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BIODIVERSITY RESEARCH

Distribution of alien plant species in relation to human disturbance on the Georgia Sea Islands

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Abstract. This study investigates the effects of human disturbance and environmental factors on the distribution of alien plant species on the Georgia Sea Islands (GSI), USA. We sampled the absolute cover of native and alien plant species on two tourist islands (St. Simons Island and Jekyll Island) and on two protected National Wildlife Refuge Islands (Blackbeard Island and Wassaw Island). On each island, vegetation composition and environmental variables (soil properties and salt spray) were measured in two habitats that differed substantially in their degree of environmental stress, the more exposed primary dune and the more sheltered and inland maritime forest. Sites were further stratified within each habitat into areas that had different levels of human disturbance. Many alien species were present on all islands and the absolute cover of alien species was not significantly different among islands even though they varied substantially in their degree of accessibility and overall land use. Alien plant cover was appreciably greater in severely disturbed sites than in less disturbed sites on all islands and within both habitats. However, the difference between disturbance categories was much less pronounced in the primary dunes where human disturbance agents do not mitigate the harsh environmental conditions of this habitat (salt spray and saline soils). Alien plant abundance on the GSI is evidently more dependent upon the availability of disturbed ground than the degree of accessibility or overall island development. It appears that human disturbance increases alien cover in general, but in environments where the stress levels are not mitigated, human disturbance does little to foster alien invasions.

Key words. Alien plants, biological invasions, environmental stress, Georgia Sea Islands, human disturbance.

INTRODUCTION

The traits that make a community invasible by alien species have been widely discussed in the ecological literature, yet there is still ambiguity regarding why some communities are more invasible than others (Crawley, 1987; Lonsdale, 1999; Williamson, 1999). Traditionally it was believed that invasions are less successful in species-rich communities because of intense competition with the existing native species (Elton 1958; Tilman, 1997). More recently, however, research has shown that there may be a positive association between species richness and alien invasibility (Levine, 2000; Brown & Peet, 2003). Communities that have high species richness often have more available resources, and thus would be more readily invaded by all species regardless of native or alien status (Huston, 1994; Lonsdale, 1999; Stohlgren *et al.*, 1999).

The association of invasibility and resource availability is applicable to habitats that have high levels of environmental stress. For the purposes of this paper, stress is defined as any physical process that inhibits or constrains plant production (Grime, 1979). It has been shown, for

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example, that alien species are more abundant in mesic habitats than in habitats where moisture availability is more extreme (Rejmanek, 1989). Xeric sites are less conducive to alien seed germination or establishment, and hydric sites support strong competitors that exclude invasion. Similarly, Wiser *et al.* (1998) showed that alien invasions in the Southern Alps of New Zealand were more frequent in plots that were more fertile, more sheltered, and at lower elevations. Additionally, Harrison (1999) reported that alien species, common throughout most grasslands of California, were significantly less abundant within the nutrient-poor serpentine grasslands. Alien invasions in Australia have also been shown to be associated with more fertile soils (Armor & Piggin, 1977). In these cases, the physically harsh habitats had limited alien invasions because environmental stress reduces the ability of species to utilize available resources (Davis *et al.*, 2000).

Human disturbance, on the other hand, often increases resource availability and thus makes disturbed habitats more susceptible to invasion (Davis *et al.*, 2000). In fact, the long-held notion that alien invasions are tied to human disturbance (Hobbs & Huenneke, 1992; Mack & D'Antonio, 1998; Davis *et al.*, 2000) is possibly related to the changes in available resources. Human disturbance facilitates the invasion of alien plants by opening and creating available grounds for invasion, by severely reducing native species that previously excluded alien colonization, by selectively eliminating long-term relationships between organisms, by creating vacant niches, and by changing the natural disturbance regimes (Orians, 1986; Mack & D'Antonio, 1998).

Both human disturbance and environmental stress affect alien invasions by changing resource availability. It would seem, then, that the interaction of these two factors would play an important role in the distribution of alien species. For example, Forcella & Harvey (1989) reported that alien plants extend their range from lower montane zones, which have a warmer climate, into the higher elevations of Montana, which have a much cooler climate, using roadsides as avenues of migration. Kuhn & Zedler (1997) similarly found that aliens have invaded Californian coastal marshes along storm drains and sewage spills where human-induced freshwater runoff has lowered salinity levels. Greenberg *et al.* (1997) showed that alien species used roadside soils as corridors to invading xeric habitats. Huenneke *et al.* (1990) showed that the addition of nutrients on serpentine soils of California elevated alien plant abundances. Burke & Grime (1996) discovered that nutrient enrichment increased the number of alien plants within limestone grasslands of Great Britain. On the Tiwi Islands of Australia, alien species were most prevalent on clay-rich soils but were found in drier sandy soils in areas around human settlement (Fensham & Cowie, 1998). These results suggest that human disturbance and environmental stress interact in controlling alien distributions, but more work is needed to determine the nature of these relationships.

