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BIODIVERSITY RESEARCH

Dominance of non-native species increases over time in a historically invaded strandline community

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ABSTRACT

Aim We lack a robust understanding of whether exotic species, in addition to causing changes immediately after establishing, might continue to increase in dominance long after invasion events occur. To address this, we resurveyed strandline plant communities, which are likely to have been invaded for over two centuries.

Location Northeastern USA.

Methods We resurveyed the richness and cover of native and exotic plants in 2008 and 2009 at 18 sites, which had originally been surveyed in 1998. We examined whether native and exotic dominance had changed, whether native-rich sites were less likely to be impacted by exotics over time, whether changes in dominance were driven by large changes in a small number of outlier species or by small, incremental changes among many species and whether disturbance mediated any of these relationships.

Results Exotic dominance increased across sites. Initial native diversity was unrelated to patterns of exotic dominance during resurveys. The identity of species that were outliers with respect to changes in distribution or cover varied between resurvey years. Significant changes in exotic-to-native richness ratios at sites were detectible with or without the inclusion of outlier species, but changes in abundance ratios were only significant when outlier species were included. Disturbance across sites was not correlated with species richness, cover, or changes in dominance.

Main conclusions In this historically invaded community, exotics have increased in dominance over the last decade. This change is not due solely to the success of a few hyper-dominant species, but also to the cumulative effect of small changes in distribution among many species. It remains unclear whether patterns observed are due to invasion processes that are playing out very slowly through time or to some other explanation. Our findings highlight the need for a more robust understanding of the long-term dynamics of species invasions.

Keywords

Biological invasions, conservation, disturbance, exotic, extinction, invasive species, non-indigenous species.

INTRODUCTION

Despite the proliferation of research on species invasions over the past two decades (Lodge, 1993; Rejmanek & Richardson, 1996; Sakai *et al.*, 2001; Sax *et al.*, 2007), gaps remain in our understanding of exotic species and their impacts. One of these gaps is our understanding of how exotic invasions impact local communities over time (Blossey, 1999; Strayer *et al.*, 2006). In particular, it is unclear whether we should expect long-term coexistence between natives and exotics within communities or instead whether we should expect gradual increases in exotic dominance until natives are eventually displaced. Previous studies have documented changes in native and exotic diversity that occurred

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soon after key invasion events began (Morrison, 2002; Strayer *et al.*, 2006). Few studies, however, have documented the long-term impacts of exotic invasions (e.g., Wiser *et al.*, 1998; Meiners *et al.*, 2002), limiting our ability to understand changes in native and exotic diversity that might only manifest over longer periods of time (Crooks, 2005; Jackson & Sax, 2010). Differences between short and long-term impacts should be expected whenever impacts that manifest quickly, such as changes in nutrient cycling or patterns of disturbance, lead to feedbacks that manifest slowly, such as the invasion of additional species or loss of existing ones (D'Antonio & Vitousek, 1992; Aikio *et al.*, 2010).

Long-term impacts of exotic invasions on native richness and abundance could vary in importance and detectability depending on how they manifest. Increases in exotic dominance over natives could manifest in one of the three ways. First, changes could be driven by large increases in distribution or abundance of a few species of exotic 'winners' and large decreases in distribution or abundance of a few native 'losers' (McKinney & Lockwood, 1999; Olden & Poff, 2003). For example, the proliferation of introduced game fish into lakes in the midwestern United States during the early 20th century have led to pronounced declines of specific native competitors in these same lakes (Miller *et al.*, 1989; Rahel, 2002). Second, changes in exotic and native dominance could be driven by the cumulative effects of small incremental changes among many species (Didham *et al.*, 2005). For example, within several community types, increases in temperature have been shown to selectively favour incremental increases in exotic dominance (Stachowicz *et al.*, 2002b; Rahel & Olden, 2008; Vila *et al.*, 2009). Third, changes could be driven simultaneously by a combination of these large pronounced shifts in winners and losers as well as through small incremental changes among many species. Currently, it remains unclear whether any one of these possibilities more commonly occurs than the others. While large changes in a few prominent species should be relatively easy to detect, the cumulative effect of many smaller incremental changes would be much harder to detect without good census records (Pauly, 1995).

