

Landscape-scale patterns of biological invasions in shoreline plant communities

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Little is known about the patterns and dynamics of exotic species invasions at landscape to regional spatial scales. We quantified the presence (identity, abundance, and richness) and characteristics of native and exotic species in estuarine strandline plant communities at 24 sites in Narragansett Bay, Rhode Island, USA. Our results do not support several fundamental predictions of invasion biology. Established exotics (79 of 147 recorded plant species) were nearly indistinguishable from the native plant species (i.e. in terms of growth form, taxonomic grouping, and patterns of spatial distribution and abundance) and essentially represent a random sub-set of the current regional species pool. The cover and richness of exotic species varied substantially among quadrats and sites but were not strongly related to any site-level physical characteristics thought to affect invasibility (i.e. the physical disturbance regime, legal status, neighboring habitat type, and substrate characteristics). Native and exotic cover or richness were not negatively related within most sites. Across sites, native and exotic richness were positively correlated and exotic cover was unrelated to native richness. The colonization and spread of exotics does not appear to have been substantially reduced at sites with high native diversity. Furthermore, despite the fact that the Rhode Island strandline system is one of the most highly-invaded natural plant communities described to date, exotic species, both individually and as a group, currently appear to pose little threat to native plant diversity. Our findings are concordant with most recent, large-scale investigations that do not support the theoretical foundation of invasion biology and generally contradict small-scale experimental work.

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The large and increasing number of plant, animal, and pathogen species artificially added to habitats outside of their former geographical range poses a major challenge to conservation biology (Usher et al. 1988, Lodge 1993, OTA 1993). Such non-native, or “exotic” species, are considered to be a leading cause of species endangerment and are presumed to have large effects on the composition and diversity of native communities and on the functioning of ecosystems (Simberloff 1981, Vitousek et al. 1987, Cronk and Fuller 1995, Luken and

Thieret 1997, Wisser et al. 1998). Despite an enormous number of contributions on various aspects of the colonization, spread, and control of exotic species, surprisingly little information is available at landscape to regional spatial scales for many habitats (Hobbs and Humphries 1995, Blossey 1999, Stohlgren et al. 1999, Mack 2000). For several reasons, this dilemma has limited our understanding of the causes and effects of exotic invasions (Byers et al. 2002). First, testing hypotheses that make predictions about the

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characteristics of highly invadable habitat types or sites or successful exotic colonizers requires quantitative, large-scale data on the identity, diversity, and abundance of native and exotic species. The absence of such information has permitted the general yet erroneous acceptance of a number of paradigms in conservation and invasion biology (Simberloff 1986, 1988). In many instances, such “rules” are supported only by small-scale experimental and observational data and are rejected once adequate sampling is performed (Levine and D’Antonio 1999, Lonsdale 1999, Stohlgren et al. 1999, Levine 2000). Second, the impact of successful exotic invasions on native species richness at site to regional scales has not been evaluated for most habitat types (Parker et al. 1999, Mack 2000, Byers et al. 2002). Third, identifying locations with exceptional conservation value and highly-invaded sites that may act as exotic propagule sources can help managers optimally design and implement effective exotic eradication programs.

The purpose of this study was to quantify the presence (identity, abundance, and diversity), characteristics, and potential effects of exotic plant species in estuarine strandline plant communities and to test some of the basic predictions of invasion biology. Our quantitative sampling was conducted at a landscape spatial scale across 24 sites within Narragansett Bay, Rhode Island, USA. Specifically, we addressed the following questions: (1) do exotic species differ from native species in growth form, life history traits, taxonomic grouping or patterns of spatial distribution or abundance? (2) How spatially variable is the cover and richness of exotic species and are these variables related to site attributes including the presence of legal protection, substrate type, the disturbance regime, and the type of neighboring landward habitat? (3) Are exotic and native cover or richness negatively related and if so are the relationships scale-dependent? And do these spatial patterns suggest that high native richness is an effective deterrent against exotic invasion or that exotic species, either individually or as a group, have reduced native cover or richness?

Study area and habitat

All sampling was performed within Narragansett Bay, Rhode Island, USA (Fig. 1); a well-mixed estuary with semi-diurnal tides (range = 0.8–2.0 m). Narragansett Bay covers 342 square kilometers and includes 412 kilometers of shoreline, a large majority of which consists of beaches of unconsolidated, glacially-deposited boulders, cobbles, pebbles, and sand. Waves in the middle and upper bay are generated by local winds and boat traffic and rarely exceed 1 m in height. The strandline plant community sampled in this study is

