

# Positive Species Interactions as Drivers of Vegetation Change on a Barrier Island

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## ABSTRACT

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Positive species interactions have been shown to occur in a variety of plant systems, and the importance of these interactions is expected to vary with resource availability and abiotic stress. The processes by which these types of relationships operate and influence plant communities in coastal environments, however, are not fully understood. Positive species interactions were observed in areas of St. George Island, Florida, shortly after transplanting dune species for a restoration experiment designed to encourage the growth of foredune, interdune, and backdune vegetation. The dune habitats in St. George are subject to abiotic stresses that vary in type and magnitude, and the environmental factors responsible for ameliorating these conditions and encouraging positive vegetation change operate differently across these areas. We (1) investigated if transplants encouraged positive changes in vegetation across dune habitats, (2) determined whether disturbance (through transplanting) played a role, and (3) tested environmental factors involved in positive interactions to explain the changes in vegetation observed across dune habitats. The presence of transplants positively modified vegetation (*e.g.*, species richness or cover) across all dune habitats. Experimental disturbance had no strong overall positive effect on vegetation change. Shading and soil moisture redistribution had differential effects on vegetation change among habitats, suggesting that these environmental factors interact with the abiotic characteristics unique to each dune habitat in complex ways. Our results suggest that experimentation over a longer time scale might be required to fully understand the extent at which positive interactions affect vegetation patterns along stressful environmental gradients.

**ADDITIONAL INDEX WORDS:** *Disturbance, dune vegetation, facilitation, shading, soil moisture redistribution, species richness.*

## INTRODUCTION

Coastal systems are structurally important for protecting shorelines and are ecologically important habitats for many endangered and endemic species. Despite the economic and ecological relevance of these areas, we still have an incomplete understanding of how ecological factors might shape vegetation in these habitats.

In coastal habitats such as barrier islands, abiotic stresses can vary considerably as a function of distance from shore, and these stresses alter the composition of native plant communities (Bertness and Callaway, 1994). The presence of a stress gradient on barrier islands is due, in part, to the role these islands play as a protective buffer for the mainland against various storms including hurricanes (Walker and Willig, 1999), which bring high winds and rainfall, along with significant saltwater storm surge. These infrequent disturbance events often interact with more regular stresses such as high temperatures, constant wind, and wave actions (Fagherazzi, Wiberg, and Howard, 2003). Understanding the processes plants use to maintain

overall community structure under variable stresses found in coastal habitats is particularly important because storm prevalence and intensity is expected to increase with global change (Parmesan, Root, and Willig, 2000).

Barrier islands systems provide a unique opportunity to study potential processes that modify the changes in vegetation that affect plant community patterns and zonation. In these environments, for example, many stresses occur, including salt spray, substrate movement, high temperatures, and low nutrient and water availability; they change along a gradient of unique habitats (Brooker *et al.*, 2008; Hesp, 1991; Lopez, Larrea-Alcazar, and Ortuno, 2009; Noy-Meir, 1973). Barrier islands can be partitioned into three habitat zones: foredune, interdune, and backdune habitats (Ehrenfeld, 1990; Lewis, 1982). Vegetation in the xeric, species-depauperate oceanside facing foredune is mostly affected by temperature and high wind speeds that encourage sand movement and tall dune development. Behind the foredunes is the flat, saline interdune habitat, where vegetation is most sensitive to storm surge and precipitation (Miller, Gornish, and Buckley, 2010). These two zones protect the older and stable dunes of the species-rich bayside-facing backdune habitat, where increased vegetation change appears to be driven primarily by precipitation (Miller, Gornish, and Buckley, 2010). Although the habitats are

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continuous, clear differences in dune height generally make distinctions between habitats fairly evident. Because these habitats are characterized by a variety of stressors (Boughey, 1957), it is likely that dune plant species are interacting with their environment to modify conditions that might allow them and other neighboring species to survive (Bruno, Stachowicz, and Bertness, 2003; Odum, 1988; Stallins, 2005).

Positive species interactions, such as facilitation, have been proposed to occur in stressful environments such as intertidal communities, salt marshes, and dune environments (Bertness and Callaway, 1994; Tewksbury and Lloyd, 2001). Facilitation often works in these areas in the form of nurse-plant relationships, where benefactor species that are best adapted to overcome stress might provide more favorable environmental conditions for proximal individuals of similar or different plant species (Bertness and Callaway, 1994). For example, as a result of their morphological characteristics (*e.g.*, extensive root systems), some plant species encourage the development of sand dunes, and these topographic modifications then provide more ideal conditions for the further establishment and growth of other native species (Ehrenfeld, 1990; Lewis, 1982). Plants can also create water and nutrient reservoirs by shading the soil surface and reducing evaporation (Kidron, 2009). The result could be an increase in soil water content, which could serve to irrigate buried seedlings (Chacon and Bustamante, 2001) and facilitate plant growth in areas of the gradient where water availability is low. In addition, plants in desert environments can affect soil moisture by intercepting available water with their roots (Noy-Meir, 1973), producing differences in the vertical distribution of soil moisture. This redistribution of water has been shown to facilitate the germination of seeds and the growth of neighboring individuals (Caldwell, Dawson, and Richards, 1998; Harper, 1977; Horton and Heart, 1998).

In 2008, several dune-plant species were transplanted into storm-damaged areas in each of the three habitat zones in St. George Island State Park on the Florida Gulf Coast in a test of their potential as restoration candidates. Unexpectedly, unmanipulated native plant abundance increased in response to the transplanted species in the restoration quadrats but not in any control quadrats where no transplants were installed. This observation suggested that positive plant interactions could be taking place, providing the unique opportunity to explore the resulting environmental factors responsible for positive community-level changes in vegetation among dune habitats that are characterized by different types of abiotic stress (Brooker *et al.*, 2008; Lopez, Larrea-Alcazar, and Ortuno, 2009). Our goals were (1) to investigate if transplants significantly increased vegetation cover or species richness, possibly indicating positive species interactions (Bertness and Shumway, 1993; Callaway, 1995; Stachowicz, 2001); (2) to determine whether disturbance effects from transplanting played a role; and (3) to test two environmental factors involved in positive interactions (*e.g.*, shading and fluctuations in soil moisture) to explain changes in vegetation across the three habitat zones.

