EFFECTS OF HUMAN DISTURBANCE ON THE DUNE VEGETATION OF THE GEORGIA SEA ISLANDS

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Abstract: This research investigates how human disturbance has affected foredune vegetation of the Georgia Sea Islands (GSI) in the United States. The cover of native dune-building grasses (*Uniola paniculata* L. and *Panicum amarum* Ell.) was more abundant within less-disturbed sites than in sites that had higher levels of human disturbance. In contrast, dunes in human-disturbed areas had significantly higher cover of alien plants and native generalist taxa, and they also had higher overall species diversity. Additionally, the cover of native dune-building grasses was significantly greater on protected National Wildlife Refuge islands than on more frequently visited and developed tourist islands. In addition to the ANOVA, nonmetric multidimensional scaling (NMS) analysis showed that the vegetation composition differed between disturbed and less-disturbed plots and between plots on tourist islands and protected islands. Both ANOVA and NMS analyzes agree that dunes in human-modified areas have lower dune-grass cover and greater cover of species that are not adapted to building and stabilizing dunes. Therefore, human disturbance may indirectly reduce dune stability by altering the dune vegetation. [Key words: dune vegetation, human disturbance, Georgia Sea Islands.]

INTRODUCTION

Coastal dune communities are developed and maintained through a complex interaction of vegetation colonization and sand accumulation. Initially, beach sand is colonized by low-growing plants termed "dune initiators" that grow by spreading laterally across the sand. The vegetative bodies of the dune initiators act as a substrate for coastal dune formation because they trap and protect seeds and other propagules of the subsequent colonizers, the perennial rhizomatous grasses (Woodhouse, 1982). When these perennial grasses become established, they intercept wind-borne sand with their tussocks and trap it with their extensive root/rhizome system (Wagner, 1964), which causes dunes to grow. In this way, these grasses act as "dune builders" and they are a crucial factor for coastal dune formation (Woodhouse, 1982; Heyligers, 1985).

Dune formation is a positive feedback cycle where the accumulation of sand stimulates the growth of dune grasses, which in turn results in the further accumulation of sand (Woodhouse, 1982). Previous work has shown that dune morphology is linked to the type of vegetation that colonizes the dunes (Heyligers, 1985; Nordstrom, 1990). On the Georgia coast, for example, dunes that develop under tall

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grass species obtain larger size and steeper dip angles (>25%) than dunes that are colonized by smaller grasses and forbs (Oertel and Larson, 1976).

Because coastal dune morphology and vegetation are strongly linked, any alteration of the species composition or cover can have profound effects on the dune size and shape. Human disturbance (defined here as human activities that have resulted in changes in community and ecosystem structure and composition through the alteration of the physical environment; Drake et al., 1989; Pyle, 1995) is a factor that has been known to affect dune vegetation. For example, introduction of the European beachgrass (*Ammophila arenaria* L.) in southeastern Australia has transformed the morphology of many coastal dunes (Heyligers, 1985). Dunes that were once small (<2 m) and had gentle slopes have become larger (up to 6 m) with steeper slopes (>30%) within only 20 years as a result of colonization by alien species. The arrival of *A. arenaria* in Australia also has caused new dunes to form in areas where they had not previously occurred (Heyligers, 1985). Similarly along the Pacific United States, dunes have formed along the Oregon coast where they have been historically absent due to the introduction of *A. arenaria* and *A. breviligulata* Fern. (Cooper, 1958; Wiedemann and Pickart, 1996) and dunes in California have changed from being low and parabolic to becoming vertical and immobile from the introduction of *A. arenaria* (McPherson, 1994).

Besides introduction of species, humans also have physically damaged the vegetation cover of dunes in many coastal areas. For example, trampling by foot and by vehicles directly destroys native dune vegetation and alters dune soil properties (e.g., soil moisture), which leads to lower overall dune stability (Rickard et al., 1994; Rust and Illenberger, 1996). Furthermore, dunes with lower native species cover become unstable and eventually deflate because many of these species cannot maintain themselves on eroding sand surfaces (Wagner, 1964). Therefore, human modification of dunes, by providing habitats for alien species, by changing the dune environment, and/or by disrupting the accretion feedback cycle, can have profound influences on coastal dune ecosystems.

The objective of this research is to investigate the role of human disturbance on the dune vegetation of the Georgia Sea Islands (GSI). The specific questions I address are: (1) Does the cover of native dune builders, the cover of alien species, the species diversity, and the openness of vegetation differ between dune sites that have a high degree of human disturbance and sites that have a lower degree of human disturbance? (2) Do broad-scale, island-level human use patterns (tourist islands versus protected islands) affect local site vegetation cover? By addressing these research questions, I provide insight into how human disturbance can affect the southeastern United States coastal dune ecosystems.