It is also likely that the ultimate impacts of invaders will vary among communities. In particular, there is evidence to suggest that the diversity of native species within communities may mediate the outcome and success of exotic invasions (e.g., Levine & D'Antonio, 1999; Stachowicz *et al.*, 2002a). Experimental work has generally supported the contention that species-rich native communities should be less invaded than species-poor ones (Levine, 2000; Kennedy *et al.*, 2002). In contrast, observational studies have generally shown that sites rich with native species have more invaders than species-poor sites (Stohlgren *et al.*, 1999; Fridley *et al.*, 2007). Very few studies have examined how richness of natural systems influences exotic success over time (but see Wiser *et al.*, 1998; Cleland *et al.*, 2004; Wiegmann & Waller, 2006). Therefore, it remains unclear whether in natural systems we should generally expect species-rich sites to be less impacted over time by invasions.

The impact of species invasions on local communities may also be mediated by the properties of the physical environment that simultaneously affect native and exotic species (Huston, 1994, 2004). In particular, disturbance can either facilitate or preclude increases in exotic dominance depending on the type of community and its existing level of species diversity (Sousa, 1984; Davis *et al.*, 2000; Sax, 2002; Didham *et al.*, 2005; MacDougall & Turkington, 2005). For example, invasion theory predicts that disturbance may decrease the dominance of exotic invaders in physically stressful communities that are unproductive, but increase exotic dominance in highly productive communities where diversity is low because of competitive exclusion (Huston, 1979, 2004; Proulx & Mazumder, 1998). To date, there have been numerous studies examining the short-term impacts of disturbance on native and exotic diversity (e.g. Hobbs & Huenneke, 1992; Burke & Grime, 1996; Brown & Peet, 2003; Tierney & Cushman, 2006). However, there have been few that have examined the long-term consequences of disturbance on historically invaded communities (but see Smith & Knapp, 1999; Sax, 2002). As such, it remains unclear whether we should expect frequently disturbed communities that have been invaded historically to follow the predictions of invasion theory.

Our ability to document and understand the long-term impacts of invasions on native communities has been restricted by three principal limitations in the ecological literature. First, as previously mentioned, many studies of exotic impacts have been conducted within a few years following invasions, and cannot demonstrate the dynamics that occur over longer periods of time (Blossey, 1999; Strayer *et al.*, 2006). Second, of studies that examine the impacts of exotic species that invaded historically, relatively few of these studies incorporate recent resurvey data, making it difficult to distinguish whether changes in native and exotic dominance occurred immediately or whether they manifested only over longer periods of time (but see Knapp *et al.*, 2010). Third, even though many communities have been invaded by a large number of species (e.g., Cohen & Carlton, 1998; Sax & Gaines, 2003), relatively few studies have investigated long-term impacts in these communities that occur as a cumulative result of the entire suite of established exotics, with many more studies of long-term dynamics focused on the impact of just one or a few invading species (Wiser *et al.*, 1998; Sanders *et al.*, 2003; Strayer, 2009).

One community type where long-term impacts of invasions can be studied is the strandline plant community. These communities are found along shorelines, where they occupy the habitat between intertidal and upland zones; they are influenced strongly by disturbance and are frequently invaded by exotic species (Ehrenfeld, 1990; Walmsley & Davy, 1997; Bruno *et al.*, 2004). Historically, these communities were likely to have been some of the first in North America to be invaded, as they are in areas where ship ballast would have been discarded (Ruiz & Carlton, 2003). In particular, the strandline plant communities of Narragansett Bay (within Rhode Island and Massachusetts, USA) are ideal for examining long-term effects of species invasions for five main reasons. First, in 1998, Bruno *et al.* (2004) characterized 24 strandline plant communities, providing baseline data for estimating changes in native and exotic diversity over time. Second, the exotic species in this system have been present within the region for a long period of time (Bennett, 1888; IPANE, 2010) and most have presumably been integrated into these communities for many decades or longer. Third, these communities are invaded by a great number of exotic species (Bruno *et al.*, 2004), allowing for the possibility of detecting both large changes among a few species and incremental changes among many species. Fourth, these communities span a gradient from being dominated by natives to being dominated by exotics, allowing us to examine the potential influence of native diversity in mediating changes in exotic dominance. Fifth, these communities are distributed along a disturbance gradient, from exposed coastline to protected coves, allowing for the opportunity to determine the impact of disturbance in these historically invaded communities. Further, in addition to the utility of addressing long-term changes in the strandline plant communities of Narragansett Bay, this system is also of applied conservation importance as these communities support several species that are threatened or of critical concern, e.g. *Polygonum glaucum* and *Honckenya peploides* (Enser, 2007).