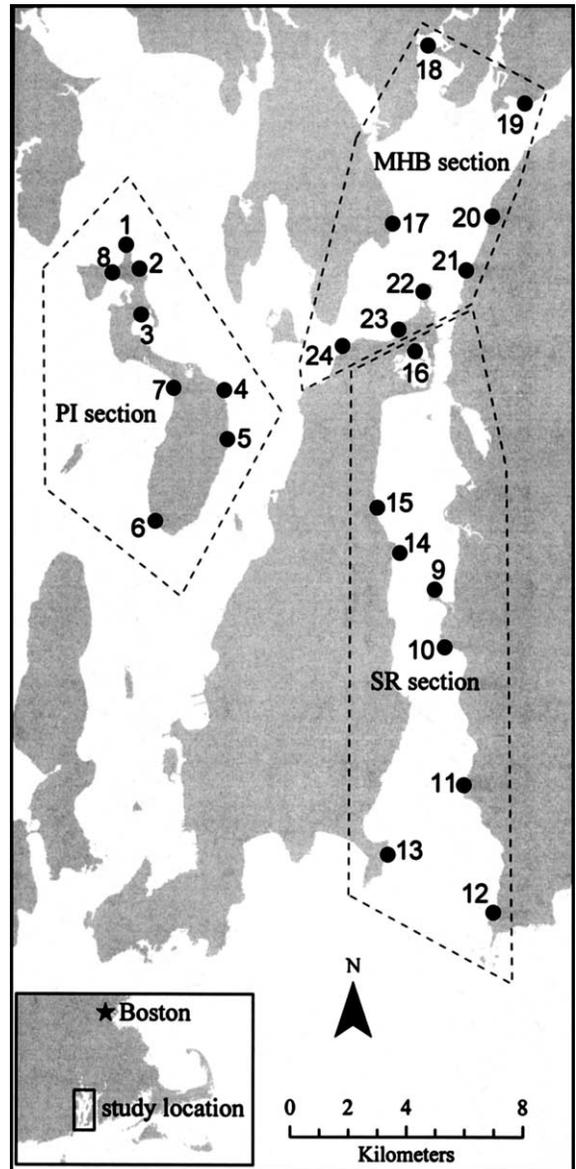


Fig. 1. Map of study sites and sections in Narragansett Bay, RI.

found between 2.5 and 4.0 m above mean low water, above the normal high water mark. In general, the habitat is submerged only during storms and is usually found on the 3–10 m wide storm berm that delineates the upper beach and lower terrestrial borders. The strandline plant community is loosely synonymous with foredune communities (Ehrenfeld 1990, Bertness 1999) and shingle plant communities (Walmsley and Davy 1997). The strandline habitat should not be confused with salt marsh, fringing salt marsh, or cobble beach plant communities, all of which occur well below the strandline community in Narragansett Bay (Rand 1999, Bruno 2000).

Methods

We sampled eight sites within each of three sections/landscapes of Narragansett Bay (i.e. $n=24$ sites; Fig. 1, Table 1): Prudence Island (PI; sites 1–8), Sakonnet River (SR; sites 9–16), and Mount Hope Bay (MHB; sites 17–24). Sections were defined by spatial and hydrographic isolation. Five of the study sites on Prudence Island were within the Narragansett Bay National Estuarine Research Reserve (Fig. 1). All sites were separated by >1 km and were randomly selected from a large pool of accessible sites. A site was defined as a 100 m long section of the shoreline based on preliminary data and observations indicating that this was the approximate scale of spatial continuity of site characteristics such as species and substrate composition.

We used two techniques to sample each of the 24 sites in July 1998 at the time of annual peak biomass. Quadrat sampling was performed to quantify the percentage of the ground covered by each species (cover was considered a proxy for abundance). This method was also used to quantify species richness within quadrats. Twenty independent quadrats (ten above and ten below the transect) were placed at random points along a 100 m transect that ran parallel to the shoreline, 1 m above the seaward (lower) boundary of the community. The quadrats were 0.25 m^2 and were divided into 100 small squares with string. The two-dimensional cover of each species was estimated by counting the number of squares

in which it was present, producing a net cover of $>100\%$ in densely populated quadrats with multiple levels of vegetation. This method may have overestimated the abundance of some species, but it was chosen over the point-intercept method to avoid under-representation of the less common species. We found that this level of quadrat sampling could not adequately quantify richness at the scale of a site because many species were uncommon. Therefore a belt transect technique was used to quantify species richness (i.e. total number of species present) of native and exotic plant species at each site. This was done by identifying and recording all plant species within a single 100 m belt transect placed parallel to the shoreline, that extended landward 5 m from the lower community border (total search area/site = 500 m^2). All sites were searched for >60 min, and we continued to search for unrecorded species for >15 min after finding the last species. Rarefaction analysis, using search time as the independent variable and cumulative number of species as the dependent variable, indicated that this method adequately described site richness.

It is often assumed that physical characteristics of the environment can affect invasibility (Orians 1986, Hobbs and Huenneke 1992, Hobbs and Humphries 1995). We tested this prediction by characterizing each site in respect to wave exposure, the dominant substrate type, the type of adjacent landward habitat, and whether the site was within a legally protected area. Variability in the

Table 1. Descriptions of study sites in Narragansett Bay, RI.