STUDY AREA

The GSI (Fig. 1) have varying degrees of human use, but for this study I classified islands as either tourist islands or protected islands depending on the overall land use and accessibility from the mainland. I sampled the vegetation cover from two tourist islands and from two protected islands. Even though the location of these islands varied in latitude, the island flora was rather uniform across the entire study

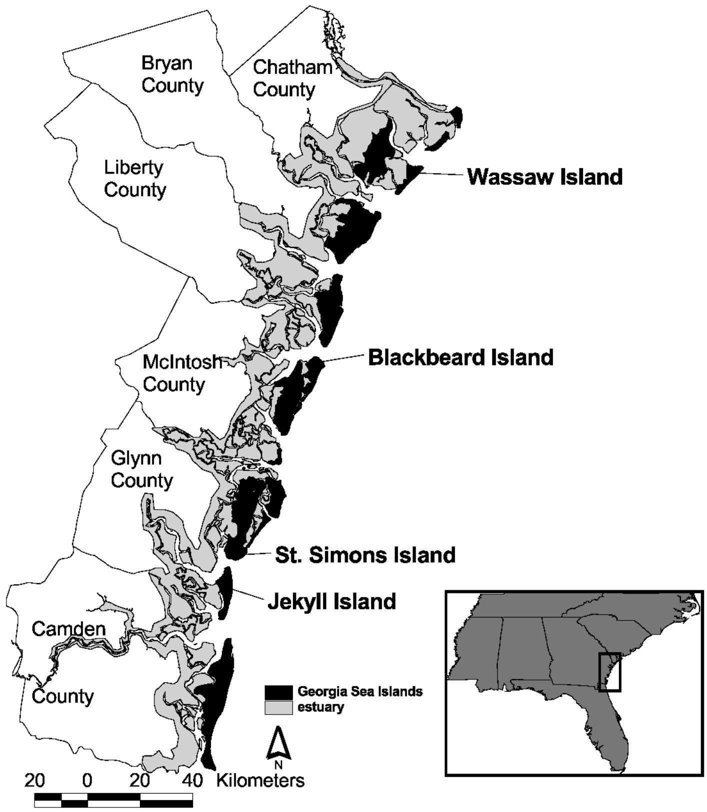

Fig. 1. Georgia Sea Islands used in this study.

region because north-south climatic gradients on the Georgia coast are muted and because each island had essentially the same set of potential colonists (Stallins, 2001). Compositional differences on these islands, then, are probably related to other factors, like human disturbance history.

The two tourist islands were Jekyll Island and St. Simons Island. Jekyll Island is managed as a state park through a board of trustees, the Jekyll Island Authority. Within the developed areas, Jekyll Island has many hotels, residential areas, and businesses. The island is accessible by vehicle via a causeway, and in 1997 Jekyll Island had 1.5 million visitors (Jekyll Island Convention and Visitors Bureau, pers. comm., April 1999). The island is approximately 20.4 km^2 in area and 16 km in length. St. Simons was the other tourist island used in this study. Like Jekyll Island, St. Simons is connected to the mainland via a causeway and it has many hotels and residential areas. It was the largest island (80.3 km^2 in area and 17 km long) and it was perhaps the most heavily developed island used in this study. But even though it was heavily developed, there existed pockets of less-disturbed dunes. During 1997, over 1.7 million people visited St. Simons Island (Brunswick and The Golden Isles of Georgia Visitors Bureau, pers. comm., April 1999).

The two protected islands were Blackbeard and Wassaw Islands. Blackbeard Island is a National Wildlife Refuge that is managed through the U.S. Fish and Wildlife Service (USFW). It is approximately 11 km long and has an area of 22.7 km^2. The island is one of the oldest National Wildlife Refuges and has been protected since 1924. Although the island is open to the public, it is only accessible by boat and transportation is not provided by USFW. According to the Savanna Coastal Refuge USFW office, very few visitors come to the island because of its inaccessibility (USFW, pers. comm., October 2002). Except for a few residents who stay on the island to monitor sea turtle nesting and for a few USFW officers, Blackbeard Island is uninhabited. Wassaw Island also is a National Wildlife Refuge that is only accessible by boat. Until recently, the entire island was privately owned, but in 1976 the owners donated most of the land to the USFW. Today a small part of the island is still privately owned by the original family, but most of the island is uninhabited. Wassaw Island is approximately 10 km long and has an area of 43.5 km^2. Like Blackbeard Island, the Wassaw Refuge is open to the public but few visitors come to the island because of its inaccessibility. However, both Blackbeard and Wassaw Islands have deer hunts for a few weeks during the fall and winter months when 50 to 100 hunters camp on the islands.