The purpose of this paper is to investigate the interacting effects of human disturbance and environmental stress on the distribution of alien plant species on the Georgia Sea Islands (GSI). Specific questions addressed include: (1) Does the distribution of alien plant species vary with respect to human disturbance, both at a broad scale among islands with different visitation patterns, and at a more local scale within islands, among habitats receiving different levels of human use? (2) Does the distribution of alien plant species vary with soil cation concentrations, soil pH, and soil organic matter content? (3) Do habitat types characterized by different degrees of environmental stress and human disturbance regime interact in their influence on the abundance of alien plants?

STUDY AREA

The GSI are a group of 15 barrier islands that are separated from the mainland of Georgia, USA, by saltwater estuaries, tidal creeks, and sounds (Fig. 1). Although the smaller islands and the parts of larger islands that currently face the open ocean are mid-Holocene in age (*c.* 4000–5000 BP), the bulk of the larger islands were actually part of the mainland during the last glacial maximum (*c.* 18 000 BP) (Walker & Coleman, 1987). They became isolated when sea level rose following the melting of the ice sheets. Because they were once joined to continental North America, the biota of these barrier islands is considered to be a subset of the mainland (Ehrenfeld, 1990).

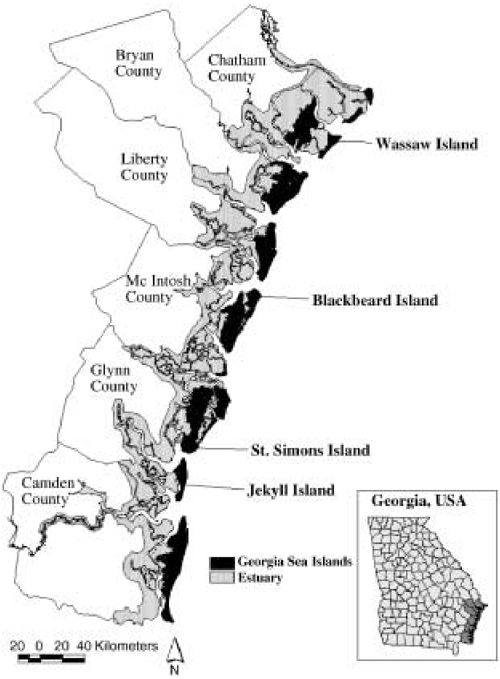

Fig. 1 The Georgia Sea Islands used in this study.

Primary foredune habitats on the GSI are relatively stressful for plants. Stresses characteristic of these sites include poor soils, due to lower organic matter content and higher salinity; salt spray from ocean winds; local-scale sand movements that cause burial and sand blasting of vegetation; high winds; broad-scale changes in island geomorphology; and susceptibility to washover events (Ehrenfeld, 1990; Stallins, 2001). The GSI also contain maritime forest habitats that are inland and less exposed to the harsh coastal conditions. These areas are more protected from salt spray and have richer, moister soils. However, available light and access to open ground is more limiting in the forest than in the primary foredunes.

Most of the GSI have been inhabited at some time in the past and they have a long history of human use by Native Americans, and more recently, by people of European and African descent (Vanstory, 1956). Today, the GSI have varying degrees of accessibility and human use. Four islands were selected for study to represent both highly visited islands as well as those that have been granted some type of protection. Jekyll Island and St. Simons Island are tourist islands that are accessible by vehicle via a causeway and have many hotels, golf courses, and residential areas. In 1997, several million people visited these islands (Jekyll Island Convention and Visitors Bureau, personal communication, April, 1999 and Brunswick and the Golden Isles of Georgia Visitor Centre, personal communication, April 1999). Both Jekyll and St. Simons Island are heavily developed, but they each contain pockets of maritime forest and dunes that have little human use. For example the Calm Creek Park on Jekyll Island and the Fort Frederica National Monument site on St. Simons Island are areas where few people venture off-trail into the surrounding forest. Similar pockets of dunes with little human use exist in areas far from accesses to public beaches. Blackbeard Island and Wassaw Island, on the other hand, are National Wildlife Refuges that have very little human development and are managed through the US Fish and Wildlife Service (USFWS). Blackbeard Island was acquired by the US Navy in the 1800s as a source of live oak timber. The island was protected and uninhabited throughout the 19th and 20th centuries. In 1940 the island was donated to the USFWS to be managed as a National Wildlife Refuge (Savannah Coastal Refuge, 2003a). Wassaw Island was owned by one family for over 100 years, during which time it remained mostly undeveloped. In 1969, the majority of the island was donated to the USFWS to be managed as a National Wildlife Refuge, excluding a small parcel of land in the centre of the island that is still privately owned (Savannah Coastal Refuge, 2003b). Today both Blackbeard Island and Wassaw Island are only accessible by boat and special permission from the USFWS is needed to visit these islands. Approximately 10 000 people visit them annually (Savannah Coastal Refuge, 2003a). Both islands are mostly undeveloped; however, numerous vehicle trails exist in both the forests and dunes that are used by USFWS personnel, hunters, hikers, and sea-turtle volunteers.