In this study, we examined the long-term impacts of species invasions in the historically invaded strandline plant communities of Narragansett Bay. Within these communities, we assessed changes in native and exotic diversity over 10 and 11 years (1998–2008 and 1998–2009) by conducting historical resurveys. In these resurveys we examined patterns of change in native and exotic richness and percent cover. Collectively, this approach allowed us to examine four related, but distinct questions: (1) Are these historically invaded communities increasing in exotic and decreasing in native dominance over time? (2) If changes have occurred, were these changes driven by the proliferation of a few winners and the decline of a few losers or by incremental changes among many species? (3) If changes have occurred, were sites rich in native species less likely to be impacted by exotic species over time? (4) If changes have occurred, were these changes influenced by differences in disturbance across sites?

METHODS

This study was conducted in strandline plant communities of Narragansett Bay, in both Rhode Island and Massachusetts (Fig. 1). Narragansett Bay is the largest estuary in New England and has a surface area of 380 km^2 and over 412 km of shoreline. Strandline plant communities occupy the narrow band of shoreline space between intertidal and upland zones – typically extending a few meters inland (depending on substrate slope) from the normal high-water mark. These communities are only regularly submerged during winter storm events. While strandline plant communities are highly heterogeneous, with substrate types ranging from course sand to cobble stones, they often have similar vegetation and physical properties to foredune (Ehrenfeld, 1990) and shingle beach communities (Walmsley & Davy, 1997).

We replicated the methodology of Bruno *et al.* (2004) to resurvey strandline plant communities at 18 of their 24 sites (the remaining six have been lost due to development or are no longer accessible due to changes in property ownership). We conducted resurveys in the summers of 2008 and 2009. Sites were permanently marked with rebar and GPS coordinates between resurveys in 2008 and 2009. These site locations approximated, within a few meters, those originally surveyed in 1998 by Bruno *et al.* (2004). At each site, we estimated native and exotic plant richness by recording all species within a 5 × 100 m belt transect oriented parallel to