METHOD

Field Sampling

I used the point intercept method (Goodall, 1957) to sample the absolute cover of all herbaceous and woody taxa (<1.5 m in height) on the foredunes of Blackbeard, Jekyll, St. Simons, and Wassaw Islands. On each island, I had a total of 10 dune sites; 5 sites were located in areas that had a high degree of human disturbance (hereafter referred to as disturbed sites) and 5 sites were located in areas that had a lower degree of human disturbance (hereafter referred to less-disturbed sites). Aerial photographs, orthophotoquads, and ground reconnaissance were used to identify potential sites before sampling. The criteria for accepting sampling sites were that disturbed sites occurred within 1 m of heavily used boardwalks; hiking trails and vehicle access roads that cut through dunes (which existed on both the protected and tourist islands); dunes with high foot traffic; or, in the case of a few sites on Blackbeard Island, dunes that had been mechanically smashed to foster the nesting of sea turtles. Less-disturbed dune sites were at least 30 m away from disturbed areas. Even though not as common, less-disturbed dunes existed on both tourist islands. Owing to within-island longitudinal differences in sediment accretion and erosion on the GSI (Hayes, 1994), all sites were located on the southern half of the islands where dunes were more prominent. Vegetation sampling was conducted in 1997 during September and October, when the dune vegetation is at its most mature stage (Wilbur Duncan, University of Georgia, Athens, pers. comm., September 1997).

Data Analysis

In the following analyses, key dune species were placed into several vegetation classes. First, the principal native dune-building species in this study were the perennial, rhizomatous grasses *Uniola paniculata* L. and *Panicum amarum* Ell., both of which are commonly responsible for the development and stabilization of dunes in the southeastern United States (Woodhouse, 1982). I investigated differences in cover of this vegetation class as a whole and for each individual dune-building species. Second, alien species included those species that were described as either "nonnative," "alien," "exotic," or "introduced." Alien status was determined from descriptions in Small (1913), Godfrey and Wooten (1979, 1981), Hitchcock (1950), Sanders (1987), and U.S. Department of Agriculture (1971), and the species encountered in this study that met these descriptions were *Chloris patrea* Swartz., *Cynodon dactylon* (L.) Pers., *Digitaria sanguinalis* (L.) Scop., *Paspalum notatum* Flugge., *Sorghum halepense* (L.) Pers., *Lantana camara* L., and *Lonicera japonica* Thunb. Not all of these species were present on all the islands (see the Results section). Analysis of this group was based on the combined cover values of all the alien species present at a particular site. Third, generalist species were those native species that occur in many different inland habitats besides coastal dunes (Castillo and Moreno-Cassasola, 1996). This vegetation class consisted of *Rubus* L. spp., *Smilax* L. spp., *Cenchrus tribuloides* L., and *Hydrocotyle bonariensis* Comm. These species were placed into a single group for discussion purposes, but the statistical analyzes were performed on the individual taxon because they were each commonly found within the study area.

Differences in cover were examined for certain individual species. As mentioned earlier, *U. paniculata* L. and *P. amarum* Ell. were tested individually to investigate the extent to which the cover of each dune-building grass varied. I examined differences in cover of one particular alien species, *C. dactylon*, because it was the most frequent and dominant dune alien species on all islands. I also examined differences in cover for native dune taxa that were common (frequency = 50%) or that had high cover values (cover = 30%) in at least five sites. These important species included *Spartina patens* (ait.) Muhl, *Heterotheca subaxillaris* (Lam.) Britt. and Rusby, *Iva imbricata* Walt., *Ipomoea stolonifera* (Cyr.) Gmel., and *Croton punctatus* Jacq. Besides these vegetation classes and individual species, I calculated species diversity for each site using the Shannon-Weiner Index (Barbour et al., 1999) and the absolute cover of bare ground (area where no species were recorded) for a proxy, but inverse relationship with vegetation density.