No.	Name	Section	Substrate	Adjacent habitat	In marine protected area?
1	Providence Point	PI	CS	W	Yes-NBNERR
2	Bear Point	PI	CS	F	Yes-NBNERR
3	Potter Cove	PI	SS	F	Yes-NBNERR
4	Prudence Ferry	PI	CS	F	No
5	Sandy Point	PI	S	R	No
6	South Prudence	PI	CS	F	Yes-NBNERR
7	Sandy Beach	PI	S	W	No
8	Ferry Point	PI	S	W	Yes-NBNERR
9	Fogland Point	SR	CS	W	No
10	High Hill Point	SR	C	R	No
11	Church Point	SR	C	CS	No
12	Sakonnet Harbor	SR	C	R	No
13	Sachuest	SR	C	CS	Yes-SNWR
14	Sandy Point	SR	S	R	No
15	McCorrie Point	SR	C	R	No
16	The Cove	SR	C	F	No
17	Haffenreffer	MHB	C	F	Yes-BUHRR
18	Pleasure Cove	MHB	S	W	No
19	Brayton Point	MHB	S	W	No
20	Fall River	MHB	C	F	No
21	North Tiverton	MHB	SS	REST	No
22	Common Fence Point N	MHB	SS	W	No
23	Common Fence Point	MHB	CS	REST	No
24	Mt. Hope Bridge	MHB	SS	W	No

Region codes: PI = Prudence Island; SR = Sakonnet River; MHB = Mount Hope Bay.

Protection codes: NBNERR = Narragansett Bay National Estuarine Research Reserve; SNWR = Sachuest National Wildlife Refuge; BUHRR = Brown University Haffenreffer Research Reserve.

Substrate codes: CS = cobbles and sand; SS = shells and sand; S = sand; C = cobble.

Adjacent habitat codes: F = forest; R = residential; CS = cobble scrub; REST = restoration; W = wetland.

composition of strandline substrate types (sand, cobbles, or shells) has important implications for the availability of belowground resources and may influence the exotic and native components differently based on their species pools. The type of adjacent habitat (forest, residential, coastal scrub, habitat restoration, and wetland) likely influences the propagule supply at a given site with possible effects on strandline community composition (Lonsdale 1999, Levine 2000, Brown and Peet 2003). The frequency and intensity of disturbance may affect the likelihood of exotic establishment (Hobbs and Huenneke 1992, Huston 1995). Legal protection status (seven of the sites were within a research or nature reserve; Fig. 1, Table 1) has implications for the degree and character of anthropogenic disturbance at a site that may influence the propagule supply and the establishment probability of exotic species. We also classified sites according to wave exposure based on the assumption that substrate instability due to wave action is an important form of disturbance in the strandline habitat (Ehrenfeld 1990). We used data from a previous study (Kopp et al. 1995) on the relative exposure to waves at each site estimated from shoreline fetch and orientation and local wind data in 100 m² cells for all of Narragansett Bay, RI.

Plant species identifications and origins were based on Gleason and Cronquist (1991) and Gould et al. (1998). The few plant species that could not be identified due to their phenological state at the time of sampling were not included in the data set. All of the widespread or abundant species were identifiable except *Rubus* spp., which were treated as a single species of unknown origin (below) due to the presence of both exotic and native congeners. Exotics were defined as species that are not native to North America, and native species were those that have been historically present in Rhode Island. The four species we found that are considered exotic to Rhode Island, yet native to North America, were categorized as exotic in the analysis. All statistical analyses were performed using JMP statistical software and when necessary, data were transformed according to the recommendations of Underwood (1997).

Results

We found a total of 147 plant species representing 43 families. Seventy-nine of these species are considered exotic to Rhode Island (56% of the species of known origin) and 75 species are considered exotic to North America (Gould et al. 1998). The origins of six species

were not clear, thus they could not be assigned to either category. Both groups represented 29 plant families, and frequencies of family classification were not strongly dependent on species origin (i.e. native or exotic; chi-square analysis, $\chi^2 = 49.45$, $df = 42$, $P = 0.20$). We used the morphological classification of Gould et al. (1998) to compare the frequencies of plants in each of five categories (herb, grass, shrub, tree, vine) among native and exotic species. A greater portion of exotic species were herbs, and a smaller proportion were grasses and shrubs (Kruskal–Wallis test, $\chi^2 = 10.42$, $df = 4$, $P = 0.03$), although the differences were relatively minor (Table 2). Relative frequencies of life history strategy (i.e. annual, biennial, perennial) were not dependent on species origin (Kruskal–Wallis test, $\chi^2 = 2.64$, $df = 2$, $P = 0.27$). All measured indices of spatial distribution were similar for exotic and native species. For example, the mean number of sites occupied by the two groups did not differ significantly (t-test, $t = 0.540$, $df = 138$, $P = 0.59$; Fig. 2), and the distributions of this parameter across all species in each group were very similar (Fig. 2). The same was true for percent cover (i.e. means for each species across all 24 sites; t-test, $t = 1.024$, $df = 132$, $P = 0.30$; Fig. 2) and the standard deviation of percent cover among sites (t-test, $t = 0.881$, $df = 133$, $P = 0.38$; Fig. 2), which was used as an index of among-site variability in abundance. Half of the top ten space holders were native species. Finally, species richness of both groups was similar at all three spatial scales (Fig. 3).

