exhibited very high species diversity and richness in the herbaceous understory, which contains numerous grasses (*Aristida beyrichiana* Trin.& Rupr., *Panicum* spp., *Paspalum* spp.), sedges (*Rhychospora* spp. and *Scleria oligantha* Michx.), shrubs (*Hypericum nitidum* L. and *Hypericum brachyphyllum* (Spach) Steud.), composites (*Symphyotrichum dumosum* (L.) G.L. Nesom, *Helianthus* spp.) and carnivorous plants *(Sarracenia alata* Alph. Wood, *Drosera intermedia* Hayne).

One-way ANOVA indicated a significant treatment effect of vegetation zone on species diversity (Fig. 2.4; $F_{5,54}=47.25$, $p<0.0001$). Pairwise comparisons indicated that the mean diversity in the pine flatwood was significantly higher than all other zones, and that the species diversity decreased significantly in the more seaward vegetation types. Diversity in the maritime pine island and fresh marsh diversities were similar and were higher than those in the seaward zones. The results of the ANOVA ( $F_{5,54}=40.71$, $p<0.0001$*)* and pairwise comparisons for the effect of zone on species richness showed similar patterns, with richness highest in the wet pine flatwood and successively lower in the more seaward zones (Fig. 2.4.)  PERMANOVA results determined that the six vegetation zones were in fact compositionally distinct (Pseudo-$F_{5,27}$= 24.01, p=0.001).

The NMDS ordination of the percent cover data (Fig. 2.6) (2 axes, stress value =0.0695) and vector fitting indicated that all three environmental variables were significantly correlated with trends in community composition (distance from the sea, r=0.79, p <0.0001, conductivity, r=0.89, p<0.0001, salinity, r=0.68, p<0.0001).

Indicator species analysis suggested that 36 of the 69 species are robust and significant indicators of the vegetation zones (Table 2.3). No indicators were found for the lower brackish marsh. Several species had maximum indicator values greater than 80 (*S. alterniflora*, *C. jamaicense*, *A. beyrichiana*, *H. nitidum*) suggesting that they were present only in the particular vegetation zone and in at least 80% of surveyed vegetation plots.  Large proportions of the total species in these 5 zones were deemed indicators, with almost half of all fresh marsh species being considered indicators. The presence of these indicator species in seed banks suggests that the banks do in fact reflect the associated parent vegetation.

***Seed bank composition***—

Thirty-four different species from 10 families emerged from the seed banks over the 2 year germination period (Table 2.1, 2.4). The most abundant seedlings were *J. roemerianus* (1500/$m^2$), *Panicum repens* L. (1333/$m^2$) and *H. nitidum* (1167/$m^2$). Sixteen taxa were found only once and were considered to be rare. Emergence from salt marsh seed banks was low (mean=50 individuals/$m^2$) with emergence from only 3 seed bank samples. *J. roemarianus* and *Sesuvium maritima* (Walter) Britton, Sterns & Poggenb. were the only species which emerged and brackish marsh banks contained only *J. roemarianus* and *Sonchus asper* (L.) Hill seedlings. Freshwater marsh banks contained a much higher density of seedlings (mean= 950/m$^2$, primarily *C. jamaicense, B. halimifolia* and *J. roemarianus.* Maritime pine banks were dominated by weedy or ruderal species, primarily *Cyperus polystachyos* Rottb. and *Juncus acuminatus* Michx., as well as *P.repens*, a noxious species invading the Gulf of Mexico. Weedy taxa were also common in the seed banks of the wet pine flatwoods, with *Dichanthelium* spp.*, Panicum* spp., *Digitaria sanguinalis* (L.) Scop. and *Cynodon dactylon* (L.) Pers. accounting for 55% of all taxa that emerged.

The NMDS ordination (2 axes, stress value = 0.0346; Fig. 2.7) suggests there is higher variability and more overlap in the composition of seed banks replicates than was found in the standing vegetation. Seed banks do appear structured in the same overall directionality, with marsh banks clustered together on the left and grading into the upland banks on the right. None of the environmental variables were found to correlate with the ordination based on species composition in the seed bank. It is important to note that 16 of the original 60 banks had to be omitted from the ordination due to negligible seedling emergence and 6 banks had to be omitted due to the presence of a unique species which was not found in replicate banks. In particular, the wet pine flatwood and maritime pine island had several bins each which contained a species or number of species unique to that replicate.

***Similarity assessment***—

Sørensen’s similarity scores were averaged for all plots in each zone which had seedling emergence (Table 2.5). There was an overall increase in the compositional similarity of the seed bank to the standing vegetation toward the seaward end of the gradient, with the highest mean similarity noted in the lower brackish marsh (78%) and the lowest in the wet pine flatwood (3%).

The Procrustes rotation performed on the two NMDS ordinations, based on presence/absence data, indicates an overall good fit of the standing vegetation and seed bank ordinations (RMS residual= 0.5559). The Procrustes root mean square (RMS) residual is a measurement of the average distance between a plot and its associated seed bank in ordination space. In Fig. 2.8, the two ordinations were overlain to illustrate this relationship. Only compositional data from plots whose seed banks had seedlings emerge were included and for the purpose of interpretation, the particular replicates were not matched with their corresponding seed bank but were rather assessed in terms of the trends of all plots in the vegetation zone. In general, the saline marsh ordinations exhibit the closest fit.

Regarding the similarity of the proportions of species in functional categories, grasses account for more than 40% of the total taxa in seed banks, whereas in the standing vegetation they make up only ~22% (Table 2.6). In the standing vegetation, the herbaceous component is by far the most dominant, in terms of number of taxa, accounting for 44%. No lycophytes appeared out of seed banks but sedges and woody species make up approximately the same proportion of the total taxa.

***Effect of parent vegetation and storm surge treatments***—

The ANOVA performed on mean seedling richness data suggests an effect of vegetation zone and the storm surge treatments (Fig. 2.9a). Vegetation zones varied significantly in terms of mean seedling richness ($F_{5,48}$= 6.81, P<0.0001), and pairwise comparisons indicate that richness was higher in the more inland zones. The storm surge treatment significantly reduced seedling richness ($F_{1,48}$= 6.20, p=0.0163; Fig. 2.9b ), however no interaction exists between the two treatments in terms of mean seedling richness. Results from the ANOVA directed at seedling abundance closely parallel the results found for seedling richness (vegetation zone, $F_{5,48}$= 5.26, p= 0.0006; storm surge treatment, $F_{1,48}$= 6.83, p= 0.0119), with fewer recruits out of lowland banks and suppressed germination of surged banks compared to controls (Fig. 2.10 a,b).

PERMANOVA verified that parent vegetation was a significant driver of the composition of the seed banks recruits (Pseudo-$F_{5,27}$=2.627, p=0.001), as was an interaction with the storm surge treatment for some vegetation types (Pseudo-$F_{1,27}$=1.3688, p=0.036). The PERMANOVA generated p-values indicate the pairs of seed banks that were compositionally different due to the effect of parent vegetation (Table 2.7). Due to poor germination in seed banks across some combinations of vegetation type and storm surge treatments, pairwise comparisons could not be performed to investigate this interaction. This interaction will be discussed in greater detail using patterns in the seedling emergence and ordination data.

***Heat shock pilot study***—

Two-way ANOVA suggested that there was no statistical impact of the heat shock treatments on either species richness or seedling abundance. There was neither an effect of temperature nor duration on the composition of the seedlings (temperature, $F_{3,20=}$0.9238, p=0.522; time, $F_{3,20}$=0.08391, p=0.6360). With no obvious response from the most speciose and fire-sensitive autumn seed banks, heat shock was not performed in the larger experiment.

## DISCUSSION

***Patterns in the standing vegetation***—

The salinity and inundation gradients resulting from normal tidal regimes are major determinants of species richness along the coastal plains. The saline, emergent marsh communities typically having low species diversity (Dardeau et al., 1992; Odum, 1998) and the pine-wiregrass savannas and associated flatwoods of the coastal plain being documented as some of the most species rich globally, reaching up to 50 species/m2 (Peet and Allard 1993; Kirkman et al., 2001). Analyses of the standing vegetation reveal a pattern of increasing plant species richness and diversity with distance from the sea, a feature which is correlated with declining soil salinity and frequency of inundation. This study found these pine communities to be significantly more diverse than other communities surveyed on site. They contained 49 of the total 69 species identified in the extant vegetation on the transect, 44 of which were endemic to the flatwoods. Average species richness was not as high as in other studies (Peet and Allard 1993; Walker and Peet, 1984; Kirkman et al., 2001; Meyers and Harms, 2009) (~13 species/m$^2$ ) but ranged from 12 to 18 species/m$^2$. These NMDS ordinations suggest that the sampled vegetation zones were compositionally different, with overlap driven by only a few shared species, and that they were compositionally typical of the above-ground zonation in many marine-terrestrial transitions along the Gulf of Mexico (Dardeau et al. 1992; Shirley and Battaglia, 2006). The low number of introduced species and high number of desirable and indicator species imply that the extant communities were quite ecologically intact.

***Composition of seed banks across coastal transition***—

In coastal systems, which routinely experience tidal and hurricane inundations, the recruitment of species from the seed bank and into the standing vegetation depends not only on the presence of viable seeds but also on the presence of favorable germination conditions and the competitive interactions with other biota which may limit their survival (Leck, 1989; Middleton, 2009a). Seed bank composition varies substantially across ecosystems, based on species-specific dispersal and germination patterns and the above- ground vegetation is, therefore, not necessarily representative of the total pool of species available for recruitment (Thompson and Grime, 1979; Leck, 1989; Baskin and Baskin, 2001; Hopfensberger, 2007).

Seed banks in salt marsh communities are often less developed and diverse than in more freshwater environments due to the highly stressful abiotic conditions (Hopkins and Parker, 1986; Odum, 1988). Seed banks are less important for reproduction because of the unfavorable germination conditions and recovery is typically through vegetative means (Shumway and Bertness, 1992; Ungar and Woodell, 1993). Oligohaline or freshwater marshes, which have a greater component of annuals and larger overall pool of species, often exhibit lower similarity to their seed banks than more perennial-dominated marshes (Parker and Leck, 1985; Crain et al., 2009). Studies aimed at these less saline tidal marshes have shown that where there are many shared species in the standing vegetation and seed bank, disturbances may lead to recruitment of similar assemblages (Parker and Leck, 1985; Crain et al., 2009).

This assessment found similar patterns in the marsh seed banks, with a higher abundance and richness of seed bank communities in the freshwater marsh relative to the more saline marshes. Additionally, species assemblages in the seed bank and standing vegetation are quite similar in the saline marshes but differ widely in the upland communities. Multivariate analysis indicated a correlation between the standing vegetation and its position along salinity and elevation gradients. Despite the environmental gradients which generate patterns of zonation in the standing vegetation, this correlation was not seen in the seed bank composition, probably because most species common in the upland seed banks are uncommon in the standing vegetation, with transient/weedy species dominating.  The species assemblages in the seed banks were less discrete and exhibited more species overlap than is seen in the above-ground vegetation. A few species were found in seed banks from zones in the transition from which they were not established in the vegetation, indicating that some species are quite mobile throughout the landscape. *J. roemerianus*, for example, a dominant species in the saline marshes and an indicator of the brackish marsh vegetation, was identified in the seed bank of 4 of the 6 vegetation zones, including that of the freshwater marsh, from which it was not apparent on site. In their evaluation of seed banks of the various dune ecosystems in Florida, Looney and Gibson (1995) saw similar behavior from propagules of J. roemerianus, with the indicator species found at high densities in both marsh and dry swale seed banks. On a landscape scale, seed bank compositions in the saline marshes were largely identical, due to the dominance of *J. roemerianus*. *Populus deltoides*, a tree common in the unsurveyed freshwater bottomlands at the GBNERR, appeared in three separate seed banks from the freshwater marsh, which is located more than 3 km away. *Sonchus asper* and *Panicum repens*, aggressive invasives known throughout the region (Wilcut et. al, 1988; Bryson, 2003) were not located in any of the sampled standing vegetation but were two of the most common and abundant species that emerged from seed banks.

While the broad-scale evaluation above questions the potential of the banks to act as a reservoir of diversity, on a small-scale, most seed banks were comprised of a subset of species present in the standing vegetation. Seed banks from all vegetation zones (with the exception of the salt marsh) contained species which were established as indicators of the standing vegetation. Compositional similarity between the seed bank and parent vegetation, which is a common measurement of ecological resilience, was higher in the salt-stressed marshes and substantially lower in the more species-rich landward communities, ranging from only 3% to 19%. Hopfensperger (2007) reviewed patterns in seed bank studies across ecosystem types (forests, grasslands, wetlands) and determined that seed banks of forested ecosystems are the least similar to their standing vegetation, with average similarity values less than 60%. This discrepancy between vegetation and seed bank composition is thought to be the result of a number of characteristics of forested systems, including the clonal nature of shrub vegetation, higher predation on larger seeds by birds and small mammals and the technical difficulties involved in obtaining large seeds for seed bank and greenhouse studies (i.e. the use of small diameter sampling devices and/or collection of small soil volumes; Cohen et al., 2004; Hopfensperger, 2007).

The distribution of the plots in the overlain seed bank and standing vegetation ordinations also suggests zonation may occur in the seed bank that is similar to that of the standing vegetation. Looney and Gibson (1995) found similarity between the vegetation and seed bank to be quite low, (Jaccard's Index =0 .36, ~ 37%), but at a larger scale, the seed bank composition was a good indicator of the dominant above-ground vegetation. In their evaluation of seed bank distributions across three tidal wetland associations (marsh, swamp hummock and swamp hollow), Peterson and Baldwin (2004) found discrete seed bank communities but also found some species overlap due to hydrologic connectivity.

This study found little evidence to suggest long-distance transport of seeds in landscapes that experience relatively frequent storm events. Hydrochory in tidal waterways usually occurs locally, with seeds generally deposited within the vicinity of the parent plants (Willson, 1993; Rand, 2000; Wolters and Bakker, 2002). Long-distance dispersal of seeds in ocean currents can occur over hundreds of kilometers (Nathan et al., 2008) and rafting and entrapment of seeds in storm surge events has been confirmed (Willson, 1993; Chang et al., 2007; L. Battaglia and W. Platt, SIUC, unpublished data) with seeds reportedly having moved more than 20 km from the site of release (Koutstaal et al., 1983). Chang et al. (2007) examined the effect of storm surge on patterns of seed movement throughout a salt marsh complex and found that seed entrapment was more common in the older and highly vegetated section and that long distance transport, although less common than in tidal action, appears to be happening in a seaward direction. Also, patterns of seed rain more strongly affected the younger sections of the salt marsh. Huiskes et al. (1995) also determined that in normal tidal events, there is a net export of seeds through the seaward communities and out to the open ocean, where they appear to only rarely be moved back inland. Additional research will be needed to discuss the apparent absence of seaward species in the inland seed communities. If there is a natural tendency of seeds to be exported out to sea, rather than deposited inland, it would be unlikely that any such species would be found inland. This may also be due to differences in the timing of storm events relative to the fruiting of seaward species. More likely, the rarity of these storm events and the longevity of these propagules in the soil result in patches of transient seeds with a very small window for recruitment.

***Storm surge and seed bank response***—

Due to the unpredictable nature of tropical storms (e.g. timing and intensity), inferences about storm surge impact on seed bank communities are typically based on the known effects of inundation and salinity stress on germination and seedling dynamics. The conditions following the recession of storm surge can vary but high levels of salinity and/or inundation have been shown to reduce seed germination rates and seedling survival (Baldwin et al., 1996; Middleton, 1999), as well as growth rates of several dominant coastal species (Baldwin and Mendelssohn, 1998; Mendelssohn and Burdick, 1988) and overall plant diversity (Baldwin et al., 2001). Storm surges have been shown to influence long-distance patterns of propagule dispersal and retention in tidal communities and are capable of altering microsite characteristics for more than a year following recession (Chang, 2007).

Studies are beginning to emerge which assess patterns of recruitment and recovery of coastal communities following the retreat of natural storm surges (Middleton, 2009 a,b; Miller et al., 2010). While the initial recovery and regeneration following recession of storm surge are driven by surviving individuals and response of the potential flora already residing in the soil seed bank, patterns of recovery vary among communities. In coastal barrier island and sand dune communities, which are frequently disturbed by storm events, the spatial structure of their plant and seed bank communities has also been shown to be related to their distance from the shoreline and/or frequency of disturbance by surge events (Looney and Gibson, 1995; Miller et al., 2010). In coastal *Taxodium* swamps, saltwater influx from the storm surges can result in high mortality of many tree species but also increased seedling regeneration due to the higher light availability (Conner and Inabinette, 2003; Middleton, 2009a). Middleton (2009b) evaluated seedling regeneration in the coastal marshes following storm surges of Hurricanes Katrina and Rita and found significantly higher seedling regeneration with increasing distance from the sea in both field and seed bank studies. Additionally, the application of salinity and flooding treatments indicated that higher sea-levels and increased inundation by storm surge would probably result in lower germination and recruitment from marsh seed banks.

The results from this study suggest that storm surges may also affect the recovery and reassembly of coastal communities. Summer sampling yielded lower seedling emergence than would be expected from studies in similar systems (Ungar and Woodell, 1993; Wilson et al., 1993; Leck and Simpson, 1995), which implies that there may be a limited role of seeds in recovery from hurricane disturbances. The timing of tropical storm events in the Gulf of Mexico do not correspond to the seasons which experience peak seed bank volume and our results indicate that storm surge treatments greatly reduced seedling emergence and species richness out of seed banks. While it is not clear statistically which vegetation types are most affected by storm surge treatments, the directionality of this interaction is clear. A number of species common in control banks of the more inland communities zones (*Panicum virgatum, Centella erecta, Rhynchospora rariflora, P. deltoides)* are notably absent from surged banks (Table 2.4). While these species may not have been present in all surged samples, it is likely that the suppression of at least some of these salt-intolerant species were responsible for the reduction in overall emergence. Low emergence in the saline marshes makes it difficult to notice such interactions but the strong resemblance of the seaward seed banks to each other and to the standing vegetation suggests similar assemblages would result following storm surge disturbances.