Two-factor analysis of variance (ANOVA; Sokal and Rohlf, 1981) was used to investigate among site differences in dune-building species cover, alien species cover, species diversity, open ground, and cover of prominent taxa. Differences in vegetation were examined between disturbed and less-disturbed sites and among islands. The research hypothesis tested by these analyses was that vegetation patterns between tourist islands and protected islands and between disturbed and less-disturbed sites would be significantly different with regards to the vegetation classes, individual species, and species diversity. The absolute cover values were transformed using the arcsine of the square root (Zar, 1999) to normalize the data.

Table 1. ANOVA of the Effects of Island and Disturbance Category on the Absolute Cover of Native Dune Builders, Alien Species, Species Diversity, and Bare Ground Per Island

Source of variation	Native dune builders (Pr > F)	Alien species (Pr > F)	Species diversity (Pr > F)	Bare ground (Pr > F)
Island	.093*	.257	.38	.291
Disturbance	.0001**	.037**	.02**	.503
Interaction	.155	.303	.39	.07*

* Significant at $p < .10$.
** Significant at $p < .05$.

Nonmetric multidimensional scaling (NMS) was used to investigate overall vegetation differences among sites. NMS is an ordination technique that has been widely adopted by ecologists and is used to organize and make sense of complex compositional data sets (Kenkel and Orióci, 1986; Minchin, 1987; Clarke, 1993). NMS graphically positions sites in a multidimensional ordination space based on their species composition. Distances between sites represent compositional similarity (Kenkel and Orióci, 1986), such that sites positioned closer to one another share many of the same species in similar abundances while far away sites are more dissimilar. As an aid to interpreting the NMS results, I used Varimax rotation to collapse the multiple dimensions into a two-dimensional ordination in which each site was given specific X, Y coordinates (Clarke, 1993; Legendre and Legendre, 1998). With these coordinates, I calculated the mean center (average X, Y position) and corresponding 95% confidence interval for each disturbance category and for each island. These descriptive statistics are illustrated on the ordinations as ellipses in which the center of the ellipse represents the mean center, the polar axis represents the confidence interval around the average Y position, and the equatorial axis represents the confidence interval around the average X position. The arrangement of these ellipses helped indicate differences in composition among sites and underscore ecological responses to human disturbance. PC-ORD Version 4 (McCune and Mefford, 1999) was the software used to perform NMS ordinations.

RESULTS

Spatial Variation of Vegetation Classes and Individual Species

The ANOVA results showed significant differences between disturbance categories for the vegetation classes, but differences were not as strong among island groups (Table 1). Native dune builders were more abundant in less-disturbed sites ($p = .0001$). This vegetation class had over six times as much cover in less-disturbed sites (61% mean cover) as in disturbed sites (11% mean cover) across all islands (Fig. 2). The ANOVA results also showed significant differences in the cover of native dune builders among islands ($p = .09$). Blackbeard and Wassaw Islands had

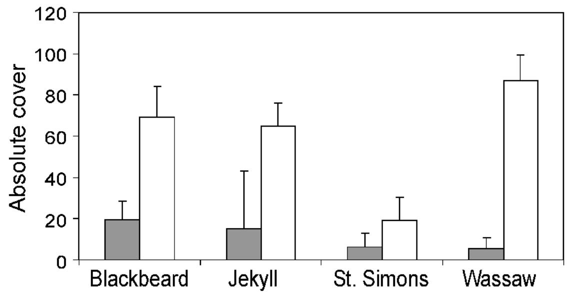

Fig. 2. Average absolute cover of native dune builders (±SD). Shaded bars represent disturbed sites and open bars represent less-disturbed sites.

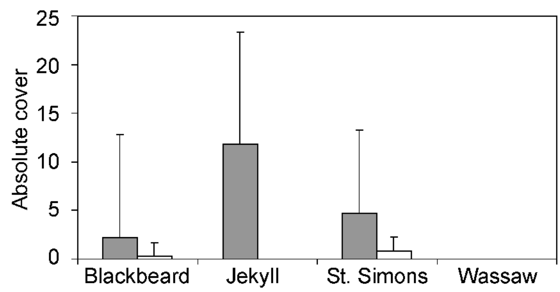

Fig. 3. Average absolute cover of alien species (±SD). Shaded bars represent disturbed sites and open bars represent less-disturbed sites.

higher mean cover values of native dune builders (43% mean cover for both islands) than Jekyll Island (38% mean cover), but all of these had higher cover than St. Simons Island (12% mean cover).