Because transplanting involved the disturbance of soils in restoration quadrats, we investigated disturbance to measure whether the observed changes in vegetation were attributable

to this process. We expected the positive effects (*e.g.*, increased diversity or vegetation cover) that could result immediately post disturbance to decrease from the foredune to the backdune habitat because species in more protected back areas are less adapted to substrate movement (disturbance associated with the transplanting process) and could therefore be more vulnerable to its potential negative effects. We also expected disturbance to have a more positive effect on species richness than on vegetation cover because soil disturbance often results in redistribution of seed-bank species to shallower depths (Thompson *et al.*, 2001), where abiotic conditions are more conducive to germination.

Additionally, we tested shading and soil moisture redistribution as potential environmental factors associated with positive interactions that might have induced positive vegetation change across dune habitats. We tested shading and soil moisture redistribution because these two factors are related to the amelioration of water limitation, a characteristic stress on barrier islands. We expected the positive effects of shading (moisture entrapment at shallow soil depths [Callaway, 1995]) to increase from the foredune to backdune habitat as stabilizer species, such as those with rhizomatous growth forms, increase in abundance (Ehrenfeld, 1990). Rhizomatous fragments, which are found exclusively at the soil surface and encompass a smaller group of existing species (Gross, 1990; Looney and Gibson, 1995), should receive a greater benefit from increased water availability than seed bank species, which are more diverse. Finally, the amount of water available for plant-mediated movement of soil moisture depends on evaporation and runoff rates, both of which can be modified by dune height (Bromley *et al.*, 1997). Therefore, we expected the degree to which transplants influence vertical redistribution of soil moisture to vary across dune habitats because of well-documented differences in dune height across habitats (Ehrenfeld, 1990). We expected an absence of soil moisture redistribution in the higher, irregular dunes in the foredune habitat where evaporation and runoff is highest. We also expected soil moisture redistribution to play the largest role in the interdune habitat, where an absence of dunes results in less runoff, consequently increasing water availability at more shallow depths.

## METHODS

### Ongoing Restoration Study

St. George Island State Park is located at the eastern end of a microtidal barrier island in Apalachicola Bay, Florida. The soil is composed of a fine sand surface over a layer of sandy silt or clay. The island receives an average of 119 cm of rain annually. In February 2008, a restoration study was initiated to test the efficacy of using six different native dune species that differed in their response to storms to stabilize and restore storm-damaged areas in the foredune, interdune, and backdune habitats (Gornish and Miller, 2013). The six species were *Centella asiatica* (Apiaceae), *Fimbristylis* spp. (either *F. spathacea* or *F. caroliniana*; Cyperaceae), *Muhlenbergia capillaries* (Poaceae), *Schizachyrium maritimum* (Poaceae), *Sporobolus virginicus* (Poaceae), and *Uniola paniculata* (Poaceae). Three replicate quadrats (6 × 5 m, each composed of 30 1-m<sup>2</sup> plots) were established in the center of foredune, interdune,

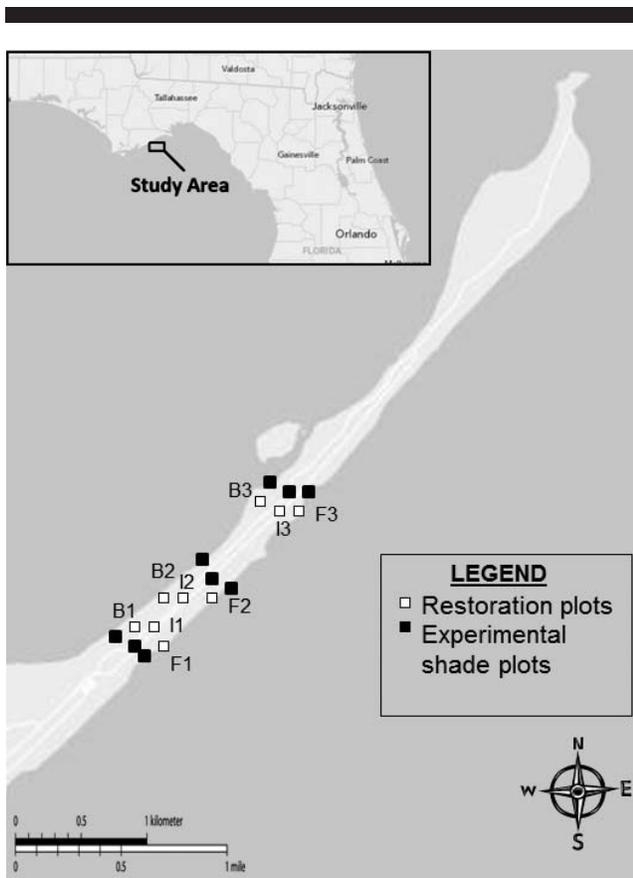


Figure 1. Map of study location of foredune (F), interdune (I), and backdune (B) restoration plots and experimental shading plots on St. George Island State Park.

and backdunes areas that were entirely devoid of vegetation as a result of a major storm the previous year (Figure 1). One mature individual of each of the six restoration species was transplanted into each of the smaller 1-m<sup>2</sup> plots (one of each of the six transplant species per plot, for a total of 180 plants per quadrat). The species were planted in a 2 × 3 array within each plot. Adjacent to each restoration quadrat, a control quadrat was established in which no transplants were installed in order to quantify effects of the transplanting process.

### Evidence of Vegetation Change

We quantified the intensity of vegetation change as the amount of colonization by extant native plants into restoration quadrats either through germination of the seed bank or dispersal into the plots. In August 2008, we visually estimated percentage vegetation cover by species and counted species richness (excluding transplanted individuals) on 10 randomly selected plots in each restoration quadrat and on the same 10 plots in each associated control quadrat. Through preliminary work, we found that vegetation data from 10 plots was sufficient to reflect trends across the entire quadrat.