Little information exists from which to determine the potential for recovery and reassembly of the inland communities. This study suggests that few species were present in seed banks across the different vegetation types and that the upland banks do not contain species from further downslope. As a result, the upland communities may not easily transition to more future adapted communities given a rapid rise of sea-level. Additionally, if the upland seed bank communities are not able to withstand altered storm surge regimes, they may not contribute substantially to community recovery following inundation.

The especially undeveloped and species-poor summer seed banks in the pine flatwoods community may make them particularly vulnerable to disturbances. The seed banks lacked the perennial co-dominant *A. beyrichiana* and the majority of other dominant graminoids and forbs which contribute to the exceptionally high species diversity typical of the ground cover (Walker and Peet, 1984; Peet and Allard 1993; Kirkman et al., 2001; Meyers and Harms, 2009). Other evaluations of seed banks in the longleaf pine dominated flatwoods have found similar results. Andreu et al. (2009) also determined the presence of relic/indicator and non-native species in the seed banks but Coffey and Kirkman's (2006) evaluation found only transient/short-term persistent seeds indicative of the historical *Pinus palustris* communities. In contrast, Cohen et al.

(2004) confirmed the presence of a persistent seed bank component in various *Pinus palustris* communities throughout coastal North Carolina, however they also found that most of the taxa represented “weedy” or “fugitive” species.

Also of serious concern is the prevalence of *Panicum repens*, an aggressive exotic grass, in numerous seed banks across the upland zones. It was not found in the standing vegetation on site but its pervasiveness in the upland seed banks suggests it is well dispersed from disturbed areas and roadsides in the region. The presence of similarly disturbance-prone species in the seed bank but not in the standing vegetation indicates that they, while currently unable to recruit into the community, may be able to establish and replace native species following future disturbances. Other research has found similar patterns in the seed banks of pine flatwoods and it is suggested that restoration of the pine flatwood communities will require outside sources of propagules (Cohen et al., 2004; Rush et al. 2008).

### ***Propagule banks and ecosystem resilience*—**

A consideration of propagule banks may provide a clearer picture of ecosystem resilience to climate-driven changes. Standing vegetation surveys suggest that 95% of taxa found at GBNERR are perennial (or both annual/perennial) and the seed banks contain a disproportionately large number of graminoids relative to the standing vegetation. Communities lacking species in the seed bank that are more adapted to future conditions will have reduced capacity to respond to rapid environmental changes. Their recovery from acute disturbances, and long-term survival in light of rising sea-levels, will also depend on the vegetative propagules which may enable rapid landward migration. In vulnerable ecosystems, the assisted dispersal of propagules may be necessary to facilitate migration of species in response to climate change (Hobbs et al., 2009; Hoegh-Guldberg et al., 2010; Vitt et al., 2010).

Further research should be focused on the total pool of propagules in the ecotone communities, which are essential corridors for landward migration and propagule dispersal. Actively assessing seed transport and deposition during and following storm surges will be necessary to better predict potential long-distance dispersal along the coasts and the potential role of increased storm surge activity in assembly of future plant communities.

Table 2.1. Species composition and community structure of the standing vegetation and seed banks along the GBNERR transect. Species are categorized by life history characteristics (A=annual, P=Perennial, A/P=occurs as both) and guild (G= grass, S=sedge, R=rush, H=herbaceous, W=woody, L=lycophyte). Species in bold indicate an introduced species. The pattern of occurrence for each species indicates its generalized range and propagule mobility throughout the complex. Several species span a variety of vegetation types and several commonly occur in seed banks of zones from which they are not evident in the vegetation.

| **Species** | **Status** | **Form** | **Salt Marsh** | | **Lower Brackish** | | **Upper Brackish** | | **Freshwater Marsh** | | **Maritime Pine Island** | | **Wet Pine Savanna** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Vegetation | SB | Vegetation | SB | Vegetation | SB | Vegetation | SB | Vegetation | SB | Vegetation | SB |
| | | | | | | | | | | | | | | |
| *Agalinis maritima* | A | H | | | | | | | X | | | | | |
| *Agalinis purpurea* | A | H | | | | | | | | | | | X | |
| *Aletris lutea* | P | H | | | | | | | | | | | X | |
| *Andropogon glomeratus* | P | G | | | | | | | | | X | | | |
| *Anthaenantia rufa* | P | G | | | | | | | | | | | X | |
| *Aristida beyrichiana* | P | G | | | | | | | | | | | X | |
| *Arnoglossum sulcatum* | P | H | | | | | | | | | | | X | |
| *Baccharis halimifolia* | P | W | | | | | | | X | X | X | X | | |
| *Balduina uniflora* | P | H | | | | | | | | | | | X | |
| *Bartonia virginica* | A | H | | | | | | | | | | | X | |
| *Bidens mitis* | A | H | | | | | | | | | | | X | |
| *Borrichia frutescens* | P | H | | | | | X | | | | | | | |
| *Carex glaucescens* | P | S | | | | | | | | X | | X | X | |
| *Centella erecta* | P | H | | | | | | | X | X | | | X | |
| *Cladium mariscus* | P | S | | | | | | | X | X | | X | | |
| *Coreopsis linifolia* | P | H | | | | | | | | | | | X | |
| *Cynanchum angustifolium* | P | H | | | | | | | X | | X | | | |
| ***Cynodon dactylon*** | P | G | | | | | | | | X | | | | |
| *Cyperus polystachyos* | A/P | S | | | | | | | | | | X | | |
| *Cyperus sp.* | P | S | | | | | | | | X | | | | |
| *Dichanthelium acuminatum* | P | G | | | | | | | | | X | | X | |
| *Dichanthelium laxiflorum* | P | G | | | | | | | | | | | | X |

Table 2.1. (continued)

| **Species** | **Status** | **Form** | **Salt Marsh** | | **Lower Brackish Marsh** | | **Upper Brackish Marsh** | | **Freshwater Marsh** | | **Maritime Pine Island** | | **Wet Pine Savanna** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Vegetation | SB | Vegetation | SB | Vegetation | SB | Vegetation | SB | Vegetation | SB | Vegetation | SB |
| *Dichanthelium sp.* | P | G | | | | | | | | | | X | | |
| *Digitaria sanguinalis* | A | G | | | | | | | | | | | | X |
| *Diodia virginiana* | A/P | H | | | | | | | | | | | X | |
| *Distichlis spicata* | P | G | X | | X | | X | | | | | | | |
| *Drosera intermedia* | P | H | | | | | | | | | | | X | |
| *Eriocaulon decangulare* | P | H | | | | | | | | | | | X | |
| *Eupatorium semiserratum* | P | H | | | | | | | | | | X | | |
| *Eupatorium leucolepis* | P | H | | | | | | | | | | | X | |
| *Fimbristylis caroliniana* | P | S | | | | | | | | X | | | | |
| *Helianthus angustifolius* | P | H | | | | | | | | | | | X | |
| *Helianthus heterophyllus* | P | H | | | | | | | | | | | X | |
| *Hypericum brachyphyllum* | P | W | | | | | | | | | | | X | |
| *Hypericum drummondii* | P | H | | | | | | | | X | | | | |
| *Hypericum nitidum* | P | W | | | | | | | | | | | X | X |
| *Hypericum tetrapetalum* | P | H | | | | | | | | | | | X | |
| *Ilex myrtifolia* | P | W | | | | | | | | | | | X | |
| *Ilex vomitoria* | P | W | | | | | | | | | X | | | |
| *Ipomoea sagittata* | P | H | | | | | | | X | | X | X | | |
| *Juncus acuminatus* | P | R | | | | | | | | X | | | | |
| *Juncus roemerianus* | P | R | X | X | X | X | X | X | | X | X | | | |
| *Lycopodiella prostrata* | P | L | | | | | | | | | | | X | |
| *Morella cerifera* | P | W | | | | | | | X | | X | | X | |
| *Muhlenbergia expansa* | P | G | | | | | | | | | | | X | |
| *Nothoscordum bivalve* | P | H | | | | | | | | X | | | | |
| *Panicum brachyanthum* | P | G | | | | | | | | X | | | | |
| *Panicum dichotomiflorum* | P | G | | | | | | | | X | | | | |
| *Panicum hemitomon* | P | G | | | | | | | | | | | X | X |
| ***Panicum repens*** | P | **G** | | | | | | | | X | | X | | X |
| *Panicum virgatum* | P | G | | | | | | | X | X | X | | | X |
| *Paspalum plicatulum* | P | G | | | | | | | | | | | X | |
| *Paspalum praecox* | P | G | | | | | | | | | | | X | |
| *Pinus elliottii* | P | W | | | | | | | | | X | | | |
| *Populus deltoides* | P | W | | | | | | | | | | X | | |

Table 2.1. (continued)

| **Species** | **Status** | **Form** | **Salt Marsh** | | **Lower Brackish Marsh** | | **Upper Brackish Marsh** | | **Freshwater Marsh** | | **Maritime Pine Island** | | **Wet Pine Savanna** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Vegetation | SB | Vegetation | SB | Vegetation | SB | Vegetation | SB | Vegetation | SB | Vegetation | SB |
| *Rhexia alifanus* | P | H | | | | | | | | | | | X | |
| *Rhexia lutea* | P | H | | | | | | | | | | | X | |
| *Rhynchospora baldwinii* | P | S | | | | | | | | | | | X | |
| *Rhynchospora cephalantha* | P | S | | | | | | | | | | | X | |
| *Rhynchospora chapmanii* | P | S | | | | | | | | | | | X | |
| *Rhynchospora corniculata* | P | S | | | | | | | | | | | X | |
| *Rhynchospora gracilenta* | P | S | | | | | | | | | | | X | |
| *Rhynchospora rariflora* | P | S | | | | | | | | | | | X | X |
| *Rhynchospora sp.* | P | S | | | | | | | | X | | X | | |
| *Rubus argutus* | P | H | | | | | | | | | X | | X | |
| *Sabatia stellaris* | A | H | | | | | | | X | X | | | | |
| *Saccharum giganteum* | P | G | | | | | | | | | | | X | |
| *Sarracenia alata* | P | H | | | | | | | | | | | X | |
| *Schoenoplectus tabernaemontani* | P | S | | | | | X | | X | | | | | |
| *Scleria oligantha* | P | S | | | | | | | | | | | X | |
| *Sesuvium maritimum* | P | H | | | | | | | | X | | | | |
| *Setaria parviflora* | P | G | | | | | | | X | | X | X | | |
| *Smilax laurifolia* | P | W | | | | | | | | | | | X | |
| *Solidago sempervirens* | P | H | | | | | X | | X | | X | | | |
| ***Sonchus asper*** | **A** | **H** | | | | X | | X | | X | | X | | |
| *Spartina alterniflora* | P | G | X | | | | | | | | | | | |
| *Spartina patens* | P | G | | | | | | | X | | X | | | |
| *Spartina spartinae* | P | G | | | | | | | | | X | | | |
| *Styrax americanus* | P | W | | | | | | | | | | | X | |
| *Symphyotrichum dumosum* | A | H | | | | | | | | | | | X | |
| *Symphyotrichum subulatum* | A | H | | | | | | | X | | | | | |
| *Triantha glutinosa* | P | | | | | | | | | | | | X | |
| *Unknown Poaceae* | P | G | | | | | | | | | | | | X |
| *Vaccinium elliottii* | P | W | | | | | | | | | | | X | |
| *Woodwardia virginica* | P | L | | | | | | | | | | | X | |
| *Xyris baldwiniana* | P | H | | | | | | | | | | | X | |
| *Xyris laxifolia* | P | H | | | | | | | | | | | X | |

Table 2.2. Community metrics from standing vegetation and seed banks taken at GBNERR.

| **Zone** | **Vegetation** | | **Seed Bank** | |
|---|---|---|---|---|
| | **Mean Species Diversity (H')** | **Mean Species Richness** | **Mean # of Seedlings/m$^2$** | **Mean Species Richness** |
| Salt Marsh | 0.34±0.09 | 1.8±0.2 | 50±25.45 | 0.3±.15 |
| Lower Brackish Marsh | 0.05±0.05 | 1.1±0.1 | 166.66±116.53 | 0.38±0.20 |
| Upper Brackish Marsh | 0.47±0.13 | 2.6±0.4 | 566.66±174.27 | 0.88±0.16 |
| Freshwater Marsh | 1.11±0.08 | 5.8±0.42 | 950±272.22 | 1.59±0.17 |
| Maritime Pine Island | 1.15±0.12 | 5±0.50 | 650±279.38 | 1.27±0.25 |
| Wet Pine Flatwood | 1.9±0.11 | 14.8±0.90 | 366.66±164.42 | 0.82±0.24 |

Table 2.3. Species from above-ground surveys which were found to be significant indicators of the parent vegetation type. Species in **bold** were also found in the associated seed bank of that parent vegetation.

| **Zone** | **Species** | **(IV)** | **p** |
|---|---|---|---|
| Salt Marsh | *Spartina alterniflora* | 100 | 0.001 |
| Upper Brackish Marsh | *Borrichia frutescens* | 60 | 0.001 |
| | *Distichlis spicata* | 49 | 0.001 |
| | ***Juncus roemarianus*** | 57.2 | 0.001 |
| Freshwater Marsh | ***Cladium mariscus var. jamaicense*** | 100 | 0.001 |
| | *Agalinis maritima* | 40 | 0.002 |
| | ***Setaria parviflora*** | 32 | 0.006 |
| | ***Sabatia stellaris*** | 30 | 0.026 |
| Maritime Pine Island | *Spartina patens* | 48 | 0.001 |
| | *Panicum virgatum* | 45.5 | 0.003 |
| | ***Ipomoea sagittata*** | 40 | 0.005 |
| | ***Baccharis halimifolia*** | 36.8 | 0.013 |
| | *Solidago sempervirens* | 27.4 | 0.02 |
| | *Morella cerifera* | 29.2 | 0.023 |
| Wet Pine Flatwood | *Aristida beyrichiana* | 90 | 0.001 |
| | *Dichanthelium acuminatum* | 78.5 | 0.001 |
| | *Drosera intermedia* | 50 | 0.001 |
| | *Helianthus heterophyllus* | 50 | 0.001 |
| | ***Hypericum nitidum*** | 80 | 0.001 |
| | *Scleria oligantha* | 60 | 0.001 |
| | *Tofieldia racemosa* | 50 | 0.001 |
| | *Vaccinium elliottii* | 60 | 0.001 |
| | *Xyris iridifolia* | 56.9 | 0.001 |
| | *Eriocaulon decangulare* | 40 | 0.002 |
| | *Styrax americanus* | 50 | 0.002 |
| | *Muhlenbergia expansa* | 40 | 0.003 |
| | *Helianthus angustifolius* | 40 | 0.005 |
| | *Rhexia alifanus* | 40 | 0.006 |
| | *Rhexia lutea* | 30 | 0.015 |
| | *Hypericum brachyphyllum* | 30 | 0.02 |
| | *Rhynchospora cephalantha* | 30 | 0.02 |
| | *Coreopsis linifolia* | 30 | 0.022 |
| | *Rhynchospora corniculata* | 30 | 0.022 |
| | *Bidens mitis* | 30 | 0.023 |
| | *Symphyotrichum dumosum* | 25 | 0.026 |
| | *Paspalum plicatum* | 30 | 0.028 |

Table 2.4. Species which emerged from seed banks according to parent vegetation and exposure to storm surge. Species in **bold** are candidates for the species which were suppressed by storm sure treatments and were not found in any surged banks.

| | Salt Marsh | Lower Brackish Marsh | Upper Brackish Marsh | Freshwater Marsh | Maritime Pine Island | Wet Pine Flatwood |
|---|---|---|---|---|---|---|
| Control | *Juncus roemerianus* | ***Sonchus asper***<br>*Juncus roemerianus* | *Juncus roemerianus*<br>***Sonchus asper*** | *Cladium jamaicense*<br>*Juncus roemerianus*<br>*Baccharis halimifolia*<br>***Panicum dichotomiflorum***<br>***Centella erecta***<br>*Rhychospora sp.*<br>*Panicum repens*<br>***Panicum brachyanthum***<br>***Fimbristylis caroliniana***<br>***Panicum virgatum***<br>*Juncus acuminatus*<br>***Nothoscordum bivalve*** | *Panicum repens*<br>*Cyperus polystachyos*<br>***Populus deltoides***<br>*Baccharis halimifolia*<br>*Juncus acuminatus*<br>*Cladium jamaicense*<br>***Ipomoea sagittata***<br>***Eupatorium semiserratum***<br>***Dichanthelium aciculare***<br>***Panicum sphaerocarpon***<br>*Carex glaucescens* | ***Hypericum nitidum***<br>***Rhynchospora rariflora***<br>***Panicum virgatum***<br>***Digitaria sanguinalis***<br>*Cynodon dactylon*<br>**Unknown Graminoid**<br>*Panicum repens*<br>***Panicum hemitomon***<br>*Dichanthelium laxiflorum* |
| Storm Surged | *Sesuvium maritima* | | *Juncus roemerianus* | *Juncus roemerianus*<br>*Cladium mariscus*<br>*Baccharis halimifolia*<br>*Sabatia stellaria*<br>*Panicum repens*<br>*Cyperus sp.*<br>*Cynodon dactylon*<br>*Sonchus asper*<br>*Hypericum drummondii*<br>*Spartina patens* | *Carex glaucescens*<br>*Sonchus asper*<br>*Cyperus polystachyos*<br>*Setaria parviflora*<br>*Rhynchospora sp.*<br>*Juncus acuminatus* | *Dichanthelium dichotomum*<br>*Dichanthelium laxiflorum* |