Disturbed sites had significantly greater cover of alien species (Table 1). Alien taxa were found in 14 of the total 40 sites, most of which (85%) were in disturbed areas. Across all disturbed sites, alien cover accounted for 3.8% of the total mean cover, whereas mean alien cover in the less-disturbed sites was less than 0.10% (Fig. 3). Significant differences in alien cover among islands were not consistent. On both tourist islands, alien taxa were found in all the disturbed sites, and alien species were present within 2 nondisturbed sites on St. Simons Island. Alien cover on the protected islands showed a different pattern. There were 2 sites on Blackbeard Island that had alien species present (46% cover in a disturbed site and 15% in a less-disturbed site), but alien plants did not occur in any of the other protected island sites. Wassaw Island had alien species present within inland areas (Rodgers, 1999), but they were not found in any of the foredune study sites. The inconsistent variation in alien cover between tourist and protected islands yielded ANOVA results that failed to reveal any significant differences in alien cover among islands ($p = .257$; Table 1).

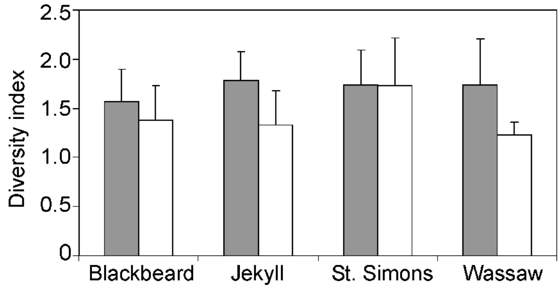

Fig. 4. Average Shannon-Weiner species diversity index (±SD). Shaded bars represent disturbed sites and open bars represent less-disturbed sites.

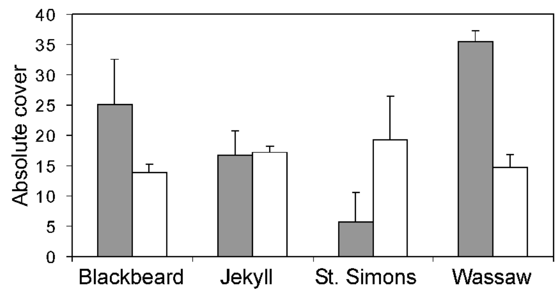

Fig. 5. Average absolute cover of bare ground (±SD). Shaded bars represent disturbed sites and open bars represent less-disturbed sites.

Additionally, disturbed sites had significantly greater species diversity (Fig. 4). On average, there were three more species in disturbed sites than in less-disturbed sites. This higher species diversity reflected the greater number of both alien species and native generalist taxa present within these sites. In terms of among-island variation, Blackbeard Island, Wassaw Island, and Jekyll Island had greater diversity in the disturbed sites, but St. Simons Island showed no difference between disturbed and less-disturbed sites. Diversity on St. Simons Island was equally high in both disturbance categories.

The cover of bare ground was not significantly different between disturbance categories (Fig. 5). This indirectly indicates that the average vegetation cover showed little difference between disturbed and less-disturbed sites across all islands. Variation in bare ground cover among islands also was not significant; however, the interaction of disturbance and island was significant ($p = .07$). The protected islands had higher bare ground cover in disturbed sites, but the tourist islands, especially St. Simons Island, had higher bare ground cover in less-disturbed sites (Fig. 5). The significance of this interaction indicates a possible disturbance-related effect on the overall dune vegetation cover of protected islands.

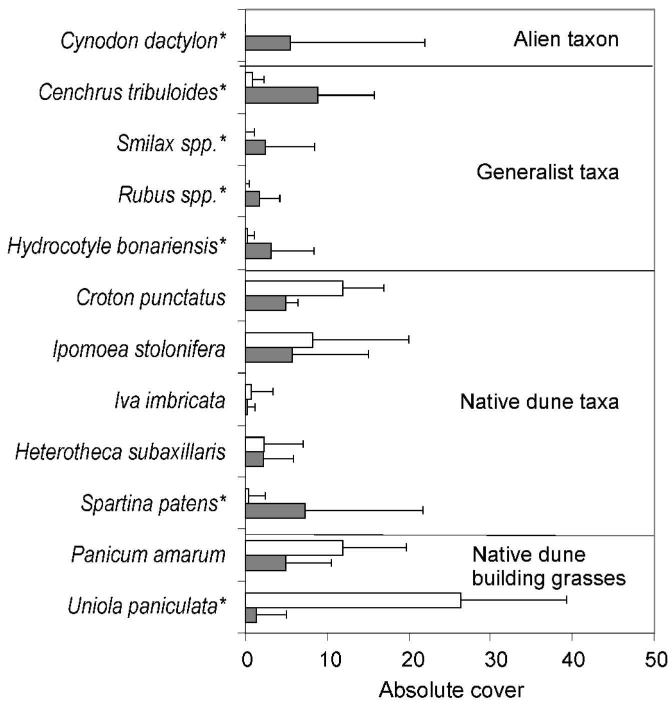

Fig. 6. Average absolute cover of frequent dune taxa (±SD) by disturbance category. Shaded bars represent disturbed sites and open bars represent less-disturbed sites. Asterisks indicate that there is a significant difference between disturbance categories ($p < .10$).