### Disturbance

To determine the effects of disturbance, we simulated the physical disturbance caused by transplanting by mirroring our

transplanting process. Specifically, we used the same transplanting tools to excavate and refill six holes with the same sand on 10 randomly chosen plots in the control quadrats of the pre-existing restoration experiment in each dune habitat in early June 2009. Species richness and percentage vegetation cover were estimated in each of the randomly chosen plots before the disturbance treatment and 3 months later (during the peak of the growing season) on disturbed plots and control plots. This time scale was deemed as an appropriate tenure for our experiments because coastal dune vegetation has been shown to germinate and develop over short time scales (*e.g.*, Brown, 1997).

### Shading

To determine the effects of shading, we created three shaded and control quadrats in areas that were relatively free of vegetation in close proximity to the original restoration quadrats (Figure 1). These quadrats were also located within the center of the dune habitats to minimize any possible effects of shading by species from adjacent habitats. Neutral-density shade cloth (50% cover, similar to the average shading by the transplants as measured with a pyranometer) was used to simulate shading of the soil by transplants. The cloth was secured to corner stakes and suspended 0.5 m above each shaded quadrat (average height of the transplants). Control quadrats received only corner stakes. The shaded and control quadrats consisted of four 1-m<sup>2</sup> plots, and three replicates were installed in each of the three dune habitats. Percentage vegetation cover and species richness were estimated visually on shaded and control plots when the quadrats were installed (April 2009) and again 3 months later at the peak of the growing season (Maurer and Zedler, 2002). The ability of the shade-cloth treatment to simulate shading by transplants was confirmed by measurement of soil surface moisture and temperature on all shaded and associated control plots 2 months after the treatment was initiated. No significant difference was found in soil surface moisture or temperature between experimentally shaded and restoration plots.

### Soil Moisture Redistribution

Differences in the soil moisture profile between restoration and control quadrats could be attributable to interception and transpiration activity by the restoration transplants. To identify these differences, we used the original restoration and associated control quadrats (different plots than those used in the disturbance study) to nondestructively measure volumetric water content ( $\theta$ ) at different depths with a Fieldscout TDR 300 soil-moisture meter (Spectrum Technologies, East Plainfield, Illinois, U.S.A.). As sand dune plants are typically shallowly rooted, with root depths ranging from about 8 to 40 cm in most species (Stalter, 1974), we took measurements from 12, 20, and 50 cm below the soil surface.

We measured water content once in the morning, twice in the afternoon, and twice in the evening at each depth on two randomly selected plots in each of the restoration and control quadrats among all three dune habitats within 24 hours in July 2009. The measurements were made at 2030 and 2330 h on one day and at 0930, 1130, and 1430 h on the following day and were used to estimate the soil-water potential ( $\Psi_s$ ) at different depths for comparison of moisture gradients on restoration and

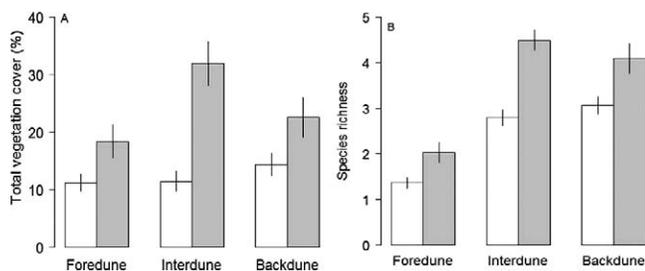


Figure 2. Mean vegetation cover (A) and species richness (B) of naturally occurring native species on control (white) and restoration plots (grey) in each dune habitat. Lines =  $\pm 1$  SE.

control plots (Donovan, Richards, and Linton, 2003). The soil moisture profiles from this single 24-h sampling period were expected to be consistent throughout the growing season (Caldwell, Dawson, and Richards, 1998). We calculated  $\Psi_S$  from measurements of  $\theta$  using a version of the Brooks and Corey equation from Campbell (1985):

$$\Psi_S = \Psi_{\text{Entry}}(\theta/\theta_S)^{-b},$$

where  $\Psi_{\text{Entry}}$  is the soil-water potential at air entry,  $\theta_S$  is the saturated water content, and  $b$  is the curve-fitting parameter. These parameters were deemed appropriate for the type of soil present on St. George Island—a high percentage of sand content ( $\geq 95\%$ ; Gornish, 2009) in all three habitats.

### Analysis

All analyses were conducted in R, version 2.10.1 (R Development Core Team, 2007). For all analyses, the plot was nested within the quadrat, which was replicated within dune habitat (main effects  $n = 3$ ). Total vegetation cover and species richness raw data were log transformed to meet assumptions of normality and variance homogeneity when necessary.

We used a linear mixed effects model (lme, R package lme4) to investigate the contribution of fixed factors (dune habitat type [foredune, interdune, and backdune] and treatment [restoration or control]) to total vegetation cover and species richness in plots. We also used an lme model to determine the contributions of experimental shading, experimental disturbance, and dune habitat type to total vegetation cover and species richness. Finally, a third lme model was used to determine the fixed effects of treatment (restoration or control), depth, and dune habitat type on soil-moisture distribution (hour included in the model as a random factor).