Exotic species were found at all sampled sites and sections. The percentage of species that were exotic ranged from 36 to 74% over the 24 sampled sites, but this parameter did not vary among sites (chi-square analysis, $\chi^2 = 21.57$, $df = 23$, $P = 0.55$) or sections of Narragansett Bay (one-factor ANOVA results, $F_{2,21} = 1.14$, $P = 0.34$; Fig. 4A). In contrast, the percentage of substratum covered by native and exotic species varied among sites (one-factor ANOVA results, native: $F_{23,456} = 6.48$, $P < 0.0001$; exotic: $F_{23,456} = 10.81$, $P < 0.0001$; Fig. 5), but again, not among sections (native: $F_{2,21} = 0.79$, $P = 0.47$; exotic: $F_{2,21} = 0.045$, $P = 0.96$; Fig. 4B). We analyzed the potential effects of categorical site characteristics on the cover and richness of exotic species with Kruskal–Wallis tests because all comparisons were unbalanced (site selection was random and was not based on site characteristics). The degree of spatial domination by exotic species (i.e. percent of plant cover of known origin at a site) was not affected by legal status (i.e. whether or not a site was within a marine protected area; $\chi^2 = 1.69$, $df = 1$, $P = 0.19$; Fig. 6A), the dominant

Table 2. Numbers and percentages of sampled native and exotic plant species in each of five morphological categories.

	Herb	Grass	Shrub	Tree	Vine
Native	34 (55%)	11 (18%)	11 (18%)	3 (5%)	3 (5%)
Exotic	62 (78%)	7 (9%)	4 (5%)	4 (4%)	3 (4%)

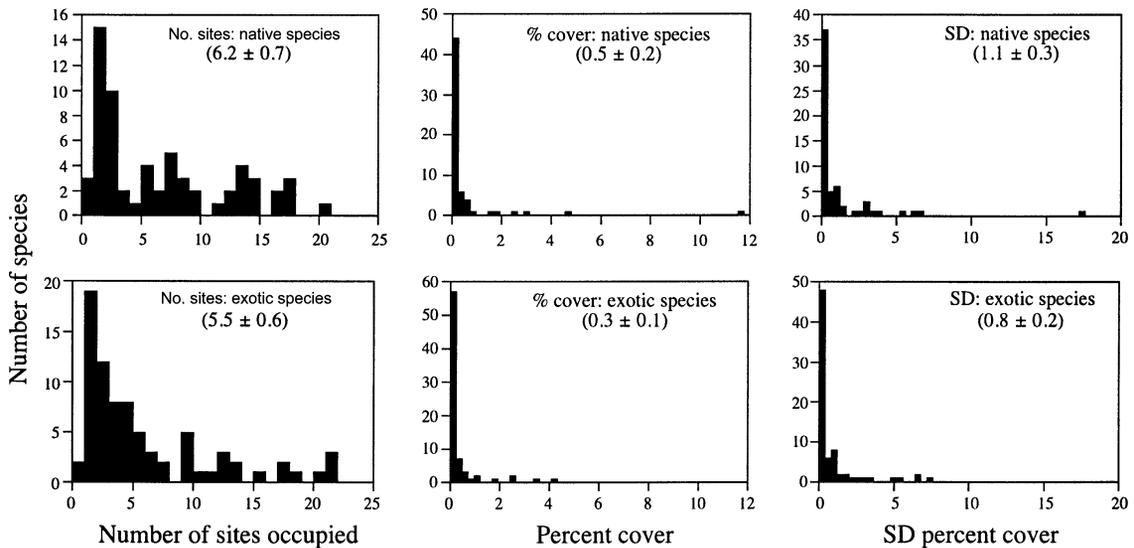


Fig. 2. Three measures of the spatial distribution of native and exotic species. Values in parentheses are mean \pm 1 SE. No. sites = number of sites occupied by each species, % cover = mean percent cover across all 24 sites for each species, SD = 1 standard deviation of % cover.

substrate type ($\chi^2 = 5.47$, $df = 3$, $P = 0.14$; Fig. 6B), the adjacent habitat type ($\chi^2 = 5.74$, $df = 4$, $P = 0.22$; Fig. 6C), or wave exposure (linear regression analysis, $F_{1,22} = 0.820$, $P = 0.38$, $R^2 = 0.04$). The percentage of total species richness that was exotic also did not vary between protected and non-protected sites ($\chi^2 = 0.001$, $df = 1$, $P = 0.98$; Fig. 6A), among sites with different adjacent habitat types ($\chi^2 = 3.71$, $df = 4$, $P = 0.45$; Fig. 6C), or with exposure to waves (linear regression, $F_{1,22} = 1.795$, $P = 0.20$, $R^2 = 0.08$), but did vary among substrate types (Kruskal–Wallis test, $\chi^2 = 10.18$, $df = 3$, $P = 0.02$; Fig. 6B).