METHODS

Field Sampling

We sampled the absolute cover of both native and alien herbaceous and woody plant taxa

(< 1.5 m in height) on each of the four study islands. On each island, we established 20 sampling sites. Ten of the sites were located in primary foredune habitats. The primary dunes presumably have a high degree of environmental stress created from greater exposure to salt spray and less fertile soils (Ehrenfeld, 1990). The remaining 10 sites were located in the inland maritime forest habitats where vegetation is less exposed to the harsh maritime conditions. The forest habitats in this study were approximately 100 m–500 m inland from the shoreline and were separated from the primary dune habitats by a secondary dune habitat (an older genetic sequence of dunes that lie landward of the primary dune and are characterized by having more woody vegetation).

The sites on each island were further stratified according to land use characteristics. The land use categories were divided into habitats that have a high degree of human disturbance (severely disturbed sites) and habitats where human disturbance is minimal (less disturbed sites). The criterion for designating a site as severely disturbed was that the habitat had a high degree of human use and visitation. In this study, roadsides, picnic areas, hiking and vehicle trails, and residential and tourist areas were selected as severely disturbed sites, with sampling occurring within 2 metres of these types of areas. Only sites that were frequently and recently disturbed were included in the sample so that variation among sites in the time since last disturbance was minimal. Less disturbed sites, on the other hand, were at least 30 metres away from disturbed areas and showed no visible signs of severe disturbance. Despite differences in their overall visitation and land use, the four islands all support sites with these levels of human modification within each of the habitat types.

At each site, we sampled vegetation in a 10-m X 10-m plot with the point intercept method (Goodall, 1957). Each plot was subdivided into four equal quadrats and within each quadrat, we randomly located a sampling point and measured the absolute cover with a 1-m long, 10-pin sampling frame placed 1 m away from the sample point. Taxa that were intercepted by the sampling pins were recorded at 10 cm intervals along the sampling frames. Sampling of vegetation was repeated in each of the four cardinal directions around the random point in each of the four quadrats. From these data, we calculated the absolute cover of each plant taxon by dividing the total number of contacts per species by the total possible number of contacts (160 total contacts per site: 10 points along the sampling frames repeated in 4 cardinal directions, repeated in 4 quadrats). Plant identification and nomenclature follow Hitchcock (1950), Radford *et al.* (1968), USDA (1971), and Duncan & Duncan (1987). Soil samples (*c.* 100 g) were also collected from the surface (*c.* 5 cm depth) and returned to the University of Georgia for chemical analysis. Field sampling occurred during October and November of 1997, a time when many of the coastal plant species are in flower (Wilbur Duncan, University of Georgia, Department of Botany, personal communication September, 1996).

We were interested in investigating the degree to which salt spray varied across the islands. However, a detailed salt spray research project was beyond the scope of this study because it would have involved analysis of many meteorological and oceanographic variables. Instead, we initiated a small-scale pilot study during one day (and thus during one meteorological setting) on Wassaw Island in October of 1998. For this pilot study, we developed our own methodology. We set out traps consisting of 3 layers of cheesecloth encased in 17.6-cm diameter, plastic hoops and attached to 1.5-m stakes. Five traps were placed at each of three locations along a 150-m linear transect (0 m, 50 m, and 150 m). This transect spanned from a primary dune to the interior forest. Traps were orientated towards the oncoming sea breezes and they were exposed to winds for exactly six hours. Cheesecloth from the exposed traps was then collected and returned to the University of Georgia Geomorphology Laboratory to be analysed for sodium concentration.

Laboratory Methods

Soil samples were analysed for cation concentration, pH, and organic matter content. Soil cation concentrations (p.p.m. of dry weight as plant available nutrients) of sodium and the plant nutrients boron, calcium, iron, potassium, magnesium, manganese, molybdenum, phosphorus and zinc were measured with an inductively coupled argon plasma emission spectrometer (ICP) at the University of Georgia Chemical Analysis Laboratory. Before analysis, soil samples were prepared with the Mehlich-1, or double acid extraction procedure (Risser & Baker, 1990). Soil pH was measured with a hand-held pH meter using a 1:1 soil to distilled water mixture (USDA, 1992). Soil organic matter content was measured using loss on ignition (Dean, 1974).

For the salt spray analysis, we soaked the exposed cheesecloth in 50 mL of distilled water for 24 h and then had the resulting solution analysed at the Chemical Analysis Laboratory with ICP analysis. Five blank samples (unexposed cheesecloth that was soaked in distilled water for 24 h) were also analysed with the salt spray samples to determine initial cation concentrations. The soil cation data and the salt spray data were both calibrated before analysis by subtracting the mean concentration of the corresponding cations from blank reagents.

Data Analysis

From the cover of individual plant species, we calculated the total absolute cover of both native and alien species within each site. Alien/native status was determined from published floras, such as Small (1903), Hitchcock (1950), USDA (1971), Godfrey & Wooten (1979, 1981), and Sanders (1987).