## RESULTS

### Evidence of Vegetation Change

Total, native vegetation cover (Figure 2A) was greater in restoration plots than in control plots across all habitats ( $F = 23.75$ ,  $p < 0.0001$ ). The interaction between dune habitat and treatment ( $F = 4.23$ ,  $p = 0.01$ ) contributed to differences in vegetation cover. Although vegetation cover was higher in restoration plots compared to controls across dune habitats (Figure 2A), it was significantly higher only in the interdune

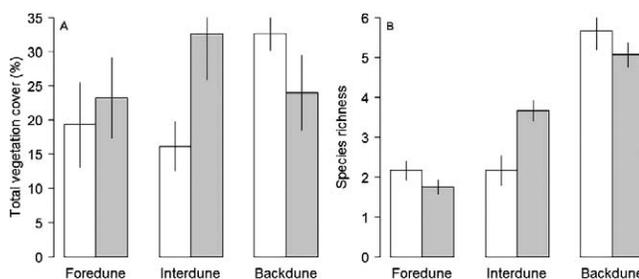


Figure 3. Mean vegetation cover (A) and species richness (B) on control (white) and experimentally disturbed plots (grey) in each dune habitat. Lines =  $\pm 1$  SE.

habitat (estimate = 0.76, SE = 0.29,  $t = 2.61$ ,  $p = 0.01$ ). Species richness (Figure 2B) was also higher in restoration plots than in control plots, overall ( $F = 32.1$ ,  $p < 0.0001$ ). Dune habitat ( $F = 62.4$ ,  $p < 0.0001$ ) also contributed to differences in species richness among plots. Species richness in the foredune habitat was smaller than richness in the interdune (estimate = 0.52, SE = 0.09,  $t = 5.64$ ,  $p < 0.001$ ) and backdune habitats (estimate = 0.6, SE = 0.09,  $t = 6.48$ ,  $p < 0.001$ ).

### Disturbance

Dune habitat type contributed to differences observed in total vegetation cover after the 3-month study period ( $F = 4.29$ ,  $p = 0.02$ ; Figure 3A). Vegetation cover overall was found to be greater in the backdune habitat than in the foredune (estimate =  $-1.81$ , SE = 0.73,  $t = -2.46$ ,  $p = 0.02$ ) and the interdune (estimate =  $-1.91$ , SE = 0.73,  $t = -2.61$ ,  $p = 0.01$ ) habitats when combining disturbance and associated control plots. Disturbance showed no main effect, but there was a significant interaction between dune habitat type and disturbance treatment ( $F = 3.35$ ,  $p = 0.05$ ) on vegetation cover. Specifically, experimentally disturbed plots in the interdune habitat had significantly greater vegetation cover than control plots (estimate = 2.63, SE = 1.03,  $t = 2.56$ ,  $p = 0.02$ ).

Dune habitat type also contributed to differences observed in species richness ( $F = 48.1$ ,  $p < 0.0001$ ; Figure 3B). Like vegetation cover, species richness in the backdune habitat was greater than richness in both the foredune (estimate =  $-1$ , SE = 0.16,  $t = -6.44$ ,  $p < 0.001$ ) and the interdune (estimate =  $-1.06$ , SE = 0.16,  $t = -6.82$ ,  $p < 0.001$ ) habitats when combining disturbance and associated control plots. The interaction between dune habitat type and disturbance treatment also contributed to differences in species richness ( $F = 8.54$ ,  $p = 0.001$ ), particularly in the interdune habitat where richness was greater in plots exposed to the disturbance treatment than in control plots (estimate = 0.83, SE = 0.22,  $t = 3.78$ ,  $p < 0.001$ ).

### Shading

Habitat type ( $F = 9.63$ ,  $p = 0.0003$ ) and the interaction between habitat type and shading ( $F = 3.25$ ,  $p = 0.05$ ; Figure 4A) contributed to differences in vegetation cover. Total vegetation cover in the backdune habitat was greater than vegetation cover in both the foredune (nonsignificant) and the interdune (estimate =  $-1.91$ , SE = 0.62,  $t = -3.09$ ,  $p = 0.003$ ) habitats when combining shaded and associated control plots.

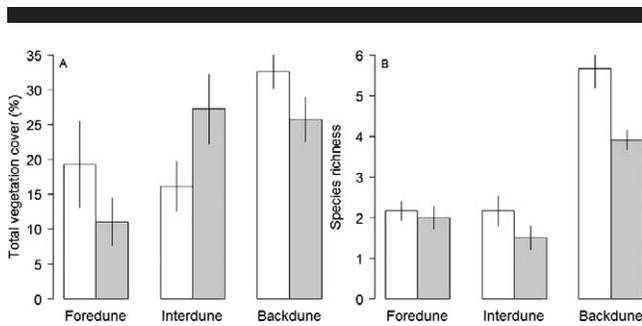


Figure 4. Mean vegetation cover (A) and species richness (B) on control (white) and experimentally shaded plots (grey) in each dune habitat. Lines =  $\pm 1$  SE.

In the interdune habitat, vegetation cover was almost twice as high in shaded plots compared to controls (estimate = 1.81, SE = 0.88,  $t = 2.07$ ,  $p = 0.04$ ). Vegetation cover was also higher in control plots in the foredune and backdune habitats (Figure 4A) compared to shaded plots (not significant).

The main effects of dune habitat type ( $F = 46.1$ ,  $p < 0.0001$ ) and the shading treatment ( $F = 7.79$ ,  $p = 0.01$ ) contributed to differences in species richness across plots. Species richness in the backdune habitat was significantly larger than that in both the foredune (estimate =  $-0.91$ , SE = 0.14,  $t = -6.76$ ,  $p < 0.001$ ) and the interdune (estimate =  $-0.94$ , SE = 0.14,  $t = -6.93$ ,  $p < 0.004$ ; Figure 4B) habitats when combining shaded and associated control plots. Unexpectedly, species richness in backdune plots exposed to the shading treatment was significantly smaller than species richness on the shaded experimental control plots (estimate = 1.58, SE = 0.65,  $t = 2.43$ ,  $p = 0.02$ ; Figure 4B).