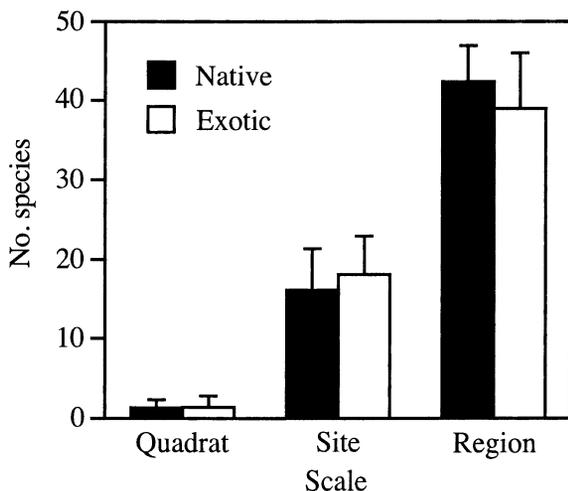


Fig. 3. Species richness (number of species) of native and exotic plant species at three spatial scales (quadrat $n = 480$, site $n = 24$, section $n = 3$). Bars represent means \pm 1 SE.

We used correlation analysis to examine the relationships between the cover and richness of native and exotic species within and among sites. Although regression analysis is traditionally used for such analyses, a regression approach is technically not appropriate since there is no clear dependent or independent variable and neither variable is under control of the experimenter or measured without error (Underwood 1997). Overall, there was only weak evidence of negative relationships between native and exotic richness and cover within or among sites (Table 3). Within most sites these factors were unrelated. Native richness was negatively correlated with exotic cover and richness within 5 and 4 sites, respectively. Across sites, native richness was not related to exotic cover and was marginally positively correlated with exotic richness (Table 3). Exotic and native cover were negatively correlated within 5 sites and among sites (Table 3). The cover of individual, spatially dominant exotic species was also generally unrelated to native cover or richness within and across sites (Table 4).

Discussion

Exotic plants are a major element of the Rhode Island strandline community, representing at least 79 (56%) of the 147 recorded species. Many of the exotic species we found in the strandline (with the exceptions of *Saponaria officinalis*, *Rosa rugosa*, and several species in the Chenopodiaceae) are generalists (i.e. ruderals) that have large geographical distributions encompassing a variety of habitats in North America (e.g. *Rumex crispus*, *Daucus carota* and *Bromus tectorum*). The

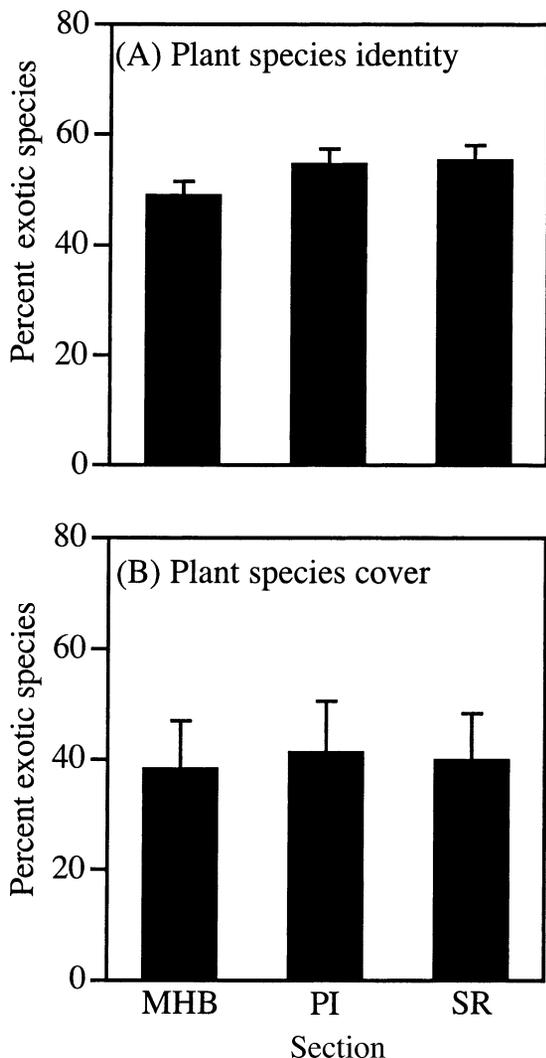


Fig. 4. Abundance of exotic plant species in three sections of Narragansett Bay, RI: (A) numerical abundance (percent of species of known origin), and (B) spatial abundance (percent of plant cover of known origin). Bars represent means +1 SE ($n=8$ sites/section).