We calculated species richness (no. species per 100 m^2 plot) for both native and alien species for each plot. We then averaged the individual plot richness values for each island, for both habitats within each island, and for each disturbance type within both habitats. In addition, we calculated the percentage of the flora comprised by alien species for each plot. Means of the percentage alien flora were determined for each island, for each habitat, and for each disturbance type within habitats.

We used a three-factor nested analysis of variance (ANOVA; Sokal & Rohlf, 1981) to test the research hypothesis that human disturbance, habitat type, and island type have an effect on the distribution of alien plant taxa on the Georgia Sea Islands. This analysis tests for significant differences in the cover of alien plants among islands, among habitats within islands, and among disturbance categories within habitats within islands. For all tests, we used arcsine transformations (Zar, 1996) of absolute alien cover so that data more closely conformed to a normal distribution.

ANOVA was also used to test for significant differences in salt spray among the three locations along the transect. Additionally, ANOVA was used to test for significant differences in soil sodium concentrations between dune and forest habitats. Spearman correlation analysis was also used to identify soil variables that were significantly related to the cover of both alien species and the more common native species. Common native species were defined as those that occurred in at least half of the plots for each habitat. Analyses were performed separately for dune and forest habitats.

RESULTS

Alien Species Encountered on the GSI

The alien species that were found in the GSI study plots are reported by habitat and by island in Table 1. This list is not a comprehensive alien flora for the entire GSI, but rather it is a list of those species encountered within the sampling frames.

The most common alien species and the ones found in both habitats and across most islands were grasses (Table 1). Most alien grass species were found within forest and dune environments, but *Echinochloa crusgalli*, *Eremochloa ophiuroides*, *Secale cereale*, and *Setaria viridis* were only found in forest sites. No alien grasses were found only in the dunes when examined across all islands. Jekyll Island had the highest number of alien grasses (9 species), followed by Wassaw Island (7 species), St. Simons Island (6 species), and Blackbeard Island (4 species).

There were substantially fewer alien forbs (Table 1), and the distribution of these forbs was more island- and habitat-specific. St. Simons Island had the highest number of alien forbs (3 species), followed by Jekyll Island (2 species) and Wassaw Island (1 species). No alien forbs were encountered in Blackbeard Island study plots. *Lonicera japonica* and *Lantana camara* were the only alien forb species found in the dune habitat, and these taxa were only present on St. Simons Island. *Sapium sebiferum* and *Lantana camara* were the only nongrass alien plant species found in both less disturbed and severely disturbed sites.

Table 1 Presence of alien taxa encountered in study plots by habitat (primary dune and forest) and by island (BB = Blackbeard Island, WS = Wassaw Island, LK = Jekyll Island, ST = Simons Island)

		Primary Dune				Forest			
	Origin	BB	WS	JK	ST	BB	WS	JK	ST
Grasses									
Cynodon dactylon (L.) Pers.	Africa	*	*	*	*		*	*	*
Digitaria sanguinalis (L.) Scop.	Eurasia/ Mediterranean			*	*		*	*	
Echinochloa crusgalli (L.) Beauv.	Eurasia/ Mediterranean						*		
Eleusine indica (L.) Gaertn.	Africa	*		*	*		*	*	*
Eremochloa ophiuroides (Munro) Hack.	South-east Asia						*		
Paspalum notatum Flugge.	Tropical America		*	*	*	*	*	*	*
Poa annua L.	Eurasia/ Mediterranean					*	*		
Secale cereale L.	Eurasia/ Mediterranean							*	
Setaria viridis (L.) Beauv.	Eurasia/ Mediterranean							*	
Sorghum halepense (L.) Pers.	Eurasia/ Mediterranean			*	*			*	
Sporobolus poiretii (Roem. & Shult.) Hitch.	Tropical America							*	*
Forbs									
Commelina communis L.	Asia								*
Lantana camara L.	Tropical America				*				
Lonicera japonica Thunb.	Asia				*				
Medicago lupulina L.	Europe/ Mediterranean							*	
Richardia brasiliensis Gomez	Tropical America							*	
Sapium sebiferum (L.) Roxb.	Asia						*		

Alien and Native Species Richness

Alien species richness varied little among the islands, with mean values ranging from 0.4 on Jekyll Island to 0.7 on Wassaw Island (Table 2). Native species richness was also similar among the four islands, ranging from 7.4 on Blackbeard Island to 8.6 on St. Simon's Island. The percentage of flora composed of alien species, however, showed a different pattern. The two protected islands had a greater percentage of alien species [Blackbeard Island (7.6%) and Wassaw Island (9.2%)] than Jekyll Island (6.0%) and St. Simons Island (5.6%).

Spatial Variation in Alien Plant Cover

Spatial variation across the study area was evident in the absolute cover of alien plant species within plots, with a significant difference occurring between disturbance types within habitats within islands (Table 3). Across all islands and habitats, severely disturbed sites had an average alien cover of 17.9%, whereas less disturbed sites had an average alien cover of only < 1%. Anthropogenic disturbance significantly increased the cover of alien species overall, but the magnitude of the increase depended upon the habitat type. Forest sites showed a greater difference in cover between severely disturbed and less disturbed sites; indeed, the highest mean cover of alien plants was in severely disturbed forests (Fig. 2a). The difference in alien cover between disturbance categories was less pronounced for primary dune habitat.