### Soil Moisture Redistribution

Soil water-potential ( $\Psi_s$ ) values were highest (least negative, indicating wetter soil) during evening hours in all three dune habitats (Figure 5) as evaporation reduced. Dune habitat ( $F = 4.99$ ,  $p = 0.01$ ) and the dune habitat by treatment (restoration *vs.* control) interaction ( $F = 3.83$ ,  $p = 0.03$ ) contributed to differences in  $\Psi_s$ . Unexpectedly, the backdune habitat appeared drier overall, compared to the foredune habitat (estimate = 29.47, SE = 12.54,  $t = 2.35$ ,  $p = 0.02$ ). As expected, however, soil in the restoration plots was wetter than soil in the control plots in the foredune (estimate = 36.19, SE = 14.89,  $t = 2.43$ ,  $p = 0.02$ ) and interdune (estimate = 31.95, SE = 14.82,  $t = 2.16$ ,  $p = 0.03$ ) habitats. Alternatively, in the backdune habitat, soil moisture was higher in control plots compared to restoration plots (estimate =  $-36.19$ , SE = 14.89,  $t = -2.44$ ,  $p = 0.02$ ).

## DISCUSSION

We documented how transplanted dune plant species, used for a restoration project, encouraged positive vegetation change and assessed how shading, soil-moisture redistribution (through positive interactions), and disturbance (through transplanting) might have played a role in vegetation change across dune habitats. Dune transplants encouraged vegetation cover and species richness of extant vegetation compared to controls in all dune habitats over a 6-month period (Figure 2).

An increase in dune plant cover, however, was only significant in the interdune habitat. Because clonal vegetation is predominantly found in this habitat (Miller, Gornish, and Buckley, 2010), it is possible that restoration species improved environmental conditions for ramets existing just below the soil surface immediately following transplanting. This might have consequently led to higher vegetation cover in the interdune habitat because some clonal dune species exhibit more rapid and extensive horizontal growth (Yu, Dong, and Krusi, 2004) compared to nonclonal species. While positive vegetation change was not as significant in the foredune and backdune areas, this result might be linked to the growth form of species associated with these habitats. For example, the long-term stability of the backdune area supports an abundance of slow-growing woody vegetation (Miller, Gornish, and Buckley, 2010). Plant species in the backdune might then not respond to the positive environmental influences of the dune transplants as quickly as faster-growing species characteristic of other dune areas.

As expected, the experimental disturbance treatment did not have a short-term significant effect on positive changes in vegetation in the foredune habitat, perhaps because this habitat is already highly disturbed by natural processes (Rodgers and Parker, 2003). Alternatively, in the much more stable sands of the interdune habitat, the disturbance treatment was documented as having a positive effect on species richness. This could be attributable to the excavation and rapid germination of seeds (Looney and Gibson, 1995) that probably accompanied the transplanting method. There was, however, an absence of an increase in vegetation cover in this habitat, which could be a result of an increase in the competitive interactions that often occur in this area toward the end of the experimental time frame (Maestre and Cortina, 2004), thereby minimizing plant growth. Finally, the lack of a significant positive effect of disturbance on vegetation cover and species richness in the backdune habitat was not entirely surprising because the effect of experimental disturbance can be difficult to quantify in a field setting (Pollock, Naiman, and Hanley, 1998). An absence of a disturbance effect in the backdune could be a result of an abiotic obstacle to plant growth and establishment (Forey, Lortie, and Michalet, 2009; Maestre, Valladares, and Reynolds, 2005), an example of which could be soil moisture availability because the extent of the treatment took place over the hottest months of the year. Moreover, the disturbance treatment temporarily disrupted any organic matter that might have been available at the substrate surface, which could have further affected moisture accretion and availability.

Shading did not appear to encourage positive vegetation change in the foredune habitat, possibly because of the considerable sand movement that occurs daily in this area (Ehrenfeld, 1990). Intense sand movement could obscure the effects of short-term shading by increasing evaporation or by burying growing seedlings (Zhang and Maun, 1990). This suggests that future studies of positive interactions in the foredune habitat should consider sediment stabilization by species as a mechanism of positive interactions such as facilitation (Gormally and Donovan, 2010; Oosting and Billings, 1942). In the interdune habitat, shading had the