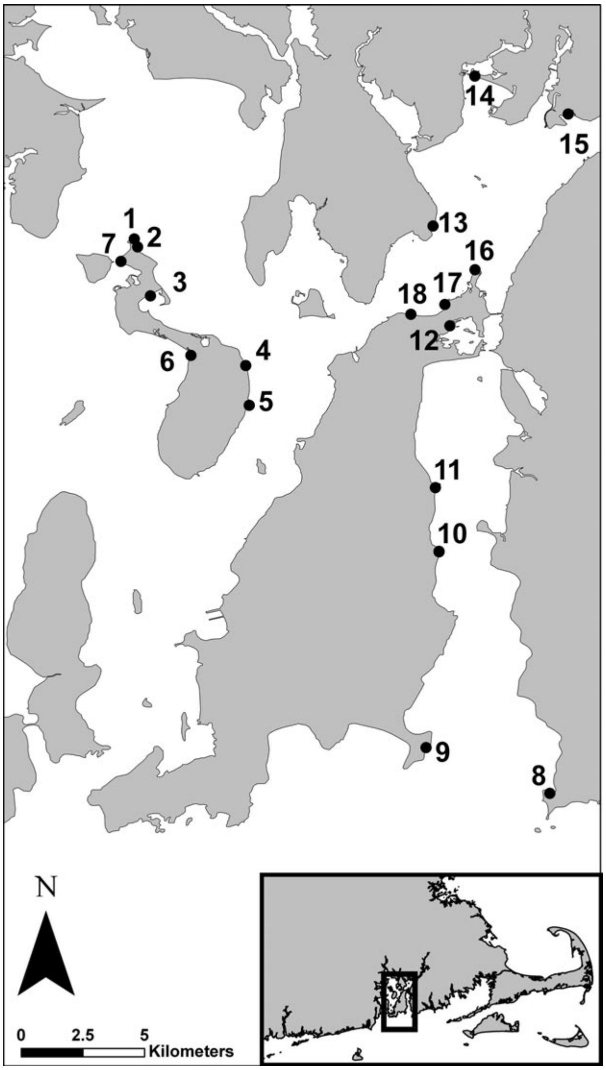

Figure 1 Map of 18 strandline plant communities surveyed from 1998 to 2009 in Narragansett Bay, RI and MA. Numbers correspond to sites analysed in Fig. 2.

the shoreline. We searched each belt transect for longer than 45 min, and looked for unrecorded species for at least 15 min after the final species was documented. Additionally, along the midline of each belt transect, we placed 10–1 m^2 quadrats spaced 10 m apart from each other (five above and five below the midline). Within each quadrat we visually estimated the percent cover of each species present by dividing quadrats into 25 smaller squares with string. Because cover was measured individually for each species, quadrats could have a net cover > 100%.

We used accounts in the literature to determine the earliest known date of presence within southern New England (Connecticut, Massachusetts, and Rhode Island) for all exotic species in our system. One exception is *Phragmites australis*, which was excluded because the exact arrival date of the exotic haplotype currently occupying our study sites is unknown. In our literature survey, we searched for specific mentions of whether each exotic species was found in southern New England. While all of our study sites are within Rhode Island and Massachusetts, we included dates of occurrence from Connecticut because of its close proximity to our sites in Rhode Island (< 30 miles) and the likelihood that shoreline plants, which frequently utilize marine dispersal methods (Walmsley & Davy, 1997; Kadereit *et al.*, 2005) should be expected, over just a few generations, to move distances as short as 30 miles (Koutstaal *et al.*, 1987; Nathan *et al.*, 2008).

We estimated changes in plant species richness and percent cover in five different ways. First, we used paired t-tests and linear regression analyses to compare mean richness and percent cover separately for both native and exotic species over time. Second, we used paired t-tests to compare changes over time in mean exotic richness and percent cover relative to changes in mean native richness and percent cover. Third, we estimated changes in the regional species pool over time separately for both native and exotic species. Fourth, we used chi-square tests for goodness-of-fit to compare the number of sites where ratios of exotic-to-native richness and exotic-to-native cover increased versus the number of sites where those ratios decreased. Fifth, we used linear regression to analyse the relationships between native and exotic richness and the changes in the ratios of exotic-to-native richness over time.

We also determined the identity of 'winners' and 'losers' for both native and exotic species and re-analysed changes in plant richness and cover over time after excluding these species, allowing us to determine whether community change was driven by a small number of outlier species. We identified winners and losers using four approaches. First, we identified species that were more than two standard deviations from mean responses across sites. We did this relative to changes in site occupancy. We also did this relative to changes in total cover, which was measured for an individual species as the sum of all percent cover records observed across sites. Second, we repeated these analyses, but considered winners and losers to be those species more than one standard deviation from mean changes observed over time. Third, we identified species at individual sites that were more than two standard deviations from mean change in cover across species at those same sites. Fourth, we repeated these analyses, but considered winners and losers to be those more than one standard deviation from observed mean changes in cover. Winners and losers were identified separately for both native and exotic species, as well as separately for 10 and 11-year periods using all methods. We also identified the number of winners and losers shared between the 10- and 11-year resurvey periods. We used linear regression to examine whether changes in site occupancy or cover over time for exotic species were correlated with their first known date of presence in southern New England.