The response of individual species to disturbance effects was variable. For native dune-building grasses, *Uniola paniculata* showed a pronounced difference between disturbance categories (41% difference in mean cover) whereas *Panicum amarum* was not significantly different between disturbance categories (7% difference in mean cover; Fig. 6). Variations in cover of other important native dune species also showed mixed results (Fig. 6). *Spartina patens* was significantly more abundant within disturbed sites across all islands (27% mean cover). *Croton punctatus*, *Ipomoea stolonifera*, and *Iva imbricata* had greater cover within the less-disturbed sites, but they were not significantly different among disturbance categories. *Heterotheca subaxillaris* showed no difference in cover between disturbance categories. Generalist taxa were clearly more abundant in disturbed sites across all islands. In particular, *Cenchrus tribuloides*, *Hydrocotyle bonariensis*, *Rubus* spp., and *Smilax* spp. had significantly greater cover within disturbed sites than within less-disturbed sites (Fig. 6).

Most alien species encountered in the study area were Eurasian and tropical grasses. These included *Chloris patrea*, *Cynodon dactylon*, *Digitaria sanguinalis*, *Paspalum notatum*, and *Sorghum halepense*. All these alien grass species, with the exception of *S. halepense*, were found on Blackbeard Island, Jekyll Island, and St.

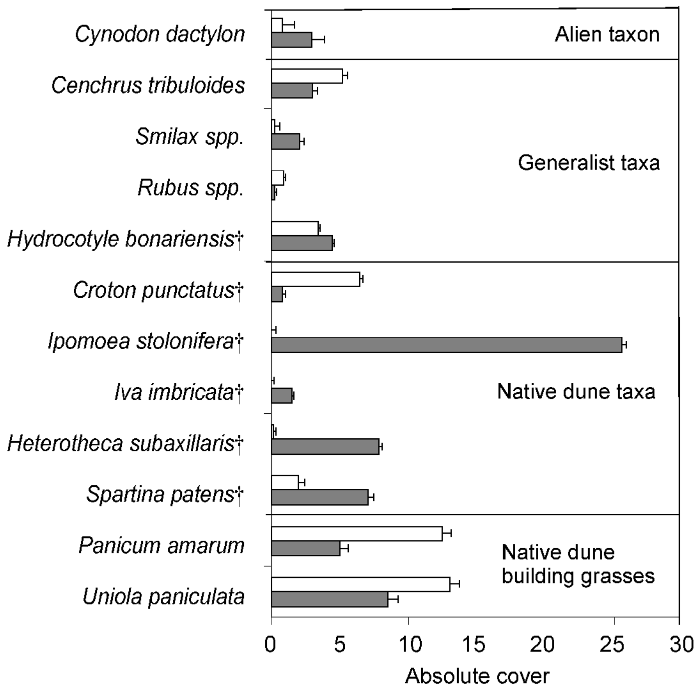

Fig 7. Average absolute cover of frequent dune taxa (±SD) by island type. Shaded bars represent tourist islands and open bars represent protected islands. Asterisks indicate that there is a significant difference between disturbance categories ($p < .10$).

Simons Island. *S. halepense* occurred on both tourist islands, but was not found on either protected island. The nongrass alien species, *Lantana camara*, and *Lonicera japonica*, were only found on St. Simons Island. *C. dactylon* was the most common alien species and had significantly greater cover in disturbed sites across all islands (Fig. 6).

Differences among islands in the cover of individual dune species were variable (Fig. 7). *Uniola paniculata* and *Panicum amarum* were not significantly different among islands. Similarly, most generalist taxa exhibited no significant differences in cover among islands with the exception of *Hydrocotyle bonariensis*, which had extremely high cover values on Wassaw Island (15% mean cover on Wassaw Island and less than 6% on the other islands). However, the cover of important native dune species showed definite distinctions among islands. For example, *Spartina patens* was substantially more abundant on St. Simons Island, where it accounted for over 60% of the absolute cover in some sites. The other native dune taxa showed clear differences in cover among protected and tourist islands (Fig. 7). *Ipomoea stolonifera*, *Iva imbricata*, and *Heterotheca subaxillaris* were more abundant ($p = .001$, $p = .05$, $p = .0001$, respectively) on the tourist islands while *C. punctatus* was more abundant ($p = .006$) on the protected islands.