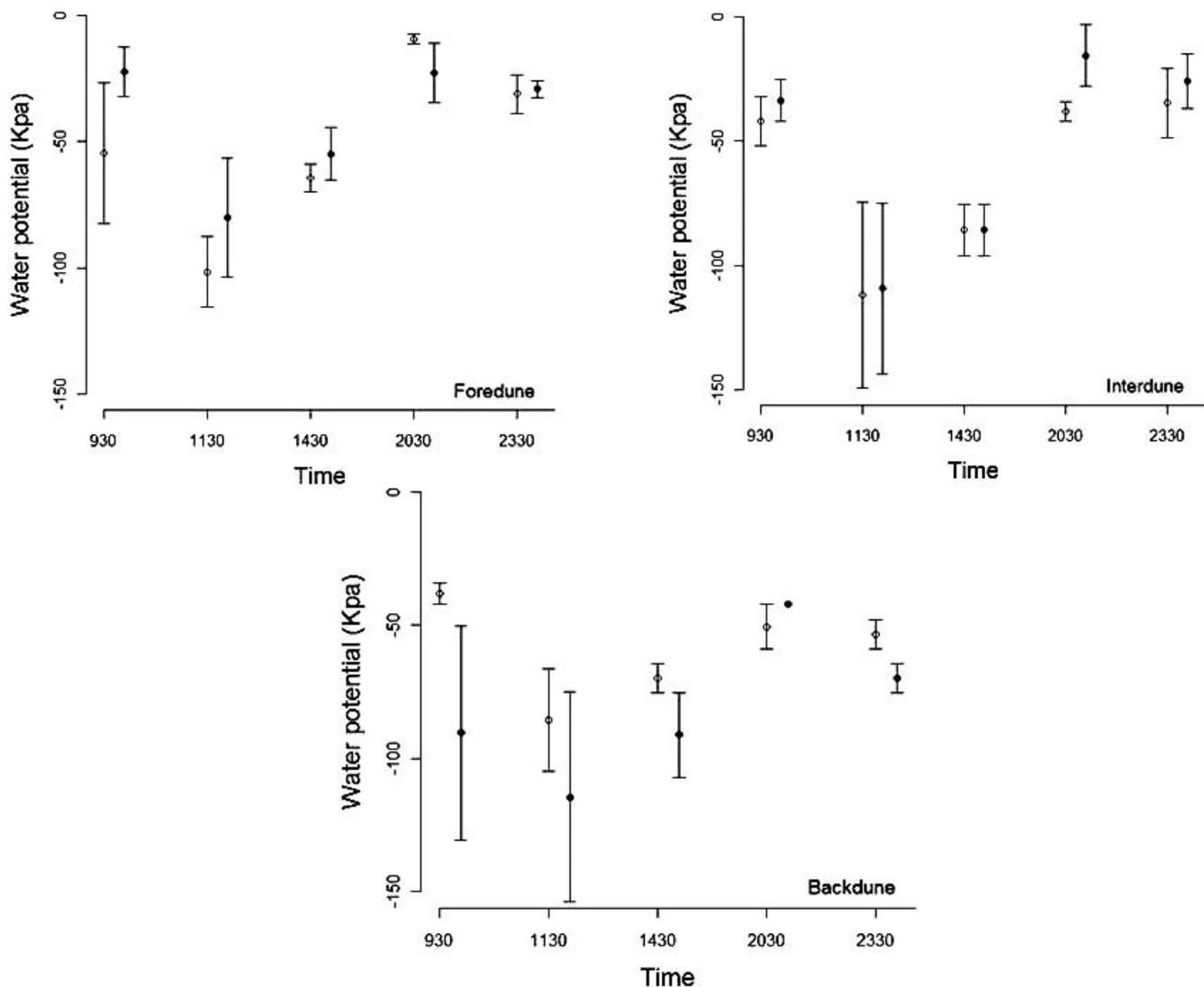


Figure 5. Differences in mean soil water potential values between control (white) and restoration plots (black) in each dune habitat. Lines =  $\pm 1$  SE.

strongest positive effect on vegetation; however, shading appeared to play a role in encouraging vegetative growth only, while actually restricting species richness. The contrasting biotic responses in this habitat suggest that other important ecological processes could be occurring there on shorter timescales, namely indirect facilitation (Connell, 1990). In this case, shading might directly influence the survival of several salt-tolerant dominant species (decreasing species richness) by reducing local salinity (Bertness and Hacker, 1994), which would subsequently permit the extensive growth of a competitively subordinate species (increasing vegetation cover) (Day *et al.*, 2004; Pennings and Callaway, 1996). In the backdune habitat, shading served to significantly reduce species richness but did not appear to play a role in modifying dune vegetation cover. The irregularity of the dune topography in this habitat could account for irregular patterns of antecedent soil moisture

(Burt and Butcher, 1985), which might obscure any effects of shading on increased vegetation cover in this area.

The signal for soil-moisture redistribution occurrence on restoration plots compared to control plots was strongest in the foredune habitat. In this habitat, transplant species such as *Uniola paniculata*, with long roots that are more effective at capturing deep water sources (Wan *et al.*, 2000), exhibited higher survival than did other transplant species. These plants probably transport moisture from deeper sources toward the surface, making the sand there more suitable for growth (Joffre and Rambal, 1993). Soil-moisture redistribution also appeared to be occurring more on restoration plots compared to control plots in the interdune habitat, although the types of species perpetuating the process are different from those in the foredune habitat. Because vegetation in the interdune habitat is characterized by species that exhibit rhizomatous growth

(Gornish, 2009; Miller, Gornish, and Buckley, 2010), plant fragments of these individuals are more likely to benefit from an increase in the availability of soil-surface moisture than seeds buried deeper in the soil profile, especially during periods of drought. Finally, in the backdune habitat, vegetation on the restoration plots did not appear to be involved in redistributing soil moisture. Perhaps the water gradient with depth was subtler in this habitat because of the higher water-holding capacity of the soil (Ehrenfeld, 1990), limiting the effects of any moisture redistribution that did occur. Alternatively, there exists a freshwater lens 0–10 m below the soil surface of St. George that is narrower and located farther below the soil surface in the backdune habitat (Ruppel, Schultz, and Kruse, 2001). The dominant vegetation in this area might be less able to redistribute deep-water sources toward the surface by, for example, hydraulic lift (Richards and Caldwell, 1987). While this study supports the presence of soil-moisture redistribution over a short period across habitats, it ignores the potential role that seasonality might play on the moisture available to vegetation for redistribution. For instance, there is a greater demand for water by plants during the growing season (the summer months), which could reduce the overall moisture provided by precipitation for redistribution, while the opposite might be true for the winter months (Weltzin and McPherson, 2000).

Results of this work highlight the complex interactions among dune habitats, which vary in abiotic stress type and magnitude, and existing vegetation that are probably involved in promoting nurse-plant and neighbor relationships in coastal systems (Nobel, 1989). Our evidence suggests that factors that serve to ameliorate stress through positive species interactions are responsible for influencing vegetation change; however, they operate differently among coastal dune habitats exhibiting different levels of stress. Other factors not investigated here but likely serve to promote positive vegetation change in coastal habitat include soil stability on highly mobile dunes and the provisioning of organic matter to the relatively nutrient-poor dune soils. For example, the outward expansion of roots or rhizomes could serve to restrict sand movement and contribute to seedling establishment (Franks, 2003). Also, organic material naturally produced by existing plants could serve to facilitate the growth of neighboring plants while fostering soil microorganisms that secondarily encourage plant growth (Berg and Steinberger, 2010). Investigating other possible factors driving positive species interactions across stressful habitats would contribute to a more comprehensive understanding of community interactions in coastal systems.

The results from our relatively short-term experiments should be interpreted with caution when extrapolating to longer time scales. Our summer-time experiments could underestimate the magnitude of environmental effects on positive species interactions, as studies have shown that these types of interactions are actually minimized under the driest environmental conditions (Holmgren and Scheffer, 2010). Moreover, results of our study are more vulnerable to the longer-term effects of seasonality, which can bias the impact of environmental factors on positive interactions (Tielborger and Kadmon, 2000).