We examined the potential influence of differences in disturbance across sites on strandline plant communities by examining three proxies for disturbance. First, we examined the relationships between the site slope, which is a proxy for disturbance in coastal habitats (Riis & Hawes, 2003; van de Koppel *et al.*, 2005), and species richness, cover, and changes in exotic-to-native ratios over time using linear and quadratic regression (Table 1). Second, we examined the relationships between spatial heterogeneity (i.e. variance in species cover or mean cover within a site), which is another proxy for disturbance (Sousa, 1984; Huston, 1994), with changes in strandline plant richness, cover, and exotic-to-native ratios over time using linear and quadratic regression. Third, we qualitatively ranked our study sites in order of disturbance level and used Spearman's Rank Correlation test to determine if these rankings were related to changes in richness and composition over time (Table 1). Our qualitative ranking of sites was hierarchical, with three nested criteria: (1) protected coves vs. exposed coastline, (2) presence or absence of *Spartina alterniflora* (cordgrass) beds, which can buffer waves and reduce disturbance in the strandline (Bruno, 2000) and (3) site slope (see Table 1). Sites were partitioned by the first criterion, and within these groupings by the second criterion, and within those groupings by the third criterion. These rankings are available from the senior author upon request.

Because our baseline data collected by Bruno *et al.* (2004) are only from a single year and our resurvey data are from just two more years, we also examined whether 1998, 2008, or 2009 had anomalous climatic conditions. We determined if the survey years were anomalous by examining temperature, precipitation records and winter storm records for Rhode Island (home to 16 of our 18 sites) from 1971 to 2010 (NOAA (National Climatic Data Center), 2012a; NOAA (National Satellite & Information Service), 2012b). We used Grubb's outlier test to determine if each survey year's temperature or precipitation values were more than two standard deviations from the mean. Finally, we used linear regression to examine how mean annual temperatures has changed over the last century (1895–2009) to determine if there has been a long-term increase in temperature that could influence community composition.

Table 1 Physical characteristics and species composition data for the 18 strandline plant communities surveyed in Narragansett Bay

Site	Slope (%)	Exposure	Spartina	Substrate	Mean native Spp.	Mean exotic Spp.	Mean native cover	Mean exotic cover
1	9.7	Open	Present	Shell/cobble	17.7 ± 1.7	21.3 ± 1.5	27.4 ± 4.5	53.0 ± 12.4
2	10.8	Protected	Present	Shell/cobble	17.7 ± 1.3	18.7 ± 2.1	30.3 ± 11.8	25.1 ± 7.5
3	7.2	Protected	Present	Sand/cobble	24.7 ± 0.9	18.7 ± 5.9	42.1 ± 19.2	12.8 ± 6.5
4	7.4	Open	Absent	Shell/cobble	11.3 ± 1.5	27.7 ± 5.7	15.3 ± 8.3	63.1 ± 7.7
5	3.0	Open	Absent	Shell/Cobble	17.0 ± 1.5	20.0 ± 3.6	40.4 ± 23.4	15.5 ± 4.4
6	4.4	Open	Absent	Sand/shell	13.7 ± 1.3	17.0 ± 2.0	33.2 ± 13.3	22.0 ± 6.0
7	11.5	Open	Present	Sand/shell	12.0 ± 1.2	15.7 ± 6.5	25.3 ± 9.4	28.4 ± 10.2
8	4.9	Protected	Absent	Sand/cobble	17.0 ± 3.0	27.7 ± 6.4	31.3 ± 16.5	46.5 ± 7.7
9	5.6	Open	Absent	Cobble	13.0 ± 0.0	20.3 ± 4.7	55.3 ± 18.4	4.8 ± 1.5
10	5.1	Open	Absent	Cobble	14.0 ± 1.5	19.0 ± 2.6	13.8 ± 9.6	36.4 ± 16.4
11	9.5	Open	Absent	Cobble	19.0 ± 0.6	22.3 ± 1.2	33.3 ± 10.7	25.0 ± 6.4
12	4.7	Protected	Present	Sand/cobble	19.3 ± 3.9	17.0 ± 2.6	34.6 ± 2.6	14.1 ± 52
13	6.1	Open	Present	Shell/cobble	22.