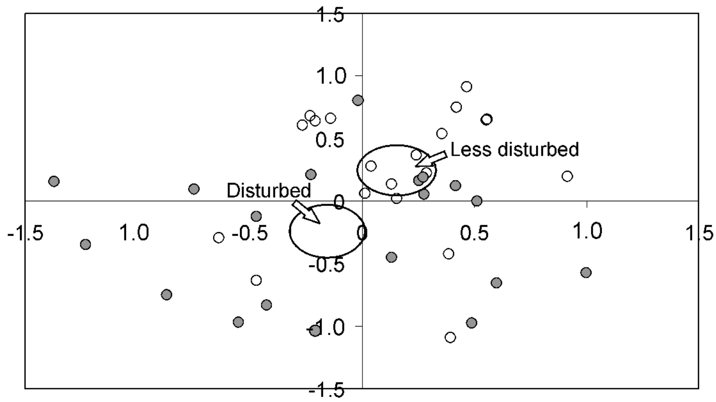

Fig. 8. Ordination results from nonmetric multidimensional scaling by disturbance categories. Open circles indicate less-disturbed sites and shaded circles represent disturbed sites. Ellipses represent the 95% confidence interval around the mean center for disturbed and less-disturbed sites.

Spatial Variation of Georgia Sea Islands Dune Vegetation

NMS ordination results showed that the overall vegetation composition clearly differed between disturbance categories (Fig. 8), but island distinctions were not as strong (Fig. 9). From the ordination, disturbed sites clustered more within the lower left quadrant while the less-disturbed sites clustered in the upper right quadrant. Island-based compositional patterns follow a similar trend, but are less distinct (Fig. 9). The tourist islands are fairly well segregated in the upper right quadrant and the protected islands are bottom and left side of the NMS diagram. This indicates that the island groups differ in their overall vegetation response to disturbance.

DISCUSSION

The Role of Human Disturbance on the Vegetation of the GSI

Results from this study indicate that dunes in human-disturbed areas had markedly different vegetation than dunes in less-disturbed areas. The ANOVA and NMS analyses showed that the vegetation composition differed substantially, even though the overall vegetation cover was similar. Disturbed dunes had reduced cover of native dune-building grasses and had higher cover of alien species, native generalist taxa, and other native dune taxa.

Disturbed dune sites, being in close proximity to boardwalks and vehicle access points, are places where human traffic is intense. Even on the protected islands, dune species composition has been affected. Trampling and other forms of human disturbances directly injure roots and rhizomes of dune grasses and damage the surface sand layers that minimize freshwater evaporation (Rust and Illenberger, 1996). By destroying the existing native dune vegetation and by disrupting the surface soils, human disturbance is providing gaps in which generalist, alien, and other

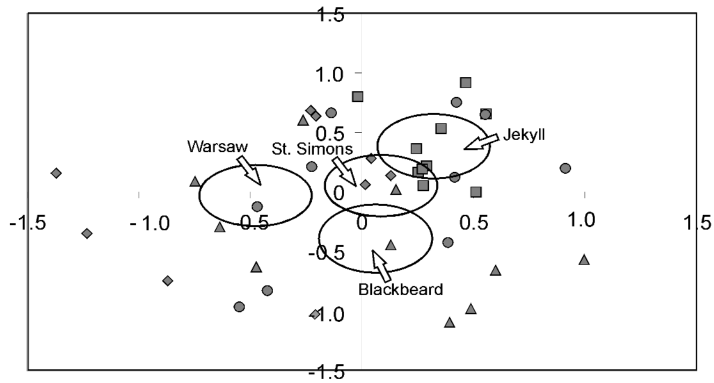

Fig. 9. Ordination results from nonmetric multidimensional scaling by island. Triangles indicated Blackbeard Island, squares represent Jekyll Island, circles represent St. Simons Island, and diamonds represent Wassaw Island. Ellipses represent the 95% confidence interval around the mean center for each island.

native dune taxa can invade from nearby areas. These other species, once established, often increase in abundance at the expense of the native dune builders.