Table 2.5. Mean Sørensen’s Coefficient, indicating compositional similarity of the seed bank and its associated standing vegetation, decreases substantially with distance from the sea. Averages include seed banks that exhibited no emergence.

| Vegetation Type | Mean Sørensen’s Coefficient |
|---|---:|
| Salt Marsh | 0.3889 |
| Lower Brackish Marsh | 0.7778 |
| Upper Brackish Marsh | 0.6625 |
| Freshwater Marsh | 0.1940 |
| Maritime Pine Island | 0.0903 |
| Wet Pine Flatwood | 0.0370 |

Table 2.6. Comparison of community structure in the standing and seed bank vegetation. The number of species and proportion of total taxa in each functional category listed below, as are the percentage of total species in each that are considered to be annuals/perennials and native/exotics.

| **Source** | | | | | | **Guild** | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Total # of Taxa | Grass | % | Rush | % | Sedge | % | Herbaceous | % | Woody | % | Lycophyte | % |
| | | | | | | | | | | | | | |
| Standing Vegetation | 69 | 15 | 20 | 1 | 1 | 11 | 16 | 33 | 48 | 7 | 10 | 2 | 3 |
| Seed Bank Vegetation | 34 | 14 | 40 | 2 | 3 | 7 | 21 | 9 | 26 | 2 | 6 | 0 | 0 |

| **Source** | **Life History** | | **Origin** | |
|---|---|---|---|---|
| | % Annual | % Perennial | % Native | % Exotic |
| | | | | |
| Standing Vegetation | 4.7 | 95.3 | 100 | 0 |
| Seed Bank Vegetation | 21.9 | 78.1 | 92 | 8 |

Table 2.7. P values from PERMANOVA indicate vegetation zones which have statistically different seed bank compositions (**bold**) (Vegetation Zone: Pseudo F=2.627 p=0.001). (Legend: SM=Salt Marsh, LBM=Lower Brackish Marsh, UBM=Upper Brackish Marsh, FM=Freshwater Marsh, MPI=Maritime pine island and WPF=Wet Pine Flatwood).

| | SM | LB | UB | FM | MPI | WPS |
|---|---|---|---|---|---|---|
| SM | | | | | | |
| LB | 0.1731 | | | | | |
| UB | **0.004** | 0.586 | | | | |
| FM | 0.195 | 0.075 | **0.001** | | | |
| MPI | **0.015** | **0.003** | **0.001** | **0.032** | | |
| WPS | 0.097 | **0.011** | **0.001** | **0.024** | **0.019** | |

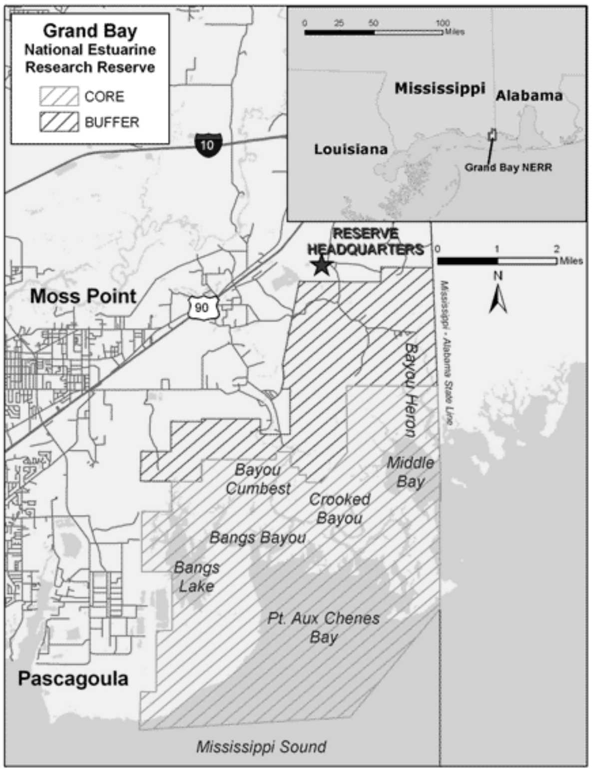

Figure 2.1 The Grand Bay National Estuarine Research Reserve (GBNERR) (hatched area) is located in Moss Point, MS and encompasses 7,284-hectares of contiguous marsh-pine forest transition. The site is exceptionally well-preserved and standing plant communities are largely intact. Map courtesy of GBNERR.

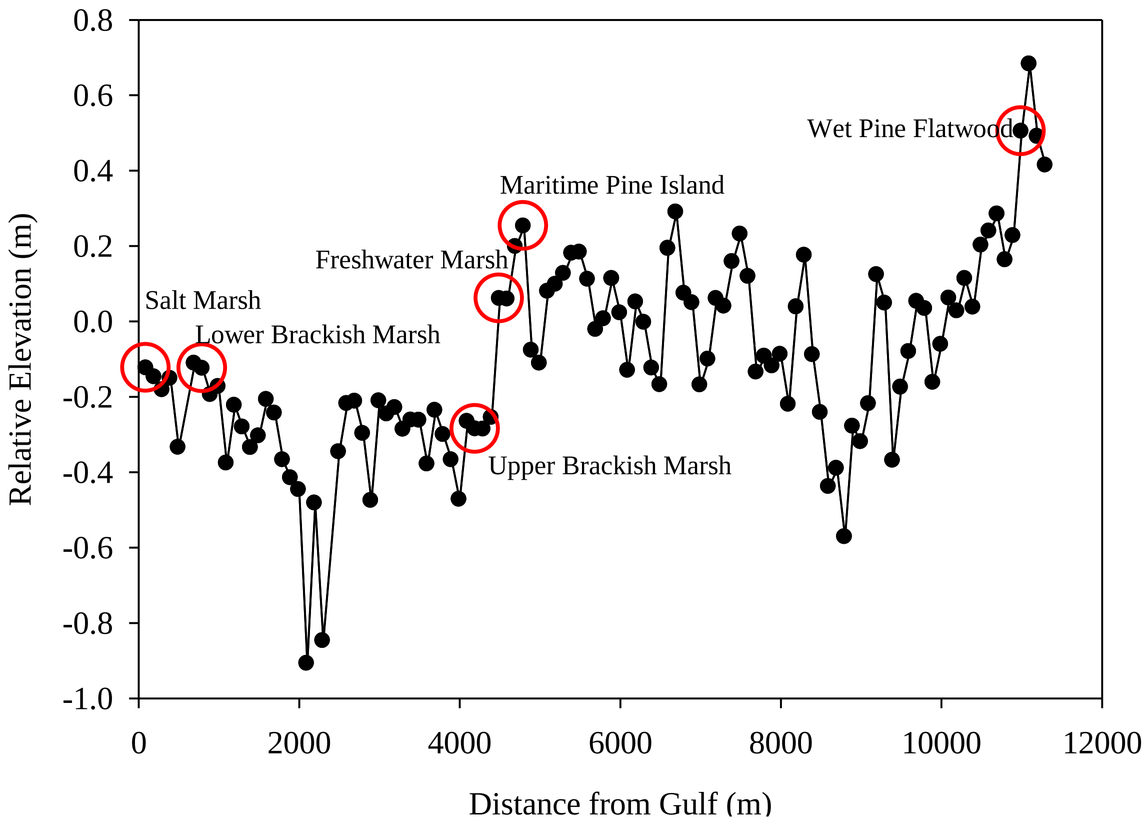

Figure 2.2. Elevational gradient across transect established at GNBERR in 2007. Circles indicate location and elevation of zones chosen for sampling in this study. Six community types are listed which describe these zones and elevation change is <2m from the edge up the sea up into the pine uplands.

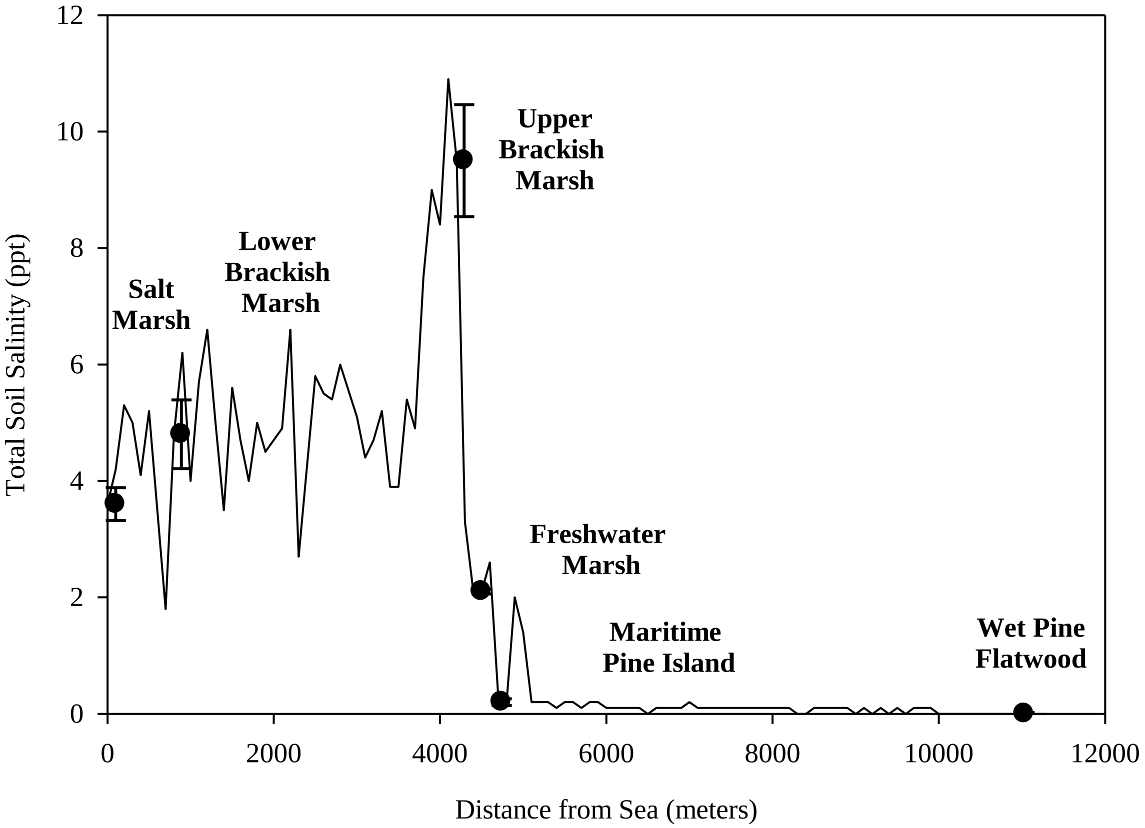

Figure 2.3. Mean total soil salinity along major turnover zones from 2007 survey of 12-km research transect in GBNERR. Black circles indicate mean soil salinity at vegetation zones from which sampling occurred in 2009. Standard error (bold) in the seaward zones was <0.1.

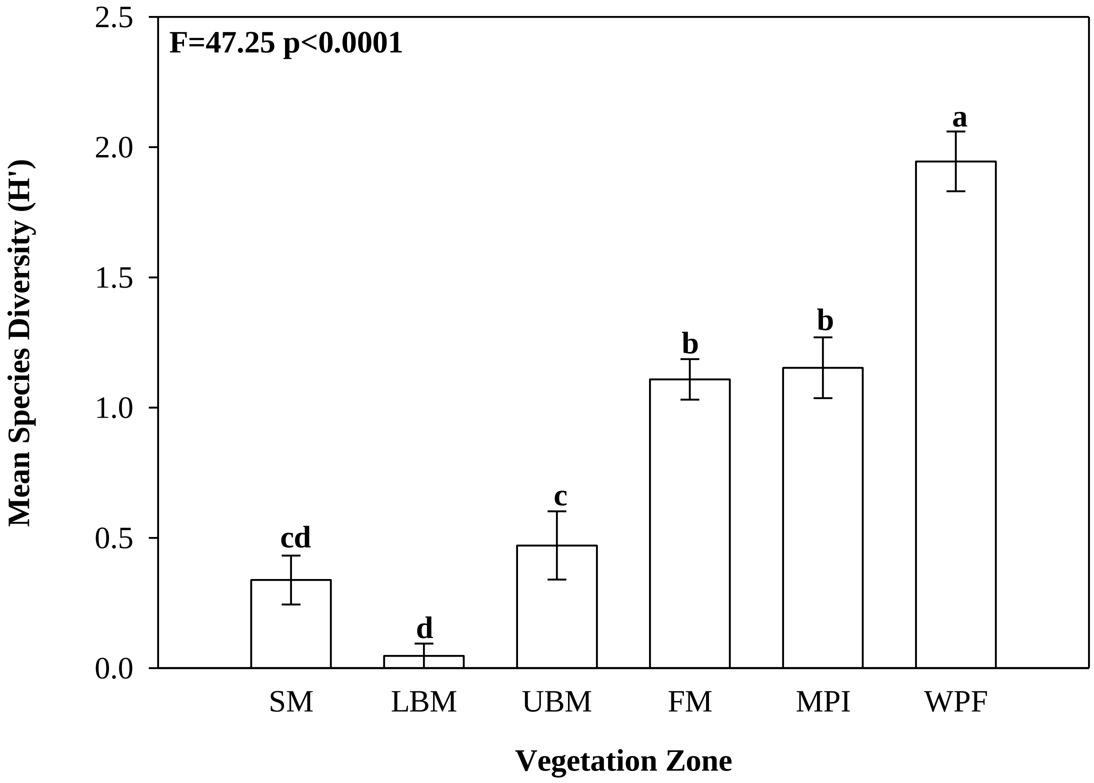

Figure 2.4. Species diversity of standing vegetation across sampled vegetation types significantly increases with distance from the sea. ANOVA and pairwise comparisons suggest that there is a strong relationship between elevational position and species diversity.

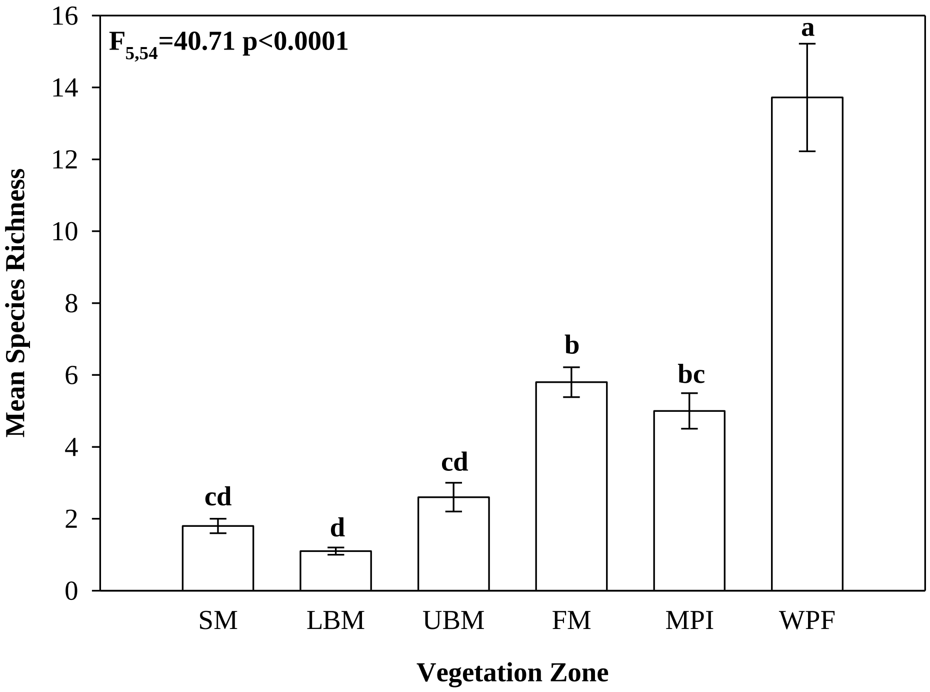

Figure 2.5. Variation in mean species richness across standing vegetation zones at GBNERR.