This study observed how species interactions play a role on vegetation change over a relatively short period; however, further work investigating the effects of shading, soil moisture redistribution, and transplanting disturbance over a longer time frame might be required to develop a more comprehensive understanding of how positive interactions operate across areas exhibiting different levels of stress. Habitat type also contributed to differences in vegetation change, which suggests that only the surviving restoration candidates best adapted to the general environmental pressures found in each of these areas might have provided suitable conditions for neighboring species. This demonstrates the degree to which environmental stress gradients can affect biotic interactions (Bertness and Shumway, 1993; Hacker and Gaines, 1997; Michalet *et al.*, 2006), which should be considered when devising projects for the restoration of damaged coastal systems (Padilla and Pugnaire, 2006).

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#### LITERATURE CITED

- Berg, N. and Steinberger, Y., 2010. Are biological effects of desert shrubs more important than physical effects on soil microorganisms? *Microbial Ecology*, 59(1), 121–129.
- Bertness, M.D. and Callaway, R., 1994. Positive interactions in communities. *Trends in Ecology and Evolution*, 9(5), 191–193.
- Bertness, M.D. and Hacker, S.D., 1994. Physical stress and positive associations among marsh plants. *American Naturalist*, 144(3), 363–372.
- Bertness, M.D. and Shumway, S.W., 1993. Competition and facilitation in marsh plants. *The American Naturalist*, 142(4), 718–724.
- Boughey, A.S., 1957. Ecological studies of tropical coastlines. I. The Gold Coast, West Africa. *Journal of Ecology*, 45(3), 665.
- Bromley, J.J.; Brouwer, A.P.; Barker, S.P.; Gaze, S.R., and Valentine, C., 1997. The role of surface water redistribution in an area of patterned vegetation in a semi-arid environment, south west Niger. *Journal of Hydrology*, 198(1), 1–29.
- Brooker, R.W.; Maestre, F.T.; Callaway, R.M.; Lortie, C.L.; Cavieres, L.A.; Kunstler, G.; Liancourt, P.; Tielbörger, K.; Travis, J.M.J.; Anthelme, F.; Armas, C.; Coll, L.; Corcket, E.; Delzon, S.; Forey, E.; Kikvidze, Z.; Olofsson, J.; Pugnaire, F.; Quiroz, C.L.; Saccone, P.; Schifffers, K.; Seifan, M.; Touzard, B., and Michalet, R., 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, 96(1), 18–34.
- Brown, J.F., 1997. Effects of experimental burial on survival, growth, and resource allocation of three species of dune plants. *Journal of Ecology*, 85(2), 151–158.
- Bruno, J.F.; Stachowicz, J.J., and Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, 18(3), 119–125.
- Burt, T.P. and Butcher, D.P., 1985. Topographic controls of soil moisture distributions. *Journal of Soil Science*, 36(3), 469–486.