Natural disturbances on barrier islands have been shown to lower species diversity (Ehrenfeld, 1990; Hayden et al., 1995). For example, overwash events on the North Carolina Outer Banks create hypersaline soils that are mostly inhabited by *Spartina patens* (Godfrey, 1976; Woodhouse, 1982). The GSI seldom experience these natural disturbance agents at this magnitude because they are under the influence of different wave and tidal regimes (Walker and Coleman, 1987). Where dune vegetation on the GSI is subjected to human disturbance, dunes have higher plant species diversity. In that same context, diversity is lower on the GSI in less-disturbed dune areas because native species tend to dominate. If one ascribes to the intermediate disturbance hypothesis (Connell, 1978), these findings suggest that human disturbance levels on the GSI are operating at centrally located values of intensity. Dune diversity is high when dunes are subjected to human disturbance and diversity is low when either disturbance is minimal (because native dune species tend to dominate) or extreme (because only a few species are adapted to harsh conditions). This is clearly an instance in which maximizing species diversity is not a sound ecological policy.

Differences in vegetation composition also were apparent between protected islands and tourist islands, albeit these differences were not as strong. Tourist islands had lower cover of native dune builders and had higher cover of other native dune taxa. The degree of trampling and other human modifications are much greater on the tourist islands because they are visited by more people and they are more developed. As a consequence, the frequency and magnitude of human disturbance are more extensive. Human disturbance is affecting dunes even in the more sheltered areas on tourist islands. Overall island land-use contrasts are reflected in species composition at the local site level.

The cover of alien species was not significantly different among islands, primarily because of large variances in alien cover values among islands. This was an interesting finding because it indicates that alien plants were present on all the islands regardless of the islands accessibility to people. The most common alien species were Eurasian and tropical grasses that are adapted to human disturbance and cultivation (Hitchcock, 1950). These species appear to be filling in gaps in the dunes that were created by human disturbance. It seems, then, that alien plant distributions on the GSI are more a function of the number of available disturbed sites on an island than the overall island accessibility or the level of human usage.

St. Simons was the most heavily disturbed and humanly modified GSI included in this study, yet the cover of alien species was much less than that of Jekyll or even protected Blackbeard islands. Several of the heavily disturbed sites on St. Simons had dunes with lower elevations, which would make them more susceptible to saltwater inundation. The native generalist and alien taxa that were present on disturbed dunes on other islands are not as common here because they are not able to tolerate overwash. Indeed, *Spartina patens*, a well-known overwash colonizer, displayed high cover values on several St. Simons Island dunes.

Implications of Human Disturbance and Dune Vegetation

The replacement of native dune builders with other native dune, alien, or generalist taxa could have profound influences on foredune dune morphology for several reasons. In contrast to the native dune builders that have an extensive and dense subsurface root/rhizome system (Woodhouse, 1982), many of the other species found on disturbed dunes lack adequate root morphology to trap and hold sand. Additionally, it has been shown that dune height is directly proportional to the corresponding height of the dune vegetation (Oertel and Larson, 1976; Heyligers, 1985). The native dune builders on the GSI are efficient at intercepting wind-blown sand (Wagner, 1964; Woodhouse, 1982), but other species probably do not extend high enough to contribute meaningfully to sand interception. *Cynodon dactylon* has been shown to increase substrate stability in other areas (Mack and D'Antonio, 1998); however, its short stature would make it less capable of intercepting sand. Lastly, native dune builders have a leaf and stem morphology well adapted to reducing drag coefficients of winds and causing wind-blown sand to settle out (Woodhouse, 1982). The other species are not as effective as the native dune-building grasses at instigating sand deposition. Furthermore, the presence of generalist and alien taxa may be interfering dune succession. Therefore, dunes in disturbed areas that have a lower abundance of native dune builders or have a higher cover of other vegetation taxa are probably be less structurally stable and potentially more susceptible to erosion than less-disturbed dunes.

CONCLUSION

This research provides evidence that human disturbance has significantly affected the vegetation composition of the foredune environments on the GSI. At the local scale, key dune species that trap and bind sand and that are important for the formation and stability of dunes have declined in areas where human disturbance has been high. Furthermore, other species that are not as adapted to building and maintaining dunes, such as other native generalist taxa and alien species, have increased in abundance on disturbed dunes. Because dune stability and vegetation cover are inherently linked, this human-induced vegetation change may indirectly be reducing the stability of coastal dunes. At the broader, island scale, human disturbance on protected islands can lead to localized alterations of foredune vegetation and environments similar to those experienced on the more heavily used islands. Likewise, protected dunes on tourist islands maintain less-disturbed remnants of a vegetation composition that are similar to less-disturbed dunes on more protected islands.

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