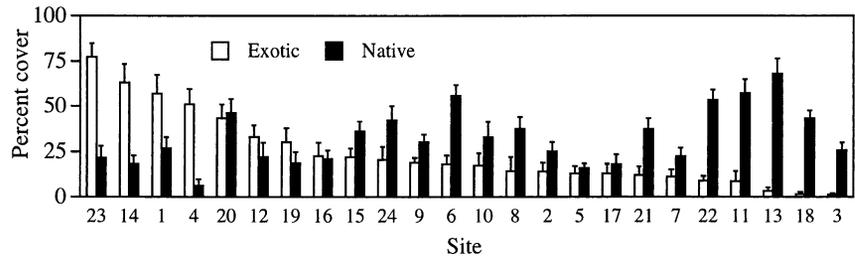
exotic species in the Rhode Island strandline were nearly indistinguishable from the native assemblage in many respects, including species richness at three spatial scales, taxonomic representation, life history, and patterns of distribution and abundance. Plant growth form was only marginally different, as a greater proportion of exotics were herbaceous, and slightly smaller proportions were grasses and shrubs (Table 2). The exotics that have become naturalized in the Rhode Island strandline essentially represent a random subset of the current regional species pool.

Comparisons with other floristic spatial pattern studies could be confounded by varying area and native species richness (Levine and D'Antonio 1999), but cautious contrasts underscore the exceptionally high

degree of exotic establishment in Narragansett Bay strandline plant communities. For example, a current flora of Rhode Island lists 1628 species, of which only 331 (20%) are exotic (Gould et al. 1998), suggesting that exotics are over-represented in the strandline habitat. Furthermore, a recent review of plant invasion research that summarized floras from 142 mainland sites found an average exotic fraction of 11% with no sites exceeding 50% (Lonsdale 1999). However, especially high exotic fractions have been reported in coastal, urban sites similar to the strandline habitats we sampled (e.g. a 60% exotic fraction on Ellis Island in New York City, Yost et al. 1991, Stalter and Scotto 1999). The success and diversity of exotic plants in the Rhode Island strandline is surprising given the perceived harshness of this and similar habitats (van der Valk 1974, Lee and Ignaciuk 1985, Ehrenfeld 1990), the low exotic fraction ($\leq 5\%$ of total species) of British seaside communities (Crawley 1987), and the view that seaside plant assemblages in general are highly resistant to invasion (Crawley 1987).

Relative exotic cover was similar among sections of Narragansett Bay, averaging 40%, but varied greatly among sites, ranging from 4% to 89%. The high site-level variation in exotic cover underscores the need to sample multiple sites across broad areas to adequately describe the identity, abundance, and potential effects of exotics. This finding also suggests that site-specific factors could affect exotic colonization and spread, in accord with an important prediction of invasion biology (Orians 1986, Crawley 1987, Hobbs and Humphries 1995). We characterized each site by legal status (i.e. protected or unprotected), adjacent habitat type, substrate type, and exposure to waves, and examined the relationship between these variables and the cover and richness of exotics. The only significant relationship was between substrate type and exotic species richness, but the effect was weak and was not significant for exotic cover. Physical disturbance is thought to increase exotic colonization (Usher 1988, Lodge 1993, Mazia et al. 2001), but we did not detect any relationship between wave exposure (as measured by Kopp et al. 1995) and either spatial or numerical exotic success. The protected sites, comprised of six sites in two federally-designated reserves and one private reserve site, did not have significantly lower exotic cover than the unprotected sites. This result suggests that the conservation restrictions at these marine reserves are ineffective for maintaining the native character of the strandline plant community (Smallwood 1994), possibly because they experience a similar degree of exotic propagule pressure as non-reserve sites (Usher 1988, Lonsdale 1999). Alternatively, the establishment of exotics may have occurred before the designation of the reserves, in which case restoration efforts may be required to reduce the exotic component of the community. Other recent land-

Fig. 5. Variation among sites in the total cover of native and exotic plants. Bars represent means+1 SE (n =20 quadrats/site).



scope to regional scale studies have also failed to detect an effect of habitat characteristics and disturbance on exotic success (Grice et al. 2000, Vanderwoud et al. 2000). Even if we were able to statistically detect subtle effects by sampling more sites and increasing our statistical power, these four site characteristics would apparently have little predictive value. However, it is possible that other unmeasured site characteristics (e.g. soil nutrients, drainage, etc.) could influence exotic success or that seed limitation could mask their effects.