The cover of alien plants was not significantly different among islands, even though Wassaw and Blackbeard Island have much lower human

Table 2 Summary of native and alien plant species occurrence on the GSI by island, habitat, and disturbance type

Island	Habitat	Disturbance category	Mean Species Richness (± SD) Native	Alien	Mean Percent Flora Alien (± SD)
Blackbeard Total			7.4 ± 2.6	0.5 ± 0.7	7.6 ± 2.6
Blackbeard	**Dune Total**		7.9 ± 2.7	0.2 ± 0.4	1.7 ± 3.7
Blackbeard	Dune	Severely	9.2 ± 2.9	0.2 ± 0.4	1.4 ± 3.2
Blackbeard	Dune	Less	7.0 ± 1.8	0.2 ± 0.4	2.0 ± 2.1
Blackbeard	**Forest Total**		6.9 ± 2.9	0.8 ± 0.7	13.5 ± 14.5
Blackbeard	Forest	Severely	5.6 ± 2.4	1.2 ± 0.8	6.8 ± 2.8
Blackbeard	Forest	Less	8.2 ± 3.0	0.4 ± 0.5	1.7 ± 3.7
Wassaw Total			8.4 ± 2.3	0.7 ± 1.2	9.2 ± 16.4
Wassaw	**Dune Total**		7.2 ± 2.3	0.1 ± 0.3	0.9 ± 2.9
Wassaw	Dune	Severely	8.4 ± 2.3	0.2 ± 0.4	1.8 ± 8.9
Wassaw	Dune	Less	6.0 ± 1.6	0.0 ± 0.0	0.0 ± 0.0
Wassaw	**Forest Total**		7.8 ± 3.4	1.3 ± 1.4	16.5 ± 20.6
Wassaw	Forest	Severely	6.6 ± 3.9	0.2 ± 0.4	30.2 ± 21.2
Wassaw	Forest	Less	9.0 ± 2.4	0.1 ± 0.3	2.9 ± 6.4
Jekyll Total			8.2 ± 2.9	0.7 ± 1.1	6.0 ± 8.9
Jekyll	**Dune Total**		7.1 ± 2.9	0.4 ± 0.7	4.4 ± 8.4
Jekyll	Dune	Severely	8.2 ± 3.7	0.8 ± 0.8	8.8 ± 3.9
Jekyll	Dune	Less	6.0 ± 2.4	0.0 ± 0.0	0.0 ± 0.0
Jekyll	**Forest Total**		9.3 ± 2.6	1.0 ± 1.4	7.6 ± 9.6
Jekyll	Forest	Severely	11 ± 2.5	2.0 ± 1.2	15.3 ± 7.9
Jekyll	Forest	Less	7.6 ± 1.1	0.0 ± 0.0	0.0 ± 0.0
St. Simons Total			8.56 ± 2.4	0.6 ± 0.9	5.6 ± 9.3
St. Simons	**Dune Total**		9.6 ± 2.4	0.7 ± 2.3	8.9 ± 6.8
St. Simons	Dune	Severely	9.8 ± 2.6	0.8 ± 0.8	6.9 ± 6.7
St. Simons	Dune	Less	9.4 ± 2.4	0.6 ± 0.9	4.9 ± 7.4
St. Simons	**Forest Total**		7.5 ± 1.9	0.5 ± 1.1	5.3 ± 11.7
St. Simons	Forest	Severely	8.0 ± 2.34	1.0 ± 1.4	10.7 ± 15.3
St. Simons	Forest	Less	7.0 ± 1.4	0.0 ± 0.0	0.0 ± 0.0

Table 3 Nested-ANOVA table of effects of islands, habitats within islands, and disturbance type within habitats within islands

Source of Variation	DF	Sum of Squares	Mean Square	*F* Value	*P*-value
Island	3	1082.02	360.67	0.281	0.838
Habitat (within Island)	4	5138.32	1284.58	0.565	0.695
Disturbance (within habitat (within Island))	8	18187.05	2273.38	8.108	**0.001**
Error	64	17944.39	280.38		

Note: boldface effects were significant at $P < 0.05$.

visitation and experience a lower intensity of overall human use (Table 3, Fig. 2b). Jekyll Island had the highest mean alien cover overall (9.5% across all habitats and disturbance categories), but this was not significantly different from values for the other islands. St. Simons Island had the lowest total cover of alien species (2%), which was lower than both protected islands (Blackbeard Island = 5.8% and Wassaw Island = 4.8%).