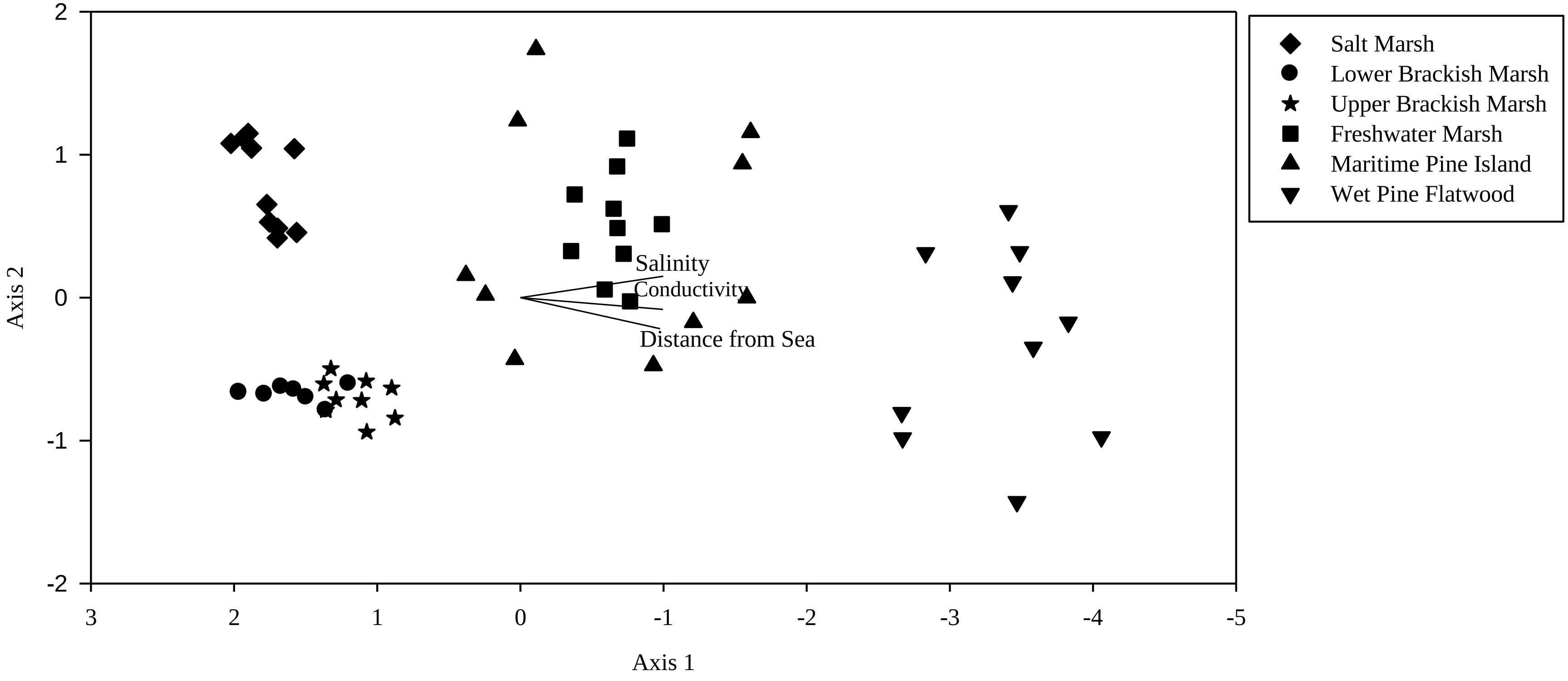

Figure 2.6. NMDS ordination of standing vegetation species composition data from vegetation types along GBNERR transect based on percent cover data. The symbols in the key indicates type of vegetation of each point and those closest together physically are compositionally most similar. Vectors of correlation indicate the directionality and magnitude of the environmental variables related to the NMDS ($p<0.05$)

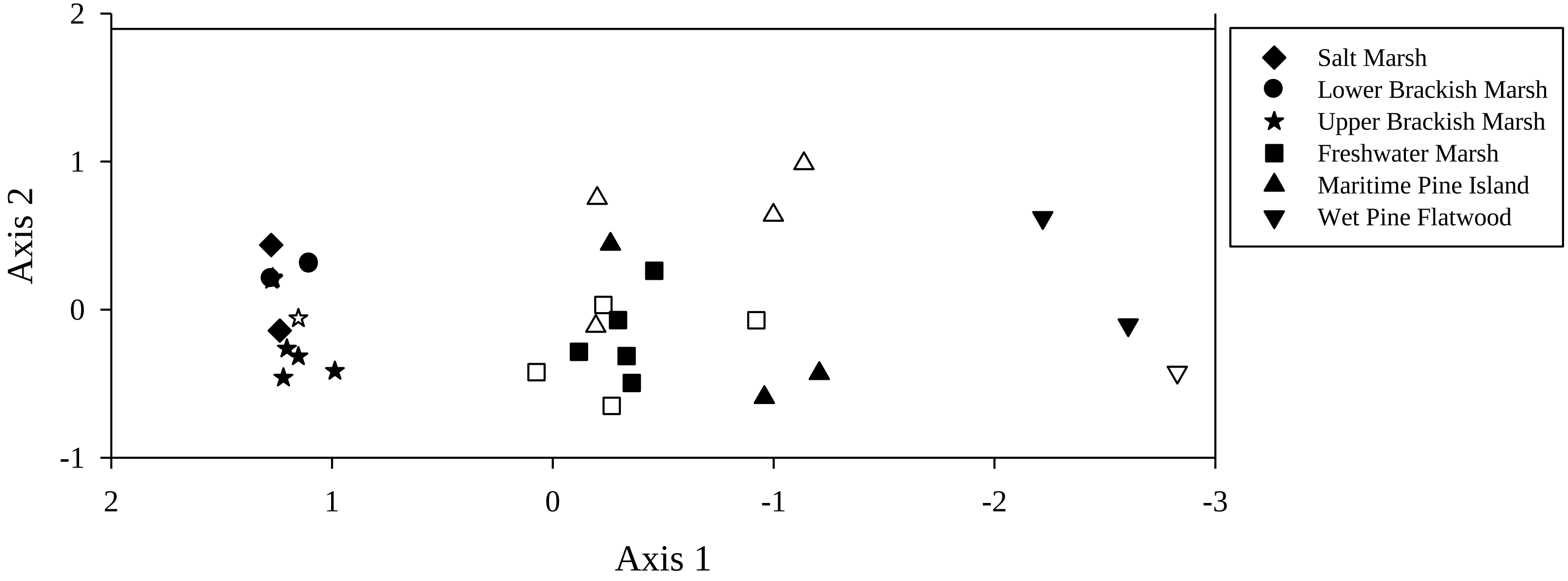

Figure 2.7. NMDS ordination of species composition of the seed bank recruits (based on presence/absence data). The symbols in the key indicate the parent vegetation from which the bank was taken and the level of fill indicates if storm surge treatment was applied (closed: control, open: storm surged). 3 surged upper brackish bins occur behind the lower brackish symbol at approximately (1.2762, 0.2091). Groupings of banks coincide with overall position of parent vegetation along the transect.

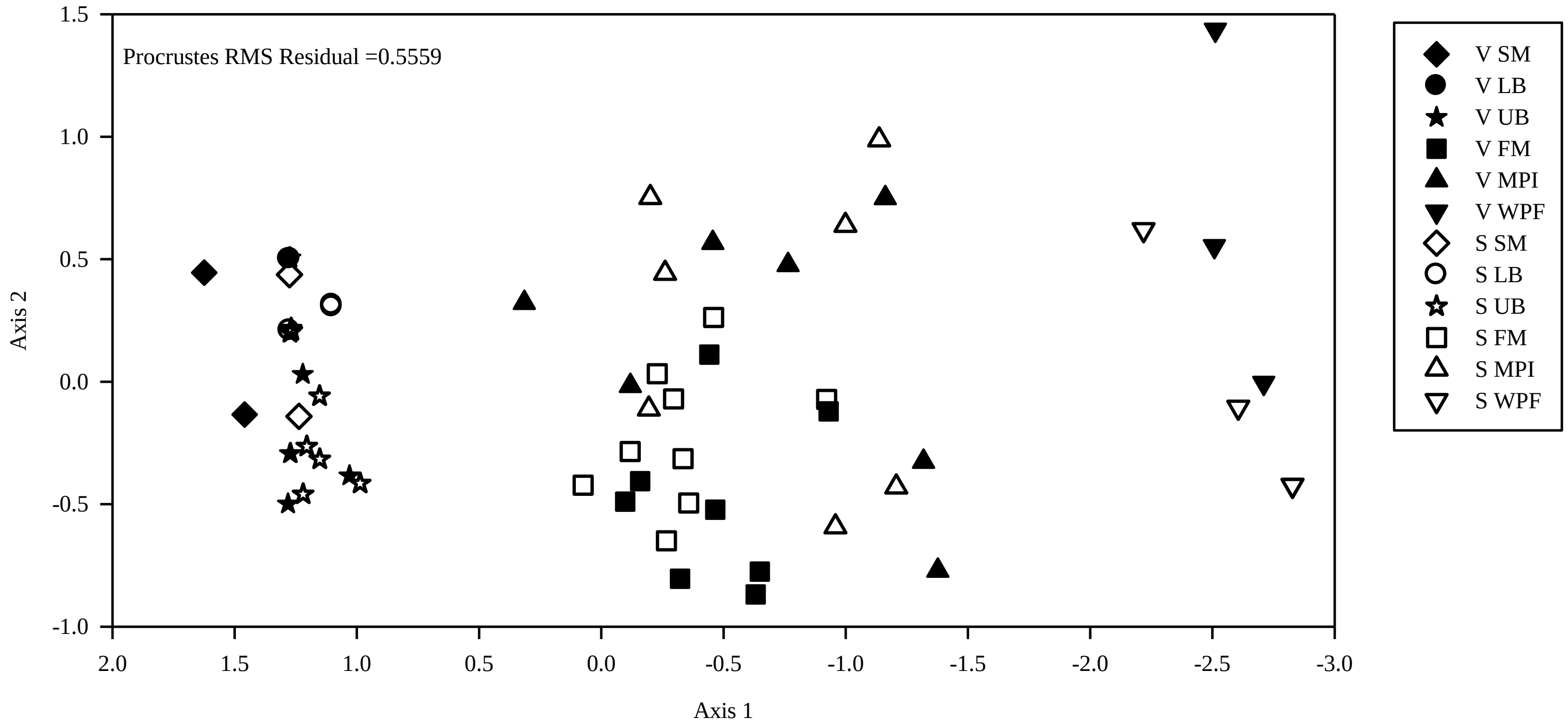

Figure 2.8. Overlay and goodness of fit of the NMDS ordinations of the standing vegetation and the seed bank samples based on absence/presence data. Closed symbols indicate the standing vegetation and open symbols indicate the seed bank. The progression of vegetation types follows their approximate position in the coastal transition, with the seaward sites (left) grading into the upland sites (right). The three plots from the Lower Brackish Marsh community have identical positions in the ordination, based only the presence of only one species, and are hidden behind the Upper Brackish Marsh symbols. Procrustes root mean square (RMS) residual indicates the average distance between the composition of the standing vegetation in a plot and the composition of the seed bank sample from that same plot in ordination space. Legend: V=Vegetation, S=Seed Bank. SM=Salt Marsh, LB=Lower Brackish Marsh, UB=Upper Brackish Marsh, FM=Freshwater Marsh, MPI=Maritime Pine Island, WPF=Wet Pine Flatwood

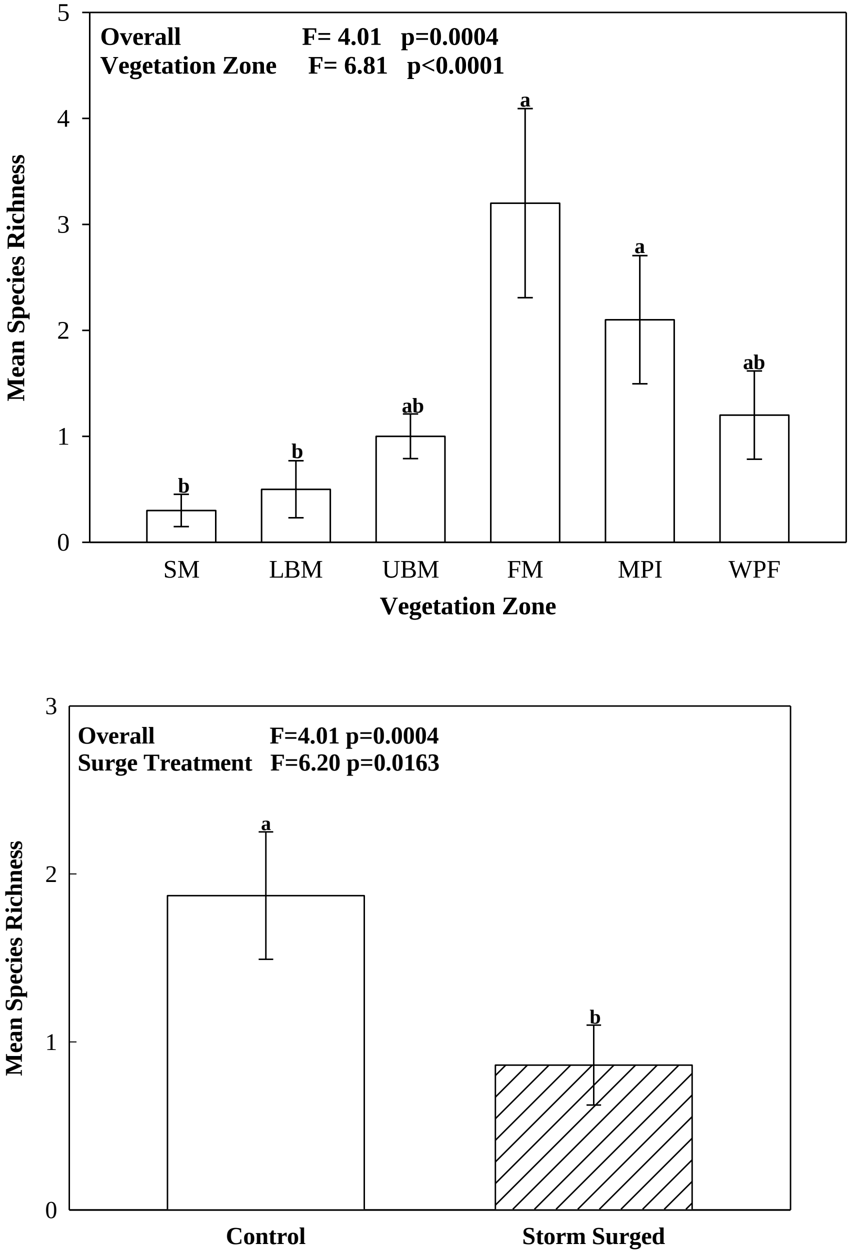

Figure 2.9. Summary of mean species richness of seedlings across a) parent vegetation zones and b) storm surge treatments using Two-way ANOVA and pairwise comparisons. No interaction was found between the vegetation type and surge treatment. Legend: SM=Salt Marsh, LBM=Lower Brackish Marsh, UBM=Upper Brackish Marsh, FM=Freshwater Marsh, MPI=Maritime pine island and WPF=Wet Pine Flatwood

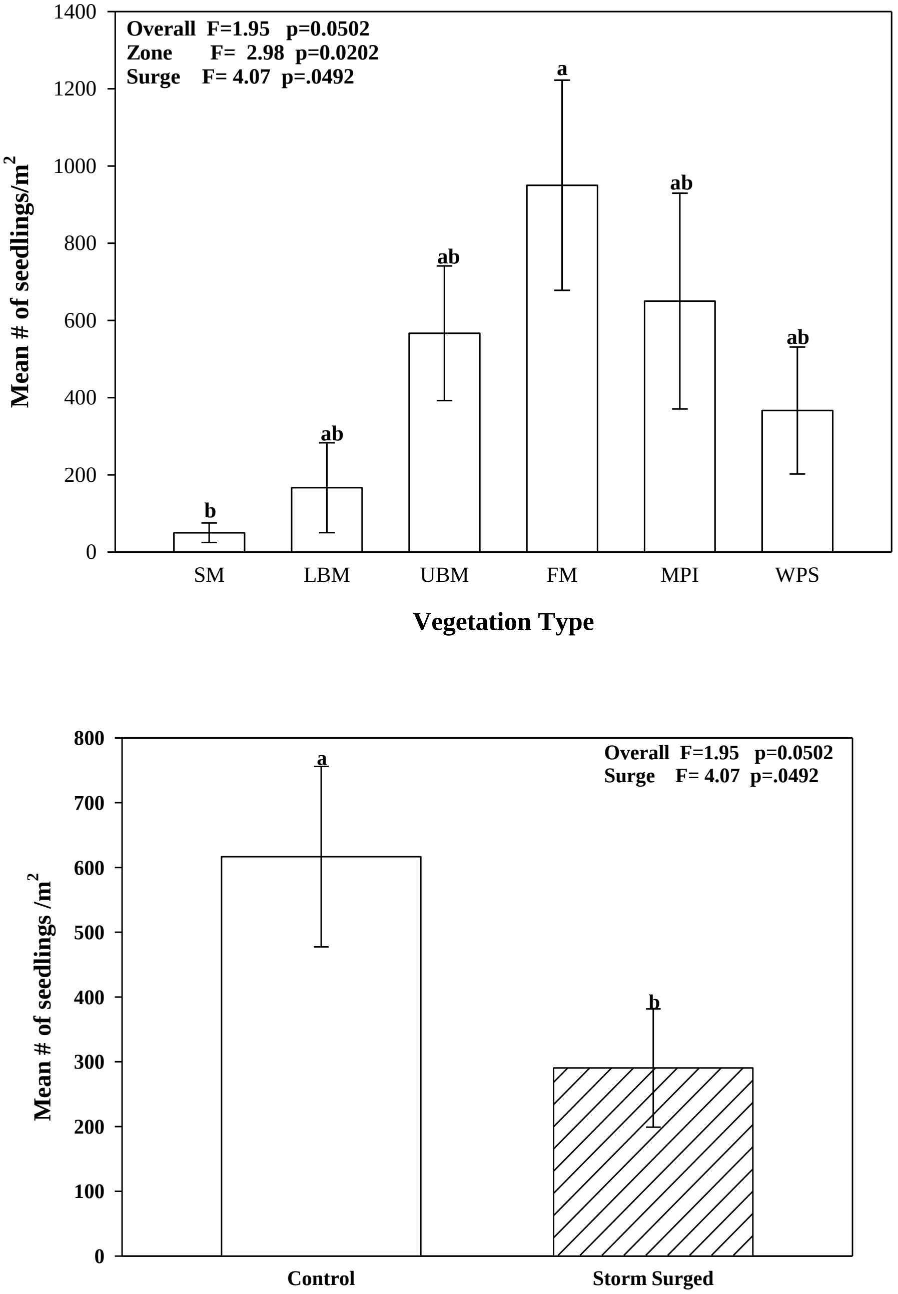

Figure 2.10. Summary of mean seedling abundance (mean # of seedlings/m$^2$) across a) parent vegetation types and b) storm surge treatments using ANOVA and pairwise comparisons. Legend: SM=Salt Marsh, LBM=Lower Brackish Marsh, UBM=Upper Brackish Marsh, FM=Freshwater Marsh, MPI=Maritime pine island and WPF=Wet Pine Flatwood.