- Caldwell, M.M.; Dawson, T.E., and Richards, J.H., 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia*, 113(2), 151–161.
- Callaway, R.M., 1995. Positive interactions among plants. *The Botanical Review*, 61(4), 306.
- Campbell, G.S., 1985. *Soil Physics with BASIC: Transport Models for Soil-Plant Systems*. New York: Elsevier, 150p.
- Chacon, P. and Bustamante, R.O., 2001. The effects of seed size and pericarp on seedling recruitment and biomass in *Cryptocarya alba*. *Plant Ecology*, 152(2), 137–144.
- Connell, J. H., 1990. Apparent vs. “real” competition in plants. In: Grace, J.B. and Tilman, D. (eds.), *Perspectives on Plant Competition*. New York: Academic, pp. 9–26.
- Day, F.P.; Conn, C.; Crawford, E., and Stevenson, M., 2004. Long-term effects of nitrogen fertilization on plant community structure on a coastal barrier island dune chronosequence. *Journal of Coastal Research*, 20(3), 722–730.
- Donovan, L.A.; Richards, J.H., and Linton, M.J., 2003. Magnitude and mechanisms of disequilibrium between predawn plant and soil water potentials. *Ecology*, 84(2), 463–470.
- Ehrenfeld, J.G., 1990. Dynamics and processes of barrier island vegetation. *Reviews in Aquatic Sciences*, 2(3–4), 437–480.
- Fagherazzi, S.; Wiberg, P.L., and Howard, A.D., 2003. Modeling barrier island formation and evolution. *Coastal Sediments*, May 18–23, Clearwater Beach, FL, 9p.
- Forey, E.; Lortie, C.J., and Michalet, R., 2009. Spatial patterns of association at local and regional scales in coastal sand dune communities. *Journal of Vegetation Science*, 20(5), 916–925.
- Franks, S.J., 2003. Facilitation in multiple life-history stages: evidence for nucleated succession in coastal dunes. *Plant Ecology*, 168(1), 1–11.
- Gormally, C.L. and Donovan, L.A., 2010. Responses of *Uniola paniculata* L. (Poaceae), an essential dune-building grass, to complex changing environmental gradients on the coastal dunes. *Estuaries and Coasts*, 33(5), 1237–1246.
- Gornish, E.S., 2009. Use of Long Term Vegetation Census Data to Inform Restoration Methods and Processes of Community Ecology on a Barrier Island. Tallahassee, Florida: Florida State University, Master's thesis, 69p.
- Gornish, E.S. and Miller, T.E., 2013. Using long-term census data to inform restoration methods for coastal dune vegetation. *Estuaries and Coasts*. doi: 10.1007/s12237-013-9617-0.
- Gross, K.L., 1990. A comparison of methods for estimating seed numbers in the soil. *Journal of Ecology*, 78(4), 1079–1093.
- Hacker, S.D. and Gaines, S.D., 1997. Some implications of direct positive interactions for community species diversity. *Ecology*, 78(7), 1990–2003.
- Harper, J.L., 1977. *Population Biology of Plants*. London: Academic, 900p.
- Hesp, P.A., 1991. Ecological processes and plant adaptations on coastal dunes. *Journal of Arid Environments*, 21(1), 165–191.
- Holmgren, M. and Scheffer, M., 2010. Strong facilitation in mild environments: the stress gradient hypothesis revisited. *Journal of Ecology*, 98(6), 1269–1275.
- Horton, J.L. and Hart, S.C., 1998. Hydraulic lift: a potentially important ecosystem process. *Trends in Ecology and Evolution*, 13(6), 232–235.
- Joffre, R. and Rambal, S., 1993. How tree cover influences the water balance of Mediterranean rangelands. *Ecology*, 74(2), 570–582.
- Kidron, G.J., 2009. The effect of shrub canopy upon surface temperatures and evaporation in the Negev Desert. *Earth Surface Processes and Landforms*, 34(1), 123–132.
- Lewis, R.R., 1982. *Creation and Restoration of Coastal Plant Communities*. Boca Raton, Florida: CRC Press, 232p.
- Looney, P.B. and Gibson, D.J., 1995. The relationship between the soil seed bank and above-ground vegetation of a coastal barrier island. *Journal of Vegetation Science*, 6(6), 825–836.
- Lopez, R.P.; Larrea-Alcazar, D.M., and Ortuno, T., 2009. Positive effects of shrubs on herbaceous species richness across several spatial scales: evidence from the semiarid Andean subtropics. *Journal of Vegetation Science*, 20(4), 728–734.
- Maestre, F.T. and Cortina, J., 2004. Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceedings of the Royal Society of London B Biological Sciences*, 271, S331–S333.
- Maestre, F.T.; Valladares, F., and Reynolds, J.F., 2005. Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology*, 93(4), 748–747.
- Maurer, D.A. and Zedler, J.B., 2002. Differential invasion of a wetland grass explained by tests of nutrients and light availability on establishment and clonal growth. *Oecologia*, 131(2), 279–288.
- Michalet, R.; Brooker, R.W.; Cavieres, L.A.; Kikvidze, Z.; Lortie, C.J.; Pugnaire, F.I.; Valiente-Banuet, A., and Callaway, R.M., 2006. Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*, 9(7), 767–773.
- Miller, T.E.; Gornish, E.S., and Buckley, H., 2010. Weather and coastal dune vegetation: effects of storms and drought. *Plant Ecology*, 206, 97–104.
- Nobel, P.S., 1989. Temperature, water availability and nutrient levels at various soil depths—consequences for shallow-rooted desert succulents, including nurse plant effects. *American Journal of Botany*, 76(10), 1486–1492.
- Noy-Meir, I., 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, 4, 25–51.
- Odum, W.E., 1988. Comparative ecology of tidal fresh-water and salt marshes. *Annual Review of Ecology and Systematics*, 19, 147–176.
- Oosting, H.J. and Billings, W.D., 1942. Factors effecting vegetational zonation on coastal dunes. *Ecology*, 23(2), 131–142.
- Padilla, F.M. and Pugnaire, F.I., 2006. The role of nurse plants in the restoration of degraded environments. *Frontiers in Ecology and the Environment*, 4(4), 196–202.
- Parmesan, C.; Root, T.L., and Willig, M.R., 2000. Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society*, 81(3), 443–450.
- Pennings, S.C. and Callaway, R.M., 1996. Impact of a parasitic plant on the structure and dynamics of salt marsh vegetation. *Ecology*, 77(5), 1410–1419.
- Pollock, M.M.; Naiman, R.J., and Hanley, T.A., 1998. Plant species richness in riparian wetlands—a test of biodiversity theory. *Ecology*, 79(1), 94–105.
- R Development Core Team, 2007. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at <http://www.r-project.org>.
- Richards, J.H. and Caldwell, M.M., 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia*, 73(4), 486–489.
- Rodgers, J.C. and Parker, K.C., 2003. Distribution of alien plant species in relation to human disturbance on the Georgia Sea Islands. *Diversity and Distributions*, 9(5), 385–398.
- Ruppel, C.; Schultz, G., and Kruse, S., 2001. Anomalous fresh water lens morphology on a strip barrier island. *Ground Water*, 38(6), 872–881.
- Stachowicz, J.J., 2001. Mutualism, facilitation, and the structure of ecological communities. *BioScience*, 51(3), 235–246.
- Stallins, J.A., 2005. Stability domains in barrier island dune systems. *Ecological Complexity*, 2(4), 410–430.
- Stalter, R., 1974. Vegetation of coastal dunes of South Carolina. *Castanea*, 39(1), 95–103.
- Tewksbury, J.J. and Lloyd, J.D., 2001. Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia*, 127(3), 425–434.
- Thompson, K.; Hodgson, J.G.; Grime, J.P., and Burke, W.J.W., 2001. Plant traits and temporal scale: evidence from a 5-year invasion experiment using native species. *Journal of Ecology*, 89(6), 1054–1060.
- Tielborger, K. and Kadmon, R., 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology*, 81(6), 1544–1553.
- Walker, L.R. and Willig, M.R., 1999. An introduction to terrestrial disturbances. In: Walker, L.R. (ed.), *Ecosystems of Disturbed Ground, Ecosystems of the World 16*. Amsterdam: Elsevier, pp. 1–16.

- 
- Wan, C.G.; Xu, W.W.; Sosebee, R.E.; Machado, S., and Archer, T., 2000. Hydraulic lift in drought-tolerant and -susceptible maize hybrids. *Plant and Soil*, 219(1), 117–126.
- Weltzin, J.F. and McPherson, G.R., 2000. Implications of precipitation redistribution for shifts in temperate savanna ecotones. *Ecology*, 81(7), 1902–1913.
- Yu, F.; Dong, M., and Krusi, B., 2004. Clonal integration helps *Psammochloa villosa* survive sand burial in an inland dune. *New Phytologist*, 162(3), 697–704.
- Zhang, J. and Maun, M.A., 1990. Effects of sand burial on seed germination, seedling emergence, survival, and growth of *Agropyron psammophilum*. *Canadian Journal of Botany*, 68(2), 304–310.