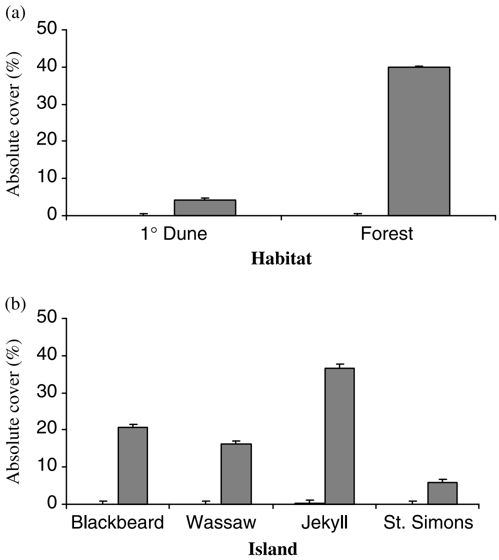

Fig. 2 Mean (±SE) absolute cover of alien plants by habitat (a) and by island (b). The shaded bars on the right indicate the mean cover of disturbed sites and the open bars on the left indicate mean cover of the less disturbed sites.

Spatial Variation in Environmental Variables

Salt spray and soil salinity were significantly higher in the primary dune habitats than in the forest habitat ($P < 0.001$) when analysed with ANOVA. During the salt spray investigation, winds were shifting from westerly to easterly flow and were blowing between 5 and 10 mph. Under these reasonably calm weather conditions, the mean accumulation of airborne sodium from the five traps in the primary dune habitat, at 0 m along the transect, was 190 mg Na/cm^{-2}/h [standard deviation (SD) = 45 mg Na/cm^{-2}/h]. Sodium concentrations dropped off substantially at 50 m along the transect to a mean of 40 mg Na/cm^{-2}/h (SD = 96 mg Na/cm^{-2}/h). In the forest habitat, at 150 m along the transect, sodium concentrations were approximately one-eighth of that measured in the primary dune (mean = 25 mg Na/cm^{-2}/h and SD = 60 mg Na/cm^{-2}/h).

The primary dune also had significantly greater concentrations of sodium in the soil (Fig. 3). The average concentration in the dune habitat (145.4 p.p.m.) was three times as high as in the forest (33.8 p.p.m.). The greater abundance

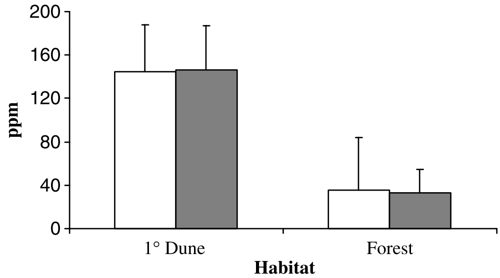

Fig. 3 Mean (±SE) sodium concentration (ppm) of Georgia Sea Island soils by habitat and by disturbance category. Shaded bars on the right represent severely disturbed sites and open bars on the left represent less disturbed sites.

of sodium in the soil and the higher amount of salt spray suggest that the primary dune habitat was more stressful in these environmental properties than the forest habitat.

Relationships of alien cover to environmental concentrations

The ANOVA results indicated a significant difference ($P < 0.05$) between the dune and forest soils for all variables except molybdenum and zinc (Table 4). Forest soils had significantly higher organic matter and manganese contents, whereas dune soils had significantly greater pH values and concentrations of boron, calcium, iron, potassium, magnesium, sodium and phosphorus.

The correlations between soil properties and alien cover showed responses that differed between dunes and forests (Table 5). Alien cover in dunes was significantly negatively correlated with soil pH and positively correlated with organic matter content. Alien cover in the forests sites, however, showed the opposite trends. Additionally, six of the nine plant nutrients tested were significantly positively related to the alien cover in forest sites, whereas none of these nutrients was linked to alien cover in the dunes. Lastly, alien cover was negatively correlated with soil sodium concentrations in the dune sites but was not significantly related to sodium in the forest sites.

Native species cover was less responsive to the soil variables (Table 5). Forbs and grasses in the dunes were significantly correlated with only molybdenum. In the forest plots, the native herbaceous species cover was significantly negatively

Table 4 Means (± SE) for the soil properties examined by habitat type

Soil Property	Dune	Forest
pH*	7.1 (± 0.1)	4.6 (± 0.1)
Organic matter (g)*	0.5 (± 0.8)	7.1 (± 0.8)
B (p.p.m.)*	13.1 (± 4.9)	1.55 (± 4.9)
Ca (p.p.m.)*	3563.2 (± 182.0)	466.4 (± 182.0)
Fe (p.p.m.)*	148.0 (± 6.4)	76.0 (± 6.4)
K (p.p.m.)*	45.6 (± 3.9)	27.7 (± 3.9)
Mg (p.p.m.)*	112.3 (± 8.4)	83.8 (± 8.4)
Mn (p.p.m.)*	9.0 (± 2.9)	16.0 (± 2.9)
Mo (p.p.m.)	0.03 (± 0.2)	0.09 (± 0.2)
Na (p.p.m.)*	145.4 (± 6.2)	33.8 (± 6.2)
P (p.p.m.)*	1904.7 (± 74.9)	163.04 (± 74.9)
Zn (p.p.m.)	2.8 (± 0.4)	3.7 (± 0.4)

* indicates that means are significantly different between habitats ($P < 0.05$).