# CHAPTER 3

# COMMUNITY TRANSLOCATION AS A TOOL FOR ASSESSING RESTORATION TARGETS AND INSTILLING ECOLOGICAL RESILIENCE WITH CLIMATE CHANGE

## ABSTRACT

Accelerated sea-level rise and increased intensity of tropical storm events have challenged the conventional approaches to the conservation and restoration of coastal ecosystems. In coastal communities, where survival will depend largely on the ability of species to adapt to rapidly shifting conditions or become established farther inland, historic assemblages may be lost. Climate change is already affecting coastal communities and storm surge disturbances in the Northern Gulf of Mexico have resulted in the federal buyout of hundreds of properties for which appropriate restoration targets are unclear. Community translocation, the intentional relocation of suites of species within or outside of their native range, may provide an opportunity to instill ecological resilience and ease the transition of these sites to futuristic communities, which may be more adapted to future conditions. In this study, translocation of propagule sods from a number of historical plant communities across the coastal transition onto degraded properties resulted in the establishment of diverse and variable communities, containing indicator species from a number of historic communities. Species diversity and richness increased, and noxious species were greatly reduced on all restoration plots relative to untreated areas. The response of vegetation following application of freshwater marsh and maritime pine island sods indicated that they were probably the community best suited to the degraded environments. Propagule banks of wet pine flatwoods, which are of particular conservation concern, also responded favorably on the restoration sites. Variation among replicate sites suggests that local environmental conditions and proximity to source populations of ruderal species may also drive

the resulting community composition and dynamics. Long-term monitoring of community change and reproductive output of target species may indicate the utility of community translocation in creating resilient and future-adapted communities.

## INTRODUCTION

As climate change alters the ecological template on which plant communities develop, new approaches to restoration will be essential for the survival of vulnerable species and ecosystems (Choi et al., 2008, Harris et al., 2006; Hobbs et al. 2009). Ecological restoration conventionally involves making *a priori* decisions about a desirable outcome, based on historical site conditions, and then introduction of those desirable organisms. Many communities have already been so modified, both by abiotic and biotic changes, that they no longer resemble their historic state and restoration to that condition is not feasible (Hobbs et al. 2009; Williams and Jackson, 2007). For these novel assemblages, historical analog communities no longer act as appropriate restoration goals (Jackson and Hobbs, 2009; Hobbs et al. 2009, Temperton 2007, Williams and Jackson, 2007). For example, Saxon et al. (2005) have estimated that by 2100, over half of the land in the United States may experience altered moisture, soil and temperature conditions so significant that historic ecosystem features could no longer be supported. With a 1 m rise in sea-level, it is hypothesized that 26-66% of coastal wetlands will be lost to the sea (Mitsch and Gosselink, 2007), making the question of appropriate restoration targets a major priority, both ecologically and economically.

The coastal areas surrounding the Gulf of Mexico, which are experiencing rapidly rising seas (IPCC, 2007; Thieler & Hammar-Klose, 2000) and increasingly intense tropical storm disturbances (Elsner et al., 2008; Hoyos et al., 2006; Bender et al., 2010), may provide an excellent opportunity for testing hypotheses about ecological restoration in regions already experiencing the effects of climate change. Extensive human settlement in coastal areas has forever altered the landscape and has greatly reduced storm buffering capacity of coastal wetlands (Michener et al. 1997; Hopkinson et al. 2008). Tropical storms are among the costliest natural catastrophes in the U.S. (Pielke and Landsea, 1998), and, in the Northern Gulf of Mexico, have resulted in widespread destruction of private properties, displacement of coastal residents and large-scale federal buy-out of hundreds of chronically flooded properties (Cigler, 2009; LACPR, 2009). Many of these properties are unmanaged and, given their proximity to the sea and frequency of storm disturbance, major questions have been raised regarding appropriate restoration targets in light of future climate conditions.

In ecosystems in which place and species-based conservation, aimed at maintaining historic communities or protecting threatened species, may no longer be ecologically and economically feasible, many restoration professionals and ecologists are focused on assessing functional resilience and the likely pathways degraded sites might follow as climate change alters site conditions (Harris et al., 2006; Choi et al., 2009; Hobbs et al., 2009; Seastedt et al. 2009). Habitat fragmentation reduces the ability for many species to migrate or disperse and climate change-induced habitat shifts may require assisted migration of some species even within their natural ranges for their survival (Hoegh-Guldberg et al., 2010; Seddon, 2010,Vitt et al., 2010 ). Assisted migration, in which vulnerable species are intentionally moved for conservation purposes, may be especially important in the Gulf of Mexico and similar coastal systems in which there are great uncertainties about the abilities of species to migrate inland.

Community translocation, also referred by ecologists and conservationists as as assisted migration and managed relocation (Hobbs et al., 2006; Temperton, 2007; Seddon, 2010) is one conservation strategy being posed which promotes the creation of resilient, novel systems through the intentional application of different suites of species. The practice is often performed to aid in mitigation for civil engineering projects in which the donor site will no longer be appropriate habitat (i.e., excavation, road building, filling of wetlands, etc.; Bullock, 1998; Vécrin and Muller, 2003). If effective, passive restoration techniques which employ propagule banks for revegetation are efficient and low-impact; moreover, the introduction of diverse suites plant species may also  hinder the establishment of non-target species, such as invasives (McKnight 1992; Brown and Bedford, 1997). Another advantage of employing donor soil in restoration is the addition of a locally adapted microbial community necessary for the proper functioning of the given system (Zedler and Kercher, 2005; Harris, 2009). When propagule sources are not widely available or dispersal is limited, passive revegetation from the seed bank may not lead to success in meeting restoration targets. Propagule limitation has been shown to be a limiting factor in the natural regeneration and restoration of some coastal plant communities (Middleton 2009a , Morzaria-Luna and Zedler 1992, Ruth et al. 2008). Donor propagule banks have been used with varying success in the restoration or community enhancement of a variety of plant communities, including non-tidal, freshwater wetlands (Brown and Bedford, 1997; Stauffer and Brooks, 1997; McKnight, 1992; Anderson and Cowell, 2004), lakeshore vegetation (Nishihiro et al., 2006), rich fens (Cobbaert et al., 2004), abandoned sand mines (Vivian-Smith and Handel, 1996), meadows and grasslands (Bragg, 1986; Stiegman and Ovenden, 1986; Vecrin and Muller, 2003) and road verges (Nordbakken et al., 2009).

If successful, this form of assisted migration may serve a wide variety of ecological functions for both species conservation and ecosystem restoration (Seddon, 2010). It is dependent on what Mitsch and Jørgensen (2004) describe as the “self-designing” properties of an ecosystem, in which those organisms which are best adapted to the environmental conditions of a site will naturally be expressed and those which are not will eventually be filtered out. Community translocations are rarely tested experimentally but can be successful regardless of similarity of donor and recipient sites (Bullock, 1989). They may be an exceptional tool for allowing modified and dynamic environments to indicate which species and assemblages are best adapted or most appropriate in terms of restoration targets (Odum, 1989).

This study aims to evaluate the assemblages which might be supported in the future on a number of the unmanaged sites through the application of donor propagule banks from intact vegetation zones (salt marsh, brackish marsh, freshwater marsh, maritime pine island and wet pine flatwood) at the Grand Bay National Estuarine Research Reserve (GBNERR). Given their isolation from intact communities, many of these sites may no longer contain viable propagules of their former vegetation and may be too highly degraded and invaded by exotic species for passive recruitment from the surrounding landscape. It is also unlikely that they contain propagules from the seaward vegetation types and therefore may not readily transition to more seaward assemblages as the sites experience altered patterns of inundation. If the propagule banks are effective in reintroducing native species which are adapted to a variety of environmental conditions in the Gulf of Mexico, the resulting community may be more resilient to future disturbances, as well as from invasion by undesirable species. The specific goals of this study were: 1) to determine if propagule bank application is an effective tool for integrating resilience into disturbed sites and 2) to evaluate if the sites are favorable for a particular target assemblage. It is hypothesized that propagule reintroduction will contribute to higher native species diversity, greater number of desirable species and fewer non-native components than in the absence of the introduction. If the abiotic site conditions have not been substantially changed, species from the historical target communities are expected to become readily established and persist.

## METHODS

***Site description*—**

The restoration sites are located in Moss Point, Mississippi, USA and are adjacent to the Grand Bay National Estuarine Research Reserve (30°26’35.94” N, 88°25’44.62” W). The sites are homestead that were inundated by storm surge during Hurricane Georges in 1998 and Hurricane Katrina in 2005 and were, historically, a mix of longleaf pine-wiregrass and maritime pine assemblages which characterize the region before development (M. Woodrey, personal communication). Forty-seven properties were bought out at this location through FEMA’s Hazard Mitigation Grant Program (HMGP), which provides federal funding for the acquisition of private properties nationwide following natural disasters (E.Blocher, personal communication). They have sustained soil disturbance during removal of building foundations and septic systems in 2008. The sites lie within a neighborhood setting and consisted of abandoned homes with overgrown yards. Tree lines are still evident which demarcate the individual properties but they are becoming increasingly overgrown with invasive species and old field weeds. *Triadica sebifera* (L.) Small and *Imperata cylindrica* (L.) P. Beauv., two Federally Listed Noxious Weeds, and *Panicum repens* L., a noxious weed listed throughout the Gulf of Mexico, are highly established on these sites and pose a major threat to the adjacent research reserve. *I. cylindrica* is of particular concern because it produces extensive underground rhizomes which are difficult to remove in their entirety. Soils are typically sandy Plummer or loamy Harleston soils (Garofolo, 1982) but are compacted and contain large amounts of fill material deposited during construction. A pilot seed bank study performed in Fall 2009 revealed that seed banks consisted primarily of old-field weeds (H. Kalk and L. Battaglia, SIUC, unpublished data).

***Site preparation***—

Initial site visits indicated that intensive site preparation was needed to remove standing vegetation and reduce impacts by invasive species. In October 2009, five sites were randomly chosen for use in this study; a 9m x 13m plot was established on each site. Two of these sites were located on the Southern edge of the neighborhood and three on the Northern edge (approx.= 0.80 km apart). A glyphosate solution (41 % ai, 3.59 ai kg/ha) was applied to these plots and mowing and removal of above-ground vegetation was performed two weeks later in November 2009. A tractor, equipped with a rotary tiller, then broke up in situ rhizomes and aerated the soil to a depth of approximately 15cm. Coarse rhizomes and rubble were raked and removed by hand; the plot was then tilled once more. Following the removal of all vegetative material, 30 1m$^2$ subplots were established within each large plot, with1m$^2$ buffers between and outside of each subplot. Buffers were mowed in June 2010, and landscaping fabric was laid down and secured to reduce weedy invaders. To prevent outshading of desirable species, selective weeding was performed throughout the course of this experiment on any invasive species with a percent cover >75% (i.e., *Centrosema virginiana* (L.) Benth., *Cuphea glutinosa* Cham. & Schltdl., *Eupatorium capillifolium* (Lam.) Small, and *Ipomoea quamoclit* L.).

***Propagule bank application***—

Five intact vegetation types were selected to be donors of propagule bank material from the GBNERR (salt marsh, brackish marsh, freshwater marsh, maritime pine island and wet pine flatwood). In November 2009, 20 0.50m$^2$ x 0.25 m$^2$ banks were removed from each vegetation zone to a depth of 5cm. Standing vegetation was clipped off before banks were extracted but associated duff and leaf litter were collected. At each of the 5 large plots, 4 subplots were randomly assigned to each vegetation type and 4 subplots were left as controls. Each bank was broken into course pieces and applied to the subplot by hand (Figure 3.1).

***Environmental data collection and analysis***—

Soil samples were taken adjacent to the study plots at the 5 selected sites for an initial assessment of soil salinity and conductivity in Fall 2008, just prior to Hurricanes Gustav and Ike. Soil samples were later taken in Fall 2010 for assessing soil salinity, conductivity, gravimetric water content and soil texture. Replicate soil cores were removed from each 9m x 13m plot at a depth of 5cm using a 2cm diameter soil corer. Soil salinity and conductivity were measured using a YSI 30 salinity meter and water content was calculated based on amount of water lost following drying of the soil at 105°C for 24 hours (Gardner, 1986). The proportion of sand, silt and clay were determined through a modified Bouyoucos hydrometer method (Bouyoucos, 1936). Characterization of soil texture from the donor propagule vegetation sods was performed in Fall 2007 (S. Paudel and L. Battaglia, SIUC, unpublished data). One-way ANOVA was used to assess differences in gravimetric water content across the sites.

***Community data collection and analysis***—

Surveys aimed at assessing the presence/absence of all above-ground species were conducted at each subplot in June, September and November 2010. In November 2010, $1m^2$ plots were established randomly in the area surrounding the study plot at each of the 5 sites to assess what the plant community would have looked like in the absence of site management.

All on-site species were placed into one of four categories based on native status and overall desirability. Ranging from most to least desirable in native restorations, these categories consist of i) targets, native species that are known components of intact, historic community types in the transition (H.Kalk and L.Battaglia, SIUC, in prep.)), ii) generalists, native species with a more broad geographic range or characteristic of more disturbed environments, iii) aliens, introduced species that form self-sustaining populations and are often weedy but not considered noxious and iv) noxious, non-native species which are Federally and State listed to pose a considerable ecological and economic threat along the Gulf of Mexico.

The Shannon-Wiener index was used to calculate species diversity based on vegetation surveys within each plot, and mean diversity and richness were calculated within the propagule sod treatments. Two-way analysis of variance for fixed-effects (ANOVA) was used to test for differences in site and sod treatment on species richness, diversity and the proportion of species in each category (SAS ®9.1) (Sokal and Rohlf, 1995). When differences were indicated by the ANOVA, post-hoc multiple mean comparisons were performed using Tukey's HSD test to assess which site or propagule sod treatments were different. The frequency of each target species was determined by calculating the total subplots in which it was present across all replicates and treatments.

Non-metric multidimensional scaling (NMDS) was used to perform an exploratory comparison of the communities resulting from the various levels of propagule sod treatments across buyout sites. Bray-Curtis dissimilarities were computed from species presence/absence data. PERMANOVA, an analysis technique which statistically assesses the effect of one or more variables on species composition (PRIMER 6), was employed to assess the effects and potential interactions between sites and the various sod treatments on the resulting plant assemblages (Anderson, 2001). An indicator species analysis was run to identify any species which act as reliable indicators of the different sod assemblages (Dufrêne and Legendre, 1997).

## RESULTS

***Environmental characteristics***—

Soil salinity levels ranged from 0 ppt to 0.1 ppt in 2007 and from 0 ppt to 0.3 ppt in 2010 (Table 3.1.) The range of soil conductivity (at 25°C) was also much higher in the 2010 samples (Table 3.1). Soil moisture ranged from 24.3% to 39.3% and one-way ANOVA indicated a significant difference between site 2 and site 5, the wettest and driest of the sites (Figure 3.2). Sufficient replicates were not obtained to statistically analyze soil texture data but there appears to be variability among the five sites (Table 3.2). In terms of soil texture, the buyout sites were intermediate to the maritime pine community and the pine flatwood communities and are less similar to the mixed hardwood-pine forests surrounding the sites than would be expected (Table 3.3; Paudel and Battaglia, SIUC, unpublished data).

***Community response and species metric***—

The three standing vegetation surveys yielded a total species pool of 117 species from 40 different families (Table 3.4; 3.5). Unmanipulated plots were largely monocultures of *Paspalum dilatatum* Poir., *P. repens*, *Cynodon dactylon* (L.) Pers., *Digitaria* spp. or *I. cylindrica* in the groundcover and exhibited very low species richness in the herbaceous layer, averaging <5 species/plot. Of the total species, 52% were considered to be habitat generalists, with most species being fairly widespread across the sites and vegetation types (Table 3.5). The most common species were *E. capillifolium*, *Euthamia caroliniana* (L.) Greene ex Porter & Britton, *Diodia virginiana* L., *Gamochaeta purpurea* (L.) Cabrera and *Kyllinga brevifolia* Rottb.. Indicator species analysis, however, identified a number of species with high fidelity and/or constancy to specific propagule sod treatments (Table 3.6).

Species richness (Figure 3.3a) and diversity (Figure 3.3b) were significantly higher in the plots which received propagule banks from the freshwater marsh community compared to the control plots and those which received the salt and brackish banks (Richness, $F_{5,90}$=4.98, p=0.0050; Diversity, $F_{5,90}$= 4.50, p=0.0011). Data from the unprepared plots, which resulted from only one survey at the end of the growing season, were not included in the ANOVA but were far below all other treatment types in terms of diversity and richness. There was also a significant effect of site on mean species diversity, $F_{4,90}$=2.78, p=0.0317, but pairwise comparisons did not indicate the cause of this variation.

The NMDS ordination (stress value=0.1638, 3 dimensions) suggested strong clustering of plots according to site both across all axes (Figure 3.4) and results from the PERMANOVA indicate that there were significant differences between the species composition among all five sites, Pseudo-$F_{4,90}$=31.053, p<0.0010 (Table 3.7b). There was also a strong effect of the source of the propagule sods on the resulting assemblages, Pseudo-$F_{5,90}$=3.061, p<0.0010 (Table 3.7a). The plots treated with the salt marsh and brackish marsh sods were compositionally indistinguishable. Additionally, the freshwater marsh and maritime pine sod treatments result in similar assemblages. All other treatments were considered compositionally different.