Two popular paradigms of conservation biology are: (1) more diverse habitats are less susceptible to invasion, and (2) the establishment and spread of exotic species negatively affects native plant diversity and abundance. Both paradigms assume that resources are limiting and that competition is a dominant structuring force in communities, and both predict the same natural patterns. Native diversity is predicted to be inversely related to invasibility because diverse assemblages are thought

to more fully utilize resources and leave little niche space for potential colonists (MacArthur 1955, 1970, Elton 1958, Herbold and Moyle 1986, Levine and D'Antonio 1999). The diversity–invasibility paradigm is supported by some recent experimental studies in which treatment plots with few species were more easily invaded than those with greater diversity (Tilman 1997, Stachowicz et al. 1999, Levine 2000, Lyons and Schwartz 2001), but other similar studies have produced opposite results (Robinson et al. 1995, Palmer and Maurer 1997, Crawley et al. 1999, Schreiber et al. 2002). Furthermore, the spatial scale and effect sizes of most experimental studies supporting the diversity–invasibility paradigm are quite small (Lyons and Schwartz 2001). Most descriptive studies indicate that there is no relationship (Timmins and Williams 1991, Rejmánek 1996) or a positive relationship between exotic and native species richness, especially at larger spatial scales (Bridgewater and Backshall 1981, Pickard 1984, DeFerrari and Naiman

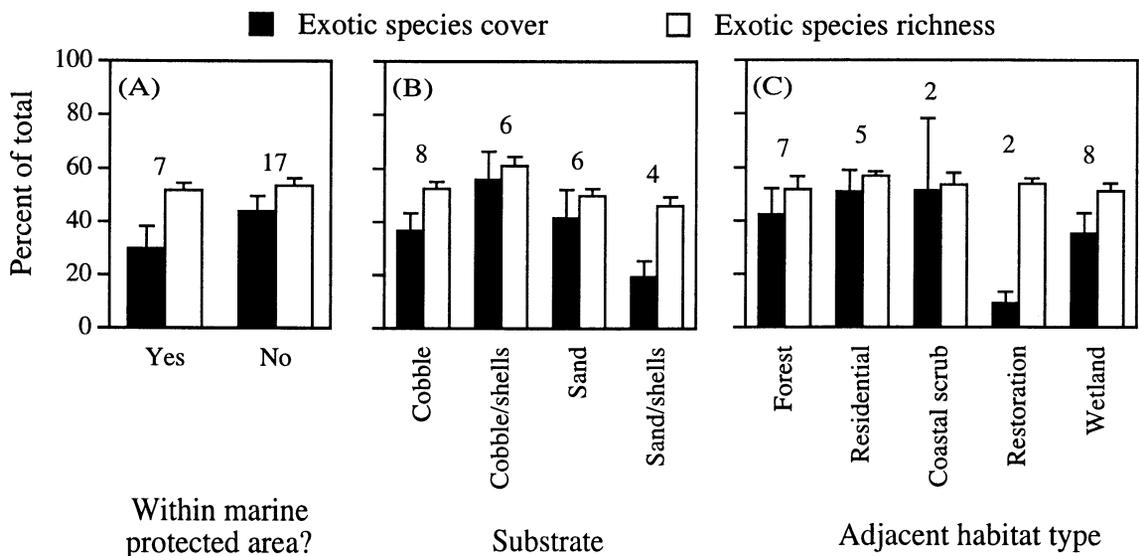


Fig. 6. The effect of three site characteristics on the spatial and numerical representation of exotic plant species (percent of total plant cover and richness): (A) legal status (whether or not a site was within a marine protected area), (B) dominant substrate type, and (C) adjacent habitat type. Bars represent means+1 SE of site means. Numbers above bars are the number of sites in each category.

Table 3. Summary of correlation analyses used to examine relationships between native and exotic richness and cover within (i.e. at the quadrat scale, n = 20, a separate test was performed for each of the 24 sites) and among sites (n = 24, using sites means).

Comparison	Within sites	Among sites ¹
Exotic cover vs native cover	negative in 5 sites** positive in 1 site***	-0.440**
Exotic cover vs native richness	negative in 5 sites**	0.166 ^{NS}
Exotic richness vs native cover	negative in 3 sites* positive in 1 site*	-0.327 ^{NS}
Exotic richness vs native richness	negative in 4 sites*** positive in 1 site***	0.386*

NS = not significant; *P < 0.06; **P < 0.05; ***P < 0.01.

¹Pearson correlation coefficient.

1994, Planty-Tabacchi et al. 1996, Wiser et al. 1998, Lonsdale 1999, Stohlgren et al. 1999, 2003, Burger et al. 2001, Brown and Peet 2003).