Table 5 Spearman rank order correlation coefficients (r_s) between soil properties examined and cover of both alien and native plant species by habitat type

	Alien Plant Cover		Native Plant Cover	
Soil Property	Dune	Forest	Dune	Forest
pH	**−0.61**†	**0.40**†	0.19	0.08
Organic matter (g)	**0.32***	**−0.30**†	−0.12	**−0.33***
B	−0.18	**0.40***	−0.26	−0.18
Ca	−0.23	**0.40***	−0.27	−0.01
Fe	0.17	**0.31***	−0.01	0.01
K	0.21	−0.07	−0.10	−0.06
Mg	−0.21	−0.06	−0.10	−0.18
Mn	−0.004	**0.43**†	−0.19	0.04
Mo	0.07	−0.28	**−0.36***	0.17
Na	−0.34*	0.16	−0.20	−0.03
P	−0.15	**0.67**†	−0.24	0.05
Zn	0.27	**0.38***	−0.16	−0.14

* Values that are significantly different between habitat groups at $P < 0.05$ are indicated with *; at $P < 0.001$ with†.

correlated with organic matter, the same response as the alien species. But unlike the alien species, native forest forbs and grasses showed no significant correlations with any of the soil nutrients.

DISCUSSION

Individual Alien Species

Grasses were the most commonly occurring alien plants found on the GSI. They occurred on both protected and tourist islands and within both dune and forest habitats, which suggests that the establishment of these species is not limited by a lack of dispersal capabilities. Many of the alien grass species that originated from the Old World, such as *Digitaria sanguinalis* and *Sorghum halepense*, have coexisted with people for thousands of years and are well adapted to human disturbance (Baker, 1986). These species are suited to invade and occupy disturbed areas on the GSI. The alien grasses of tropical origin, such as *Cynodon dactylon* and *Eremochloa ophiuroides*, have been introduced in the south-eastern United

States as lawn grasses because they are heat-tolerant and can quickly spread (Hitchcock, 1950). These growth characteristics would explain why they are also abundant in the severely disturbed sites across all islands. Like the Eurasian grasses, the tropical grass species seem to be well suited to exploiting the disturbed ground on the GSI.

There were substantially fewer alien forbs in the study plots. Those that were present are noxious weeds that occur in many different habitats besides barrier islands. *Commelina communis* and *Medicago lupulina*, for example, are weedy species that are found throughout the US Coastal Plain from Texas to Maine (Duncan & Duncan, 1987). Each alien forb was restricted to a particular island and to a particular habitat. This may indicate more limited dispersal capabilities than the alien grasses. *Lonicera japonica* is an alien species that is found in many areas of North America. It is a problematic weed in the eastern US (Robertson *et al.*, 1994) and it has been classified as a 'severe threat' by the Florida Exotic Pest Council (Floridata, 2002). It was only found in a few dune sites on St. Simons Island, but its seeds are dispersed by birds. Because this species is such a threat elsewhere and because it has the capability of quickly spreading, *L. japonica* may warrant additional research to monitor changes in distribution.

Perhaps the most threatening alien species found on the GSI was *Sapium sebiferum* (tallow tree). This species can cause widespread changes in forest structure by forming monospecific stands at the exclusion of native trees species. It can tolerate shade and will grow through existing canopies (Jones & McLeod, 1989). *S. sebiferum* also spreads very aggressively by vegetative means (producing suckers and resprouting from the stump) and by producing hundreds of seeds per year. In this study, *S. sebiferum* was only found on Wassaw Island forest sites, but it was growing in both severely disturbed and less disturbed sites. It is likely that the seeds will be carried to the other islands, and thus its distribution should also be carefully studied.

Alien species on islands with different levels of human use

The abundance of alien species on the GSI was not related to overall island land use. Many of the alien species encountered in our study plots, especially the grasses, were present on most of the islands and within both dune and forest habitats. Furthermore, the absolute cover of these species showed no significant difference among islands even though the islands differed substantially in their level of development. The cover of alien plants on the tourist islands was not significantly different from that of the more remote and protected National Wildlife Refuge islands when examined across both habitat types and disturbance types. These results differ somewhat from those of Lonsdale (1999), who reported that natural refuges usually have approximately half the number of non-native species than the surrounding unprotected areas support. It is unclear when alien species arrived to each of the islands, but many alien species may have become established on the islands prior to their respective development or protection. If propagules were already present within areas subsequently designated as nature reserves, disturbances common to both developed and protected islands, such as construction and use of roadways, may have facilitated the dispersal of aliens within natural reserves.

The abundance of alien species, however, was strongly related to the degree of disturbance. Sites subjected to human disturbance included areas that experienced the removal of existing vegetation and, through changes in available light levels and disruption of soil, alteration of the physical environment. Alien species cover was substantially greater in severely disturbed sites in both the primary dune and forest habitats. Additionally, the ANOVA results showed that alien cover among islands was not significantly different, which indicates that this contrast between disturbed and less disturbed sites was similarly evident on all islands. Therefore, the establishment of alien species on the GSI seems to be more related to the existence of human-modified areas rather than overall island land use.