The mean number of species/plot within each of the four desirability categories was found to significantly vary for some categories among the different sites and sod sources (Figure 3.5a;b). While the mean number of generalists and noxious species per plot were not different across the vegetation treatments, ANOVA results indicate there were significant differences in the proportion of alien, $F_{5,90}$=3.51, p=0.0061, and target species $F_{5,90}$= 12.11 p<0.0001 (Figure 3.5a). There was a significantly higher proportion of alien species in the control and freshwater marsh sod treatments than in the salt marsh sod treatments. The pine flatwood and freshwater sod treatments contained a greater proportion of target species than either the salt marsh or control treatment. The ANOVA directed at the effects of site variation on the mean number of species in each category/plot, indicated that all categories, except for generalists, varied among sites (Figure 3.5b). The number of targets was significantly higher at Site 1 than at Sites 4 and 5, $F_{4,90}$=4.09, p<0.0001, as was the number of noxious species, $F_{4,90}$=5.64, p=0.0004. Alien species were more numerous at sites 5 than at 1 and 4, $F_{4,90}$=9.60, p<0.0001.

The occurrences and growth pathways, emergence from seed or vegetative resprout, of the target species across the propagule sod treatments were summarized in Table 3.4. The values indicate the proportion of the 20 replicates in which the species occurs. No target species appear from the unmanipulated plots and the majority of target species were found only in the sods from the donor vegetation zones at the GBNERR for which they were deemed an indicator. Target species made up 30% of the total species pool and included 27 species that were not otherwise present throughout the buyout properties (Table 3.4). The most abundant of these species was *Spartina patens* (Aiton) Muhl., a dominant grass in coastal freshwater wetlands, (found in 85% of maritime pine treatments and 55% of freshwater marsh treatments) and *Juncus roemerianus* Scheele, a common and highly salt-tolerant rush found throughout the GBNERR (present in 25% of salt marsh plots, 40% of brackish marsh plots and 5% of freshwater marsh plots).

## DISCUSSION

### ***Possible drivers of community response***—

The structure of plant assemblages are a function of many interactions between various environmental and biological processes and are played out over long periods of time (Crawley, 1986; Morin, 1999). While this study was not focused on specific drivers of species composition, the structure of these experimental, novel communities appears to have been determined by variation in abiotic conditions on site and by the biotic interactions between local seed rain, on site propagule bank and the applied propagules. NMDS and PERMANOVA strongly suggest that despite the overlap in many taxa, different sites have largely different overall compositions (Figure 3.4; Table 3.7b). Soil texture (Robertson et al., 1978,), moisture (Yu and Ehrenfeld, 2009) and salinity (Pennings and Bertness, 2001) are all known drivers of community composition in natural systems and their variability among these sites is probably driving some of these differences. Site 2, for example, the wettest of the five sites, contains the greatest proportion of wetland indicator species (OBL, FACW+, FACW).

While the resulting communities are composed primarily of ruderal species, mobile throughout the landscape and flexible in terms of habitat preference, 30% of all non-target species were restricted either to the Southern or Northern Sites, suggesting that differences in composition may also be due to proximity to local propagule sources/patterns of seed rain. While a few families still live in the neighborhood encompassing the buyout areas, the 69 ha are unmanaged and overgrown, and are likely acting as source populations of ruderal and exotic species throughout the restoration study sites and to the adjacent GBNERR. The differences in abundances of noxious species and alien species between sites 1, 4 and 5 are probably also a result of proximity to patchy source populations, as many of these species are reproducing primarily by vegetative means. These are major challenges for the restoration of abandoned and areas because passive restoration is not usually an acceptable option for sites which are substantially modified or which are under propagule pressure and/or arrested succession by undesirable species (Prach and Pysek, 2001; De Steven et al., 2006)

***Restoration targets in a changing world***—

Species and place-based restorations have conventionally involved making *a priori* decisions about what a desirable outcome is, based on historical, baseline site conditions, followed by the introduction of “desirable” organisms and the removal of “undesirables”. In reality, plant community dynamics and the drivers of diversity are very complex, making the outcome of restoration efforts exceptionally difficult to predict and control. The pace of climate change has challenged land managers and ecologists alike to evaluate the restrictive management options associated with historic ecosystem conditions. Hobbs et al. (2009) suggests that the ability to return a site to its historical state depends not only on the degree of biotic and abiotic changes but also the inherent biological and economic thresholds. They pose that in regions in which traditional conservation options fail us, acceptance and thoughtful management actions can still yield valuable and beneficial results (conservation of biodiversity, promotion of ecological integrity and ecosystem services). Along the coasts, these biological and economic thresholds may be particularly steep and this study provides a foundation for discussing “futuristic” restoration targets for the growing number of abandoned properties in the Northern Gulf of Mexico.

The community translocation experiment indicated that the sites are environmentally capable of supporting a wide variety of species from a number of historical assemblages. Environmentally, soil salinity levels on the sites are higher than would be expected from sites 10 km inland and the soil texture is indicative of conditions somewhere between the maritime pine systems and the brackish marshes. These altered abiotic conditions are likely due to the application of fill materials following the removal of the former homestead. The communities which have resulted, in the short-term, are what Hobbs et al. (2009) have deemed “hybrids”, containing components from a number of true analog communities from the GNBERR (Table 3.4), as well as a variety of habitat generalists and non-native species (Table 3.5).

While the majority of emerging species on the recipient plots were considered to be generalists (52%), a number of positive changes resulted from the propagule treatments. Noxious species formed monocultures in many of the unprepared sites and site preparation alone notably increased species richness and diversity. Among the treated plots, the freshwater marsh banks resulted in the highest richness and diversity, with no differences between the control, salt and brackish treatments. Additionally, target species emerged from propagule banks of all donor vegetation zones across the five sites.

Donor propagule banks from the upland sods all appear to act as appropriate restoration targets, with the freshwater marsh and pine flatwood treatments resulting in the greatest number of target species on the recipient sites (Figure 3.5a). The freshwater marsh and maritime pine treatments were compositionally similar and were the most successful in terms of consistently providing target species (Figure 3.7a; Table 3.4). Based only on observations, target recruits from these sods also emerged more rapidly than in other treatments and they appeared to have the greatest biomass of target species (*S. patens, Sabatia stellaria* Pursh, *Scirpus lineatus* Michx*).*

The NMDS ordination of the composition data does not appear to suggest a strong similarity between plots with the same sod treatments. However, that PERMANOVA failed to measure any compositional differences between the control plots and those which received salt and brackish marsh sods, suggests the failure of the saline marsh propagules to become well established. The failure of translocation is either because propagule abundances in the sods are inadequate or that the site conditions were not appropriate for the target propagules (Bischoff, 2002). While *J. roemerianus* successfully recruited in some of the salt marsh plots, it was not abundant or consistent. The failure of *S. alterniflora*, an obligate salt marsh perennial which resprouted from rhizomes on a few sites, to survive through the summer months suggests that soil moisture on the sites was probably not high enough for the seaward propagules.

***Community translocation as a conservation tool*****—**

While community translocation has been widely used as a mitigation tool, often in the forms of top-soil translocation, propagule amendments, soil stockpile and mulch, few studies experimentally document its restoration objectives and/or monitor its successes (Brown and Bedford, 1997; Bullock 1998; Vécrin and Muller,2003; Anderson and Cowell, 2004 ). A review of 10 of the most well-documented translocation projects throughout Britain suggested that degree and direction of community response following translocation varies substantially by ecosystem type, translocation methodology and time since relocation (Bullock, 1998). In assessing the varying community responses following the application of intact propagule banks, this study supports the premise that while community translocation is not an appropriate tool for the preservation of intact communities (Bullock, 1998), it can serve to introduce and increase target species in degraded environments (Pywell et al., 1995; Brown and Bedford, 1997; Anderson and Cowell, 2004). Vécrin and Muller (2003) found translocation of species-rich meadow assemblages increased overall species richness but was also more successful, in terms of increasing richness, than passive restoration and seeding treatments. In one study of heathland translocations, recipient sites maintained qualities from the donor community for more than six years after initial treatment (Standen and Owen,1999).

Given the aggressive species on-site and in the surrounding properties, it remains to be seen if these propagule treatments were successful in establishing self-sustaining populations of these target species. Several studies in grassland ecosystems have found translocation experiments to increase the cover of ruderal species and to allow invasion by exotic species (Kearns, 1985; Bragg, 1986; Stiegrnan and Ovenden, 1986). The ruderal species in this study were not found to be more abundant in the treated sites then in the control plots. The ability of the target species in this study to respond rapidly to site conditions and produce seed suggests that this technique may be effective for integrating future adapted species into seed banks of systems experiencing climate change. Although not what conventional restoration might consider a desirable community, it is possible that target species may be able to persist on the sites long-term along with these rapidly colonizing, ruderal species. These ruderals may also help prevent the invasion by noxious species, which are very dominant in the untreated sites.

This study is the first step in assessing the potential for building ecological resilience into vulnerable coastal ecosystems. The growing number of abandoned coastal properties presents ecologists with an excellent opportunity to test hypotheses about the development and survival of novel ecosystems. Assisted migration may be a successful approach for accommodating the likely trajectories plant communities may follow as the environmental platform changes under them. With long-term monitoring, this study will allow researchers to envision the types of communities which are likely to develop in the future and the potential for integrating a resilient propagule source to aid in this transition. Additional studies should be performed to assess the viability and long-term populations of target species on these sites and to assess the resilience of these novel communities to impending shifts in fire, sea level and tropical storm regimes.

Table 3.1. Soil salinity and soil conductivity measurements in 2008, pre-Hurricanes Gustav and Ike, and in November 2008.

| | **Salinity (ppt)** | | **Conductivity (µs)** | |
|---|---|---|---|---|
| | 2007 | 2010 | 2007 | 2010 |
| Site 1 | 0 | 0.3 | 61.3 | 568 |
| Site 2 | 0 | 0.1 | 79.1 | 199.2 |
| Site 3 | 0.1 | 0.2 | 183.2 | 388.5 |
| Site 4 | 0 | 0.1 | 56.800 | 221.1 |
| Site 5 | 0 | 0.2 | 64.4 | 442.9 |

Table 3.2. Soil textural characteristics across 5 buyout properties.

| | **% Sand** | **% Clay** | **% Silt** |
|---|---|---|---|
| Site 1 | 69.8 | 19.6 | 10.6 |
| Site 2 | 63.8 | 23.6 | 12.6 |
| Site 3 | 62.4 | 29.6 | 8.0 |
| Site 4 | 66.4 | 25.0 | 8.6 |
| Site 5 | 56.5 | 30.9 | 12.6 |

Table 3.3. Comparison of components of soil texture (mean) from **buyout sites**, Fall 2010, to measurement from across coastal transition communities in the GBNERR, measured in Fall 2007. Locations of vegetation zones are indicated according to their distance from the shoreline.

| **Site** | **% Sand** | **% Clay** | **% Silt** |
|---|---|---|---|
| Salt marsh (100 m) | 30.4 | 43 | 26.6 |
| Brackish marsh (400-800 m) | 53.7143 | 26.8714 | 19.4143 |
| Freshwater marsh (4500 m) | 39.2 | 42.7 | 18.1 |
| Maritime pine (4600-4800) | 69.85 | 13.05 | 17.1 |
| **Buyouts (~10050 m)** | **63.788** | **25.73993** | **10.47207** |
| Mixed flatwood (10100 m) | 26.85 | 39.35 | 33.8 |
| Wet pine flatwood (10900-11100 m) | 50.4714 | 25.4286 | 24.1 |

Table 3.4. Percentage occurrence of target species, which are characteristic of a particular donor vegetation type, across all sod treatment types and all 20 replicates. No target species were located on any of the unprepared plots.

| **Donor Vegetation Type** | **Species** | **Plot Type** | | | | | |
|---|---|---|---|---|---|---|---|
| | | **Control** | **Salt Marsh** | **Brackish Marsh** | **Freshwater Marsh** | **Maritime Pine** | **Wet Pine Flatwood** |
| **Salt Marsh** | *Spartina alterniflora* | | 0.15 | | | | |
| | *Distichlis spicata* | | | 0.05 | | | |
| **Brackish Marsh** | *Juncus roemerianus* | | 0.25 | 0.4 | 0.05 | | |
| **Freshwater Marsh** | ***Sabatia stellaria*** | | | | 0.45 | | |
| | *Ilex glabra* | | | | 0.05 | | |
| | ***Panicum virgatum*** | | | 0.1 | 0.15 | | |
| | ***Setaria parviflora*** | | | | 0.05 | 0.15 | |
| | ***Symphotrichium dumosum*** | | | | 0.05 | | |
| | ***Solidago sempervirens*** | | | 0.1 | | | 0.05 |
| **Maritime Pine Island** | ***Ipomoea sagitatta*** | | | 0.05 | 0.1 | 0.15 | |
| | *Morella cerifera* | | | | | 0.05 | |
| | *Pinus elliottii* | 0.05 | 0.05 | | 0.15 | 0.2 | 0.15 |
| | ***Polygala mariana*** | | | | 0.05 | 0.15 | |
| | ***Scirpus lineatus*** | 0.15 | 0.1 | 0.1 | 0.2 | 0.5 | 0.15 |
| | ***Spartina patens*** | | | | 0.55 | 0.85 | |
| **Wet Pine Flatwood** | ***Aletris lutea*** | | | | | | 0.2 |
| | ***Andropogon glomeratus*** | 0.25 | 0.25 | 0.35 | 0.25 | 0.35 | 0.35 |
| | ***Aristida beyrichiana*** | | | | | | 0.4 |
| | ***Bigelowia nudata*** | | | | | | 0.1 |
| | ***Helianthus angustifolius*** | | | | | | 0.1 |
| | *Hypericum nitidum* | | | | | | 0.05 |
| | ***Hypericum tetrapetalum*** | | | | | | 0.1 |
| | ***Lacnanthes caroliniana*** | | | | | | 0.3 |
| | *Lycopodiella prostrata* | | | | | | 0.15 |
| | ***Muhlenbergia expansa*** | | | | 0.1 | 0.1 | 0.05 |
| | ***Paspalum plicatulum*** | 0.1 | 0.05 | 0.15 | 0.05 | | 0.1 |
| | ***Polygala cruciata*** | | | | | | 0.05 |
| | ***Rhexia alifanus*** | | | | | | 0.05 |
| | ***Rhynchospora latifolia*** | | | | | | 0.05 |
| | *Sarracenia alata* | | | | | | 0.05 |
| | ***Scleria oligantha*** | | | | | | 0.05 |
| | ***Viola lanceolata*** | 0.05 | | | 0.1 | 0.05 | 0.1 |

Table 3.5. Distribution of generalist (G), noxious (N) and alien (A) species across sites and vegetation treatments (X=presence). Wetland status according to U.S. Fish and Wildlife Biological Report 88 (26.9).

| **Species** | **Status** | **Wetland Status** | **Site 1** | | | | | | | **Site 2** | | | | | | | **Site 3** | | | | | | | **Site 4** | | | | | | | **Site 5** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | U | C | S | B | F | PI | PS | U | C | S | B | F | PI | PS | U | C | S | B | F | PI | PS | U | C | S | B | F | PI | PS | U | C | S | B | F | PI | PS |
| *Acalypha virginica* | G | FAC- | | | | x | x | x | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Acer* sp. | G | FACW | | x | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Agrostis perennans* | G | FACU | | x | x | x | x | x | x | | | | | x | | | | | | x | | | | | x | x | x | x | x | | | | x | | | | |
| *Ambrosia artemisiifolia* | G | FACU | | x | | | | | | | | | | | | x | | | | | | | | | | | | | | | | | | | x | | |
| *Ammannia coccinea* | G | FACW+ | | | | | | | | | | x | x | | | x | | | | | | | | | | | | | | | | | | | | | |
| *Ampelopsis arborea* | G | FAC+ | | | | | | | | | | | | | | | | | | | | | | | | | x | | | x | | | | | | | |
| *Andropogon virginicus* | G | FAC- | x | | | | | | | | x | | | x | x | | x | x | x | x | x | x | x | x | x | x | x | x | x | x | | | | | | | x |
| *Bacopa monnieri* | G | OBL | | | | x | x | | | x | x | x | | x | | x | | | x | x | x | x | x | | | | | | | | | | | x | | | |
| *Carex festucacea* | G | FACW | | | x | | | | x | | | x | x | x | x | x | x | x | x | x | x | x | x | | | | x | x | | | | x | x | x | x | x | x |
| *Centella erecta* | G | FACW | | x | x | x | x | x | x | | | x | x | | x | | x | x | x | | x | x | x | | | | x | x | | | x | x | x | x | x | x | |
| *Centrosema virginianum* | G | | | x | x | | x | x | | | | | | | | | | | | | | | | x | x | x | x | x | x | x | | | x | | | x | |
| *Chamaesyce maculata* | G | FACU- | | | | | x | | | | | | | | | | | | | x | | | x | | | | | | | | | | | | x | | |
| *Chromolaena ivifolia* | G | | | | | | | x | | | | x | x | | | x | | | | | | | x | | | | | | x | | | x | x | x | x | x | |
| *Conoclinium coelestinum* | G | FAC | | x | | | | | | x | x | x | x | x | x | x | | x | x | | x | x | x | | | x | x | x | x | x | | | | | | | |
| *Conyza canadensis* | G | FACU | | x | x | | x | | x | | | | | x | | | | | | x | | | | | | | | | | | | | x | x | x | | x |
| *Cuphea viscosissima* | G | FACU | | | | | x | x | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Cyperus retrorsus var. robustus* | G | FACU+ | | | | | | | | | | | | | | | | | x | | | | | | | x | x | x | x | x | | | | | | | |
| *Cyperus strigosus* | G | FACW | | | | | | | | | x | x | x | x | x | x | | x | x | x | x | x | x | | | x | | | x | | | | | | | | |
| *Cyperus virens* | G | FACW | | | x | | | | | | | x | x | | | x | | | x | | x | x | | | | | | | | | | x | | x | x | x | |
| *Dichanthelium dichotomum* | G | FAC | | x | | | x | x | x | | | | | | | | | x | x | x | x | x | x | | | | | | | | | | | | | | |
| *Dichanthelium ensifolium* | G | FAC | | | | | x | | | | x | x | | | x | x | | | | | | | | | | | | | | | | | | | x | x | x |
| *Dichanthelium scoparium* | G | FACW | | x | x | x | x | x | x | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Dichanthelium sphaerocarpon* | G | FACU | | | | | x | | | | | | | | | | | | | | | | | | x | x | x | x | x | x | | x | | | x | | |
| *Digitaria sanguinalis* | G | FAC- | x | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Diodia virginiana* | G | FACW | | | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | | x | x | x | x | x | x | | x | x | x | x | x | x |
| *Eclipta prostrata* | G | FACW- | | | | | | | | | | x | | | | | | | | | | | | | | | x | | | | | | | | | | |
| *Eleocharis tenuis* | G | FACW | | | | | | | | x | | | x | | | x | | | x | x | x | x | x | | | | | | | | | | | | | | |
| *Eupatorium capillifolium* | G | FACU | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | | x | x | x | | x |
| *Euthamia caroliniana* | G | FAC | | x | x | x | x | x | x | | x | x | x | x | x | x | x | x | x | x | x | x | x | | x | x | | | x | | x | x | x | x | x | x | x |
| *Galium tinctorium* | G | FACW | | | | | | | | | x | x | x | x | x | x | | | x | x | x | x | x | | | | | | | | | | | | | | |
| *Gamochaeta purpurea* | G | UPL | | x | x | x | x | | x | | x | x | x | x | x | x | | x | x | x | x | x | x | | | | | | | | | x | | x | x | x | x |