The apparently common positive relationship between native richness and exotic success could be driven by at least three mechanisms. First, at high levels of diversity, native communities could facilitate the colonization and persistence of exotic species (Richardson et al. 2000, Bruno et al. 2003). For example, diverse communities are more likely to contain important facilitators or habitat forming species that ameliorate environmental conditions (Stachowicz et al. 2002). Second, the factors that promote or allow high native richness (e.g. high levels of propagule supply and resource availability and favorable environmental conditions) could also enhance the success of exotic colonists (Stohlgren et al. 1999, Brown and Fridley 2003). Third, null community models indicate that sampling artifacts alone could drive positive native-exotic richness relationships (Fridley et al. in press). Yet none of these explanations preclude biotic resistance by native species – high local native richness could still suppress exotic colonization and success. In this scenario, exotics would have been even more successful in the absence of competition with the native assemblage. Therefore, a positive native-exotic relationship should not necessarily lead to the rejection of the diversity-invasibility paradigm. But this pattern does suggest that other factors are more important determinants of exotic success (Levine 2000, Stohlgren et al. 2003).

Although we sampled 24 sites, 480 quadrats, and 147 species, we found few significant correlations between the richness and cover of exotic and native species in the

Rhode Island strandline habitat. Native and exotic richness were only negatively correlated within four sites and were marginally positively related across sites. Exotic cover was slightly negatively related to native cover and richness within five sites, a pattern at least concordant with the assumption that native and exotic flora negatively affect each other. But this result also suggests that competitive exclusion is uncommon and does not translate into patterns of distribution and richness at a landscape scale (e.g. exotic cover was not related to native richness among sites). There are a number of reasons to expect that competitive processes are relatively unimportant in governing plant species diversity in strandline habitats. First, the strandline is a high disturbance habitat (van der Valk 1974, Ehrenfeld 1990) and is thus likely dominated by non-equilibrium conditions under which competitive interactions only rarely result in exclusion (Petraitis et al. 1989, Huston 1995). Additionally, and perhaps as a consequence of disturbance, strandline communities are characterized by a relatively high percentage of bare space (range of site means: 1.2–62.3%; overall site mean = 25%), suggesting that aboveground competitive interactions are likely to be spatially and temporally patchy. Furthermore, no single exotic species was spatially dominant and the cover of the most common exotics was generally unrelated to native cover and richness (Table 4). Although some of the most common exotics can cover as much as 20 to 30% of the substrate within particular sites, all exotics were distributed patchily at all three sampled scales and are thus unlikely to pose a threat to native species across sites. In fact, there was no correla-

Table 4. Summary of correlation analyses used to examine relationships between the cover of the five most common exotic space holders and native richness and cover within (i.e. at the quadrat scale, n = 20) and among sites (n = 24). Abundance statistics are the mean and maximum percent cover at the sites scale and number of occupied sites respectively.

Species	Abundance	Within sites ¹		Among sites	
		Native cover	Native richness	Native cover	Native richness
<i>Rosa rugosa</i>	4.3, 16.2, 21	1 negative*	3 negative*	ns	ns
<i>Daucus carota</i>	3.5, 29.4, 21	0	1 positive**	ns	ns
<i>Celastrus orbiculatus</i>	2.5, 19.7, 18	0	0	ns	ns
<i>Saponaria officinalis</i>	2.4, 26.1, 6	0	0	-0.425 ^{2*}	ns
<i>Melilotus alba</i>	1.8, 32.7, 7	0	0	ns	ns

ns = not significant; *P < 0.05; **P < 0.01.

¹Number of sites within which there was a significant correlation – a separate test was performed for each of the 24 sites.

²Pearson correlation coefficient.

tion between the local (% cover within a site) and regional (the number of occupied sites) abundance of exotic species (Pearson $r = 0.02$, $n = 74$, $P > 0.05$). For example, the fifth most common exotic, *Melilotus alba*, is very abundant at site 23 (32.7% cover), but its regional average cover is only 1.8% and it is only present at 7 of the 24 sites.

Rosenzweig (2001) recently predicted that exotic introductions tend to increase local diversity both in the short and long term, notwithstanding the obvious effects of particular invasive exotic species in specific habitats. Furthermore, several recent studies have failed to detect any negative effects of exotic species on native species and ecosystems (Smith and Knapp 1999, Burger et al. 2001) and suggest that invasions are often additive and can increase local diversity (Gido and Brown 1999, Sax et al. 2002, Sax and Gaines 2003). These studies support the perspective that many communities are unsaturated and propagule limited. In the Rhode Island strandline, the addition of exotic plants to the regional species pool appears to have approximately doubled species diversity at quadrat, site, and landscape spatial scales. We cannot discount the possibility that competition with exotics reduced the abundance of native plants and increased their susceptibility to extinction (Crawley 1987) or that undetected extinctions have already occurred (Blossey 1999). However, neither of these caveats seems likely. Many of the exotics in this habitat became naturalized in New England at least 100 years ago, yet there is no evidence of widespread extinction or endangerment of strandline natives after this considerable period of coexistence. The Rhode Island strandline is a highly-invaded habitat in which the patterns of invasion do not support many of the current ideas and paradigms about the nature and effects of exotic species. This and other recent studies highlight how little we still know about the factors that control community structure and suggest that processes not currently incorporated into invasion theory (e.g. seed limitation) could play a significant role in the colonization and spread of exotic species.

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