The results from this study examined the current cover of alien species in different settings, but it did not determine what factors actually led to these differences. It is unclear whether the physical disturbance (e.g. construction and use of roadways) led to the higher invasibility of disturbed sites, or whether the roadways allowed for the influx of more alien plant propagules. Propagule pressure (Lonsdale, 1999) is a major influence on habitat invasibility and future research may need to determine how this factor interacts with both human disturbance and the physical constraints of the environment. Alien species have been reported to be more extensive in disturbed areas on other US barrier islands (Miller & Jones, 1967; Anderson & Alexander, 1985; Klotz, 1986; Looney *et al.*, 1993). The invasion of alien taxa on more remote oceanic islands has also been facilitated by the availability of human disturbed sites (Cronk, 1980; Lorence & Sussman, 1986; Kloot, 1987; & Dean *et al.*, 1994). Merlin & Juvik (1992) found that on islands with similar area and proximity, alien cover was highest on islands that had been grazed. These studies suggest that although dispersal of alien taxa to invaded islands is important, the availability of suitable sites created by human modification is just as crucial in determining the abundance of alien species (D'Antonio & Dudley, 1995). The results from this study further substantiate this claim.

Alien plant species by habitat

The cover of alien plants on the GSI did not differ between habitats *within* islands. However, it was evident that alien cover showed different responses within the different habitats when examined across all islands. The suites of variables correlated with alien cover in each habitat suggest environmental controls for the patterns observed. Primary dunes had a higher abundance of salt spray and a greater concentration of sodium in the soil than maritime forests. Soil salinity is considered stressful for most plant species because it reverses plant root osmotic potentials, antagonizes the uptake of essential plant nutrients, and decreases ability of seed to germinate (Ehrenfeld, 1990). Alien cover was negatively correlated with sodium in the primary dunes, indicating that the dune sites with the highest alien cover occurred where soil sodium concentrations were lowest. Native dune cover, however, was not significantly correlated with soil sodium. Moreover, alien cover in the primary dunes was not correlated with concentrations of any of the nine essential plant nutrients, even though these nutrients varied spatially within this habitat. Therefore, the stresses associated with exposure to higher salinity may have served as a more important control of alien cover in the primary dunes than the soil nutrients examined in this study. The maritime forest understorey had much lower values of salt spray and soil sodium, and cover of alien species was significantly positively correlated with soil concentrations of six of the nine essential plant nutrients. Native forb and grass cover showed no relationship with these factors. Perhaps in the absence of saline stress, the cover of alien plants in the maritime forest responded more closely to variation in soil fertility, with greater cover in the more fertile sites. It appears, then, that the presence of saline conditions limits alien plant growth in the primary dune habitats to a much greater degree than in the maritime forest.

The maritime forest is not a completely stress-free habitat because plants on the forest floor compete for space and available light. On the GSI, human disturbance dramatically increased alien plant cover perhaps by opening available ground. In contrast to the dune habitat where disturbance does not ameliorate the stressful saline conditions, human disturbance in the forest habitat may decrease stress levels, thus making them more conducive to invasion by non-native taxa.

These results are somewhat similar to previous studies that have reported enhanced alien invasions in stressful habitats that have been disturbed (Kuhn & Zedler, 1997; Fensham & Cowie, 1998; Harrison, 1999). In most of those studies, human disturbance served to mitigate the stresses of the environment (e.g. diluting saline water, changing soil textures, or adding calcium to serpentine soils) that had evidently limited alien growth previously. In contrast, stress mitigation ssociated with human disturbance is not evident on the primary dunes of the GSI. Trampling and other mechanical alterations of the dune environment do not diminish the stresses associated with salt spray, poor soils, or sand burial. In the forest habitats of the GSI, however, human disturbance often opens sites, making them more susceptible to alien invasion by increasing light levels. Therefore, human activity enhances alien occurrence primarily in less saline habitats of the GSI (e.g. forest habitats), where the disturbance mitigates previously limiting factors. Where human activity instead does not ameliorate environmental stresses (e.g. primary dunes), disturbance does little to facilitate the establishment of the alien taxa.

CONCLUSION

This study indicates that human disturbance interacts with physical environmental conditions in determining the abundance of alien species. On the Georgia Sea Islands, human disturbance enhances the extent of alien cover in general, but alien cover increases more substantially in the maritime forest than in the primary dunes, which are exposed continually to salt spray and have soils with higher salinity values. In such habitats where the limiting environmental factors are not mitigated, human disturbance does little to facilitate alien species invasion.

On a more applied level, the spatial pattern of alien occurrence on the Georgia Sea Islands underscores the role played by localized anthropogenic disturbance in the invasion of native plant communities by alien species. Many alien species were found on all islands, regardless of their levels of human use and accessibility, which indicates that the lower visitation of the protected islands does not prevent their invasion by alien species. Therefore, the spatial arrangement of disturbed ground appears to have an important influence on the rate and extent of alien invasion across the more protected islands.

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