Table 3.5. (continued)

| **Species** | **Status** | **Wetland Status** | **Site 1** | | | | | | | **Site 2** | | | | | | | **Site 3** | | | | | | | **Site 4** | | | | | | | **Site 5** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | U | C | S | B | F | PI | PS | U | C | S | B | F | PI | PS | U | C | S | B | F | PI | PS | U | C | S | B | F | PI | PS | U | C | S | B | F | PI |
| *Galium tinctorium* | G | FACW | | | | | | | | | x | x | x | x | x | x | | | x | x | x | x | x | | | | | | | | | | | | | |
| *Gamochaeta purpurea* | G | UPL | | x | x | x | x | | x | | x | x | x | x | x | x | | x | x | x | x | x | x | | | | | | | | | x | | x | x | x |
| *Hedeoma hispida* | G | | | x | x | x | x | x | x | | | | | | x | | x | | | | | | | | x | | x | x | | | | | | | | |
| *Hydrocotyle bonariensis* | G | FACW | x | x | | | | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | | | | | x | | x | x | | x | x | | x | x |
| *Hypericum drummondii* | G | FACU | | | | | x | x | x | | | | | x | x | | | x | | | | x | x | | | | | | | | | | x | | | |
| *Hypericum gymnanthum* | G | FACW | | | | | | | | | | | | | | | | | | | | | | | x | | x | | | | | | | | x | |
| *Hypericum mutilum* | G | FACW+ | | x | | | | x | | | x | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Juncus acuminatus* | G | OBL | | x | | x | | | x | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Juncus bufonius* | G | FACW | | | | | | | | | x | x | x | x | x | | | x | x | | x | x | | | | | | | | | | | | | | |
| *Juncus coriaceus* | G | FACW | | | | | | | x | | x | x | x | x | x | x | | x | x | x | x | x | x | | | | x | | | | | | | | | |
| *Juncus diffusissimus* | G | FACW | | | | | | | | | | x | x | x | x | x | | x | x | x | x | x | x | | | | | x | | | | | | | | |
| *Juncus effusus* | G | FACW+ | | | | | | x | x | | x | | | x | | x | | x | | | | x | | | x | x | x | | | x | | x | x | x | x | x |
| *Juncus validus* | G | FACW+ | | | | | | | | | | x | x | x | x | x | | x | x | x | x | x | x | | | | | | | x | | x | x | x | x | x |
| *Kyllinga  brevifolia* | G | FACW | | | | | | | | | x | x | x | x | x | | | x | | x | x | x | x | | x | x | x | x | | x | | x | x | x | x | x |
| *Lactuca floridana* | G | FACU | | x | x | x | x | x | x | | | | | | x | | | | | x | | x | x | | | | | | | | | | | | | |
| *Ludwigia alternifolia* | G | OBL | | | | | | | | | | | | | | | | x | | | | | | | | | | | | x | | | | | | |
| *Ludwigia hirtella* | G | FACW+ | | | | | | | | | | | | | | | | | | | | | | | | | | | | | x | | x | | x | |
| *Ludwigia octovalvis* | G | OBL | | | | | | | | x | x | x | x | x | x | x | | | x | | x | | | | | | x | | | | | | | | | |
| *Mitreola petiolata* | G | FACW+ | | | | | | | | | x | | | x | | | | | | | | | | | | | | | | | | | | | | |
| *Oxalis dillenii* | G | | | | x | x | x | x | x | | x | | | | | | | | x | x | | x | x | | x | x | x | | | x | | | x | x | x | x |
| *Paspalum dissectum* | G | OBL | | | | | | | | | | | | | | | | | | | | | | | x | x | x | x | x | x | | | | | | |
| *Phyla nodiflora* | G | FACW | | | | | | | | | | | | | | | | | | | | | x | | | | | | | | | | | | | |
| *Plantago virginiana* | G | FACU | | | | | x | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *Polygonum punctatum* | G | FACW+ | | x | x | x | x | x | x | x | | | x | x | | | | x | x | x | | x | x | | | | | | | | | | | | | |
| *Polypremum procumbens* | G | FACU- | | x | | x | x | | | | | | x | x | | | | x | | | x | x | x | | x | x | x | x | x | x | | x | x | x | x | x |
| *Portulaca pilosa* | G | FACU | | | | | | | | | | | | | | | | | | x | | | | | | | | | | | | | | | | |
| *Ptilimnium sp.* | G | FACW+ | | | | | x | x | x | | x | x | x | x | x | x | | x | x | | x | | | | | | | | | | | | | | | |
| *Pyrrhopappus carolinianus* | G | | x | x | x | x | x | x | x | | | | | | | | x | | x | x | x | x | x | | | | x | | | x | | x | | | x | |
| *Rhexia virginica* | G | FACW+ | | | | | | | | | | | | | | | | | | | | | | | x | x | x | x | x | x | | | | | | |
| *Rubus argutus* | G | FACU+ | | | x | x | x | x | x | | | | | | | | x | | | | | | | | | | | | | | x | x | | x | | |
| *Sesbania herbacea* | G | FACW- | | | | | x | | | | | | | x | | x | | | | x | | | | | | | | | | | | | | | | |
| *Sida rhombifolia* | G | FACU | | | | | | | | | | | | | | | | | | | | | | | | | | | | x | | | | | | |
| *Sisyrinchium rosulatum* | G | FACU | | x | | x | x | x | x | | | | | | | x | | x | x | x | x | x | x | | x | | x | x | x | x | | x | x | x | x | x |
| *Solidago altissima* | G | FACU+ | x | | | | | | | x | | x | | | x | | | | | x | x | | x | x | x | x | x | x | x | x | x | x | x | x | x | x |
| *Sphenopholis obtusata* | G | FAC+ | | | | | | | | | | | | | | | | | | | | | | | | | x | x | x | | x | x | x | x | x | x |

Table 3.5. (continued)

| **Species** | **Status** | **Wetland Status** | **Site 1** | | | | | | | **Site 2** | | | | | | | **Site 3** | | | | | | | **Site 4** | | | | | | | **Site 5** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | **U** | C | S | B | F | PI | PS | **U** | C | S | B | F | PI | PS | **U** | C | S | B | F | PI | PS | **U** | C | S | B | F | PI | PS | **U** | C | S | B | F | PI | PS |
| *Crotalaria spectabilis* | N | | **x** | | | | | | | | | | | | | | | | | | | | | | | | | | | | **x** | | | | | | |
| *Imperata cylindrica* | N | | **x** | | | | | | | **x** | | | | | | | | | | | | | | **x** | | | | | | x | | | | | | | |
| *Panicum repens* | N | FACW- | **x** | x | x | x | x | x | x | | | | | | | | | | | | | | | | | | | | | | **x** | x | | x | | | |
| *Phyllanthus urinaria* | N | FAC | | x | x | x | x | x | x | **x** | x | x | x | x | x | x | | x | | | x | x | x | | | | | | | | | | | | | | |
| *Triadica sebifera* | N | FAC | | | | | x | | x | | x | x | x | x | x | x | **x** | | x | x | x | x | | | | | | | | | **x** | | | | | | |
| *Acmella decumbens* | A | | | | | | | | | **x** | | | | | | | **x** | x | | x | | | | | | | | | | | | | | | | | |
| *Capsella bursa-pastoris* | A | FACU+ | | | | | | | | | x | x | x | x | x | x | | | | | | | | | x | x | x | x | x | | | | | | | | |
| *Conyza bonariensis* | A | | **x** | | | | x | x | | | | | | | | | | x | x | x | x | x | x | | x | | x | x | | | | x | x | x | x | x | x |
| *Cuphea glutinosa* | A | FACU- | | | | | | | | **x** | x | x | x | x | x | x | **x** | x | x | x | x | x | x | | | | | | | | | | | | | | |
| *Cynodon dactylon* | A | FACU | | | | | x | | | **x** | | | | | | x | **x** | | | | | | | | x | x | | | | | | x | x | x | x | x | x |
| *Digitaria ischaemum* | A | UPL | | | | | | x | x | | | | | | | | **x** | x | | | | | | | x | x | x | x | x | x | | x | | x | | x | x |
| *Ipomoea hederacea* | A | FAC- | | | | | | | | | | | | | | x | | | | | | | | | | | | | | | | | | | | x | |
| *Ipomoea quamoclit* | A | FACU+ | | | | | | | | | | | | | | | | x | x | x | x | x | | | | | | | | | | | | | | | |
| *Melochia corchorifolia* | A | FAC | | | x | | | | | | | | | | | | | x | x | x | x | x | x | | x | x | x | x | x | x | | x | | | | | |
| *Murdannia keisak* | A | OBL | | | | | | | | | x | | x | | x | | | | | | | | | | | | | | | | | | | | | | |
| *Paspalum dilatatum* | A | FAC+ | **x** | x | | x | x | x | x | | | | | | | | **x** | x | x | x | x | x | x | | | | | | | | | x | x | x | x | x | x |
| *Paspalum urvillei* | A | FAC | | | | | | | | | | | | | | | | x | x | | | x | | | | | | | x | x | **x** | | x | x | x | x | x |
| *Plantago lanceolata* | A | FAC | | x | x | x | x | x | x | | x | x | x | x | x | x | | | x | | | | | | | | | x | | | | x | x | x | x | x | x |
| *Plantago major* | A | | | | | | | | | | x | x | x | x | x | x | | x | | x | x | | | | | | | | | | | | | | | | |
| *Rumex crispus* | A | FAC | | | | | | | | | | | | x | | | | | x | | | | | | | x | | | | | | | | | | | |
| *Trifolium repens* | A | | | x | | | x | | | | x | | x | x | | | | x | x | x | x | x | x | | x | | | | | | | | x | x | x | x | |
| *Verbena brasiliensis* | A | FACU | | x | | | | | | | | | | | x | | | | | | | | | | x | | x | | | | | x | x | x | x | x | x |

Table 3.6. Summary of indicator species found to be significantly faithful to the various sod treatments. Indicator value (IV) suggests how even and faithful the species is across all plots in each treatment and only species with significant p values are included. The percentage of subplots containing that species is also included

| **Sod Vegetation Type** | **Species** | **IV** | **p** | **%** |
|---|---|---|---|---|
| Salt Marsh | *Spartina alterniflora* | 15 | 0.033 | 15 |
| Brackish Marsh | *Juncus roemerianus* | 20 | 0.004 | 35 |
| Freshwater Marsh | *Sabatia stellaria* | 45 | 0.001 | 45 |
| | *Baccharis halimifolia* | 15 | 0.029 | 30 |
| Maritime Pine | *Spartina patens* | 49.8 | 0.001 | 85 |
| | *Scirpus lineatus* | 20 | 0.007 | 45 |
| | *Pinus elliottii* | 15.3 | 0.026 | 15 |
| Wet Pine Flatwood | *Aristida beyrichiana* | 40 | 0.001 | 40 |
| | *Lacnanthes caroliniana* | 30 | 0.001 | 30 |
| | *Aletris lutea* | 20 | 0.002 | 20 |
| | *Lycopodiella prostrata* | 15 | 0.027 | 15 |
| Control | *Kyllinga brevifolia* | 17.6 | 0.045 | 25 |

Table 3.7. P values from PERMANOVA on species composition data in response to a) propagule bank treatments and b) site variation. P values in **bold** are significant and indicate which treatment combinations are significantly different. Legend: C-control, S-salt marsh, B-brackish marsh, F-freshwater marsh, MP-maritime pine island, PF-wet pine flatwood.

a)

| | C | S | B | F | MP |
|---|---|---|---|---|---|
| S | **0.001** | | | | |
| B | 0.104 | 0.081 | | | |
| F | **0.001** | **0.001** | **0.001** | | |
| MP | **0.001** | **0.001** | **0.001** | 0.105 | |
| PF | **0.008** | **0.008** | **0.007** | **0.001** | **0.001** |

b)

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| 1 | | | | | |
| 2 | **0.001** | | | | |
| 3 | **0.001** | **0.001** | | | |
| 4 | **0.001** | **0.001** | **0.001** | | |
| 5 | **0.001** | **0.001** | **0.001** | **0.001** | |

Figure 3.1. Overview of the process involved in site establishment of propagule sods: a) appearance and b) removal of propagule sods from donor sites, c) application onto recipient sites, and d) site appearance in July 2010.

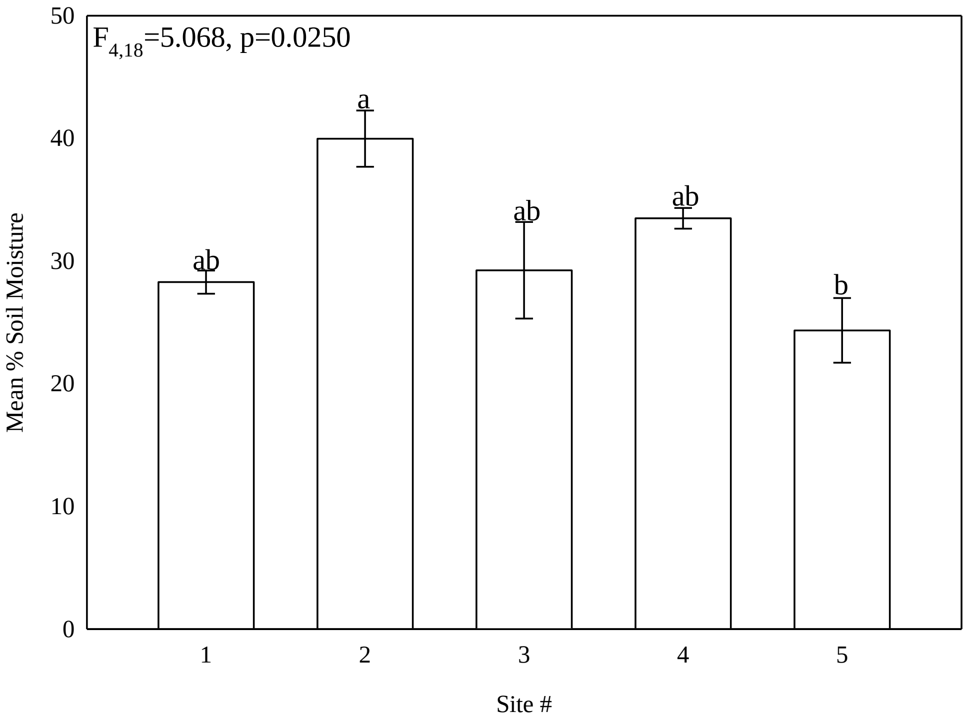

Figure 3.2. Variation in mean soil moisture among sites.

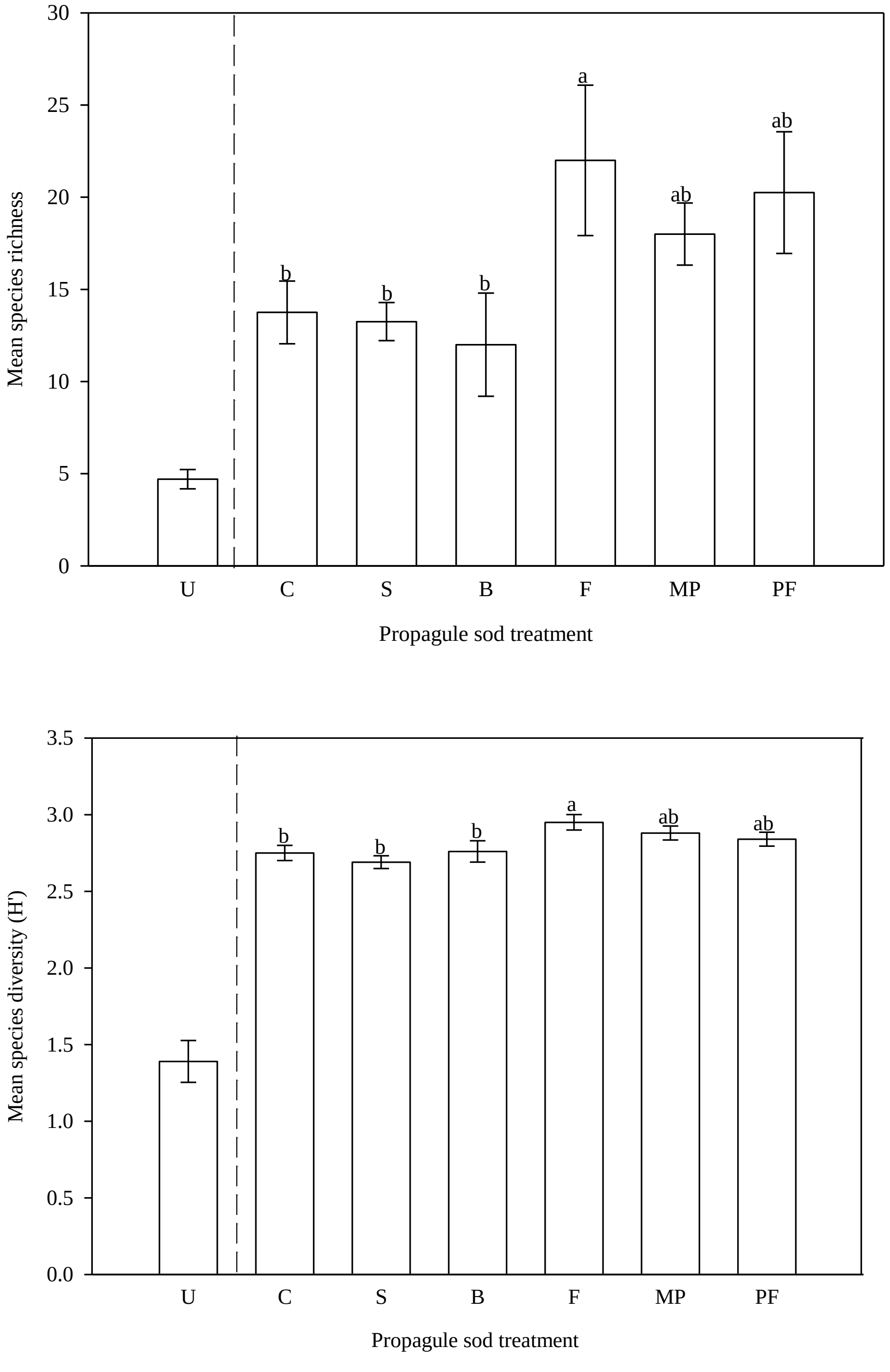

Figure 3.3. Summary of a) mean species richness and b) mean species diversity across propagule sod treatment types. While not included in the ANOVA, unmanipulated plots (receiving neither propagule addition or site preparation preparation) are included in the Figure. Legend: U-Unprepared, C-control, S-salt marsh, B-brackish marsh, F- freshwater marsh, MP-maritime pine island, PF-pine flatwood.

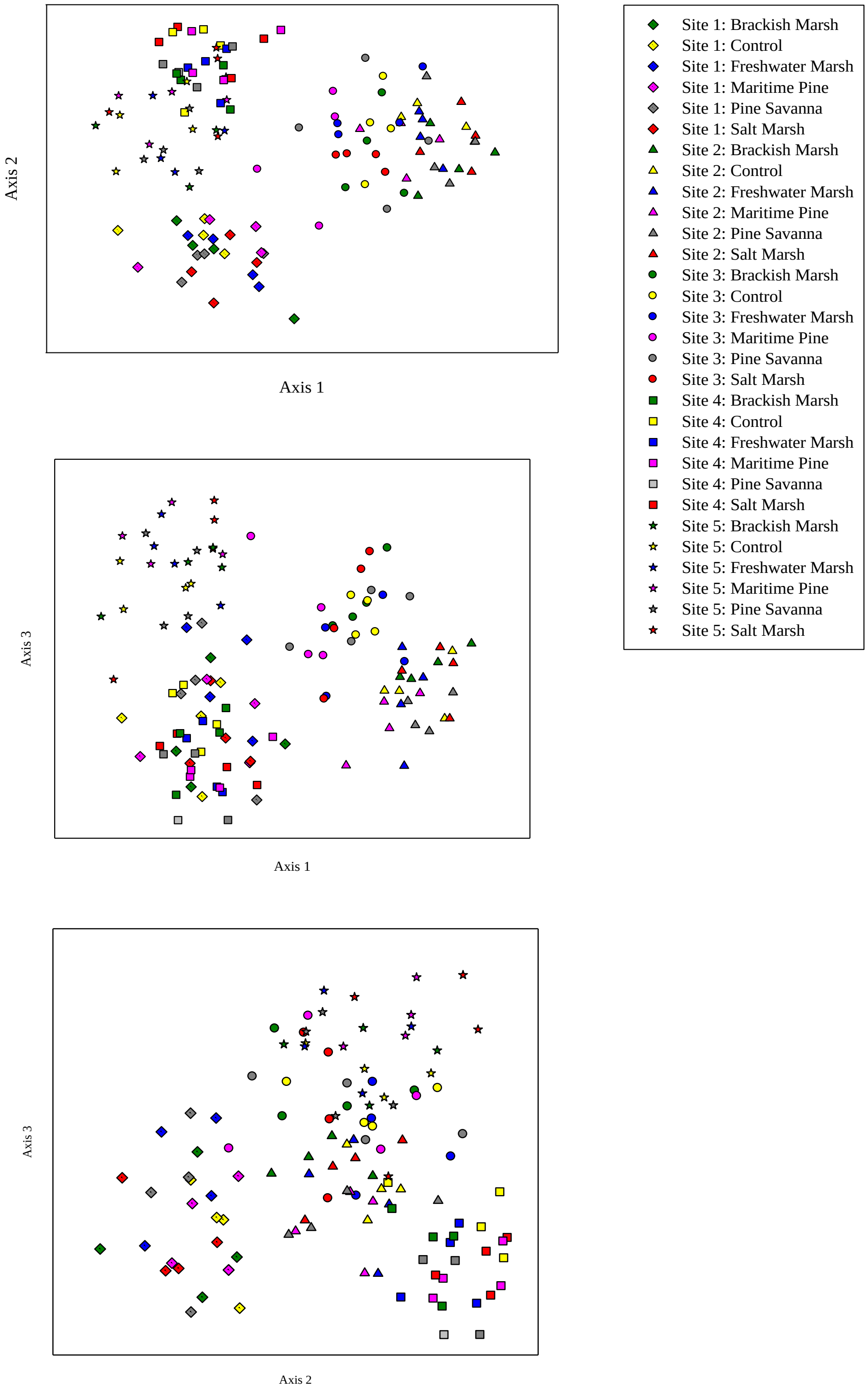

Figure 3.4. NMDS ordination of species composition of all surveyed subplots at the end of the growing season. Points which are close to each other in ordination space are compositionally similar and all three views of the three-dimensional ordination are included. Symbols indicate the site the subplot is on and color indicates which propagule treatment the plot received. Unprepared plots are not included in the ordination.

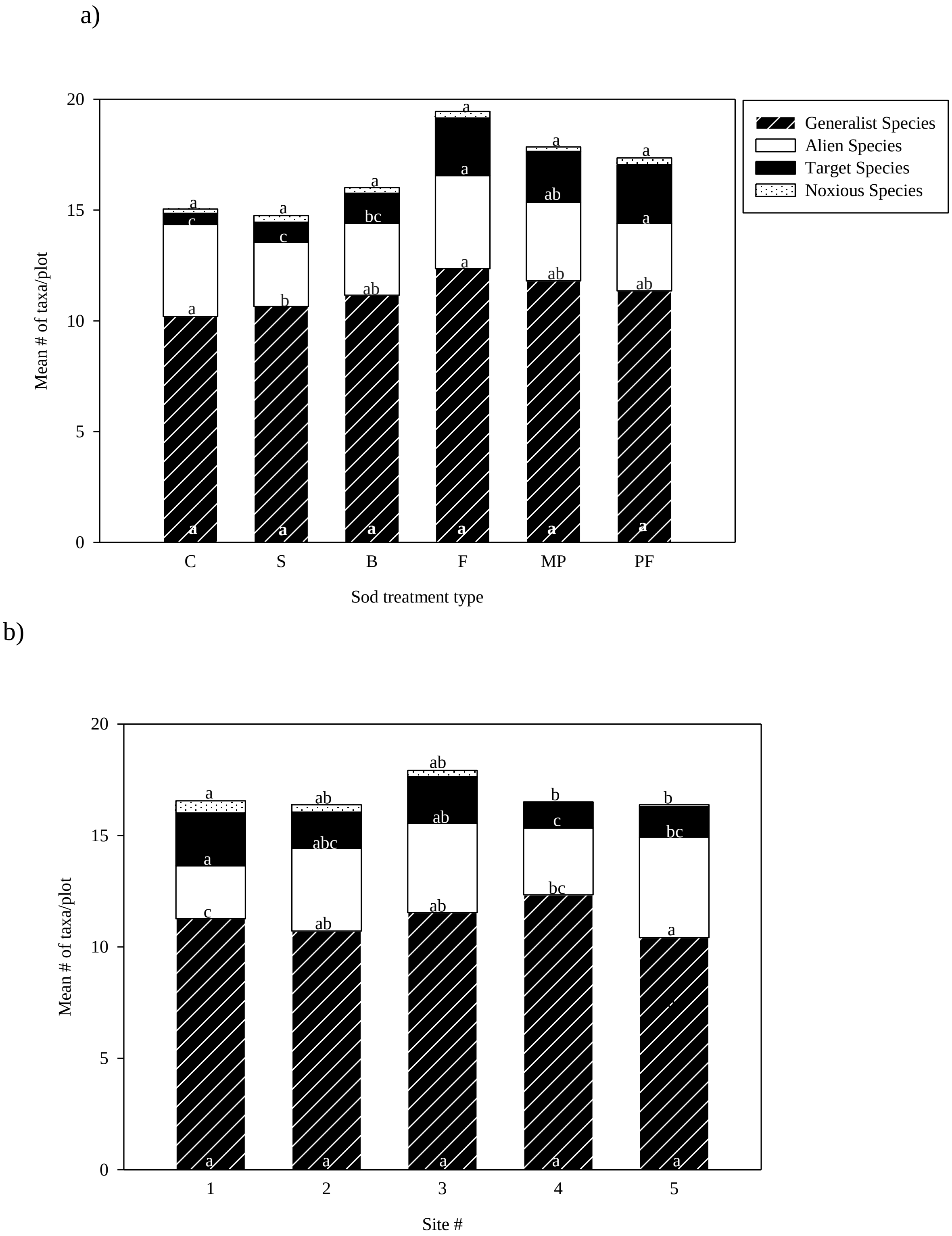

Figure 3.5. Mean # of taxa in desirability categories varies across a) sod treatment types and b) sites. Letters in each category indicate significant differences as indicated by ANOVA and mean multiple comparisons for each category. Legend: C-control, S-salt marsh, B-brackish marsh, F-freshwater marsh, MP-maritime pine island, PF-wet pine flatwood.

# CHAPTER 4

# CONCLUSIONS

Coastal ecosystems are on the front lines of climate change and will be markedly affected in a societally significant time-frame (Scavia et al., 2002; Day et al., 2008). The northern Gulf of Mexico, in particular, is one region which is considered highly vulnerable to the long-term effects of sea level rise and erosion (Thieler and Hammar-Klose, 2000) and a number of studies support the suggestion that tropical cyclone activities have increased in their strength over the last 30 years (Hoyos et al., 2006; Elsner et al., 2008; Bender et al., 2010). Accretion in coastal marshes has historically allowed the vegetation  adapt to periodic fluctuations in sea-level and the associated plant species have been able to shift gradually according to changes in ocean conditions (Brinson et al., 1995; Mitsch and Gosselink, 2007). While unmodified coastal systems have adapted to survive fluctuations in sea-level and hurricane disturbances, the pace of climate-induced change has introduced great uncertainties regarding the ability of the coastal plant communities to respond. Species which are not able to adapt or disperse quickly, may not survive the increasingly intense and further reaching storm surges.

This research was aimed at evaluating the importance of seed banks in coastal ecosystems already experiencing the effects of climate change. Specifically, it was concerned with the potential for seed banks to not only aid in the recovery following disturbances but also in the possible transition to more seaward assemblages as the environmental template changes. Plant communities with seed banks containing species able to evolve or migrate inland may be able to survive the rapid environmental changes associated with the acceleration of sea level rise and intensified storm surges. Assemblages that do not have a resilient and responsive seed bank may not be capable of surviving altered inundation regimes. If it was determined that seed and propagule banks were sufficient to “buffer” coastal plant communities from acute surge events, then they may also be important tools for instilling resilience into and guiding the restoration of degraded coastal systems.

In order to determine the potential for seed banks to guide conservation and restoration objectives in coastal ecosystems, I evaluated the composition and species distribution of the standing vegetation and seed banks in major vegetation zones along a typical Gulf Coast transition. Simultaneously, the effects of simulated storm surge on seed banks were assessed to predict possible community change with altered inundation regimes.

The results of this first study may guide future research regarding potential community trajectories and ecological resilience in a changing climate. Analyses of the species composition of the standing vegetation and seed banks reveal a pattern of increasing plant species diversity with distance from the sea that is correlated with declining soil salinity. While most seed banks were comprised of a subset of species present in the standing vegetation only the saline marshes exhibited strong resemblance to their seed bank communities. The upland seed banks contained some indicator and dominant species but largely contained transient and weedy species not present in the standing vegetation. Storm surge treatments reduced seedling abundance and richness across all vegetation zones. This study suggests that seed banks may of minor importance following storm surge events and further studies may show that vegetative growth may be more dominant. While summer seed banks are not indicative of the diversity of the propagule banks at other times of the year, the results of the hurricane season survey do imply that some of the historical plant communities may not be supported if inundation regimes were to continue changing. With ruderal species dominating and acting as the most responsive components following storm surge treatments, response from the upland seed bank communities would result, in the short-term, in replacement of native, relict species by weedy and alien species.

Climate change induced habitat shifts may require the assisted migration for the survival of some species even within their natural ranges (Hoegh-Guldberg et al., 2010; Seddon, 2010,Vitt et al., 2010 ). This study supports arguments that assisted migration, in which vulnerable species are intentionally moved for conservation purposes, may be especially important in the Gulf of Mexico and similar coastal systems. The apparent absence of seaward in the upland seed banks may make assisted migration an important tool for the survival of communities unable to keep pace. While timing and mechanisms of dispersal vary according to species and local climate, these upland species pools do not contain taxa capable of surviving frequent inundation. As site conditions change, these sites may no longer support the historical vegetation and, without a readily available pool of taxa adapted to future conditions, may not easily transition to more resilient communities. The intentional addition of propagules from throughout the landscape may provide this resilience and further studies should address the potential of this technique for the conservation of vulnerable ecosystems.

Given the growing evidence that coastal habitats are likely to be very different in the future, the conservation prospective may shift from preserving current assemblages to encouraging the development and management of more resilient, novel communities. The pace of climate change has challenged land managers and ecologists alike to evaluate the restrictive management options associated with historic ecosystem conditions. Many environments have already been so modified, both by abiotic and biotic changes, that they no longer resemble or could be feasibly returned to their historic state (Hobbs et al. 2009; Williams and Jackson, 2007). Hobbs et al. (2009) suggest that in regions in which traditional conservation options fail us, acceptance and thoughtful management actions can still yield valuable and beneficial results (conservation of biodiversity, promotion of ecological integrity and ecosystem services).

In the second study, community translocations from these historic plant communities onto the degraded buyout sites suggest that propagule banks may be an effective option for instilling biological resilience into vulnerable assemblages. The practice is often performed to aid in mitigation for civil engineering projects in which the donor site will no longer be appropriate habitat (ie. excavation, road building, filling of wetlands, etc.; Bullock, 1998; Vécrin and Muller, 2003) but does not yet appear to have been used experimentally for the creation of novel communities. These translocations resulted in the establishment of diverse and variable communities, containing many habitat generalists, alien and desirable targets from a number of true analog communities. Target species emerged from all donor communities, resulting in taxa with a wide variety of physical tolerances, life histories and functional traits. Species diversity and richness were increased, and noxious species were greatly reduced, on all restoration plots relative to the untreated areas. All upland and freshwater propagule banks responded favorably to the sites and the freshwater marsh and maritime pine propagule banks were the most stable and consistent, in terms of propagule abundances. If active management was deemed economically and biologically feasible, these assemblages would probably be the analog communities best suited to the degraded environments. Propagule banks from the wet pine flatwood assemblages, which host some of the greatest diversity of plant species globally and are of particular conservation concern, also responded favorably on the restoration sites. Variation among replicate sites suggests that environmental variation and proximity to source populations of ruderal species may also drive the resulting communities. The long-term storage of various propagules from throughout the coastal transition, however, may act to speed up succession and encourage the sites themselves to “design” a sustainable, functioning assemblage. Long-term monitoring of community change and reproductive output of target species may suggest the power of community translocation in creating resilient and future-adapted communities.

Future research may also indicate the potential to integrate these suites of species into the intact coastal transition, thereby establishing more futuristic propagule communities and allowing a more rapid response to changes in sea level and storm surge events. While historical data are still going to be important for guiding ecosystem management, climate change has introduced great uncertainties in the conservation of coastal areas which will require a greater understanding of ecosystem function and the establishment of more realistic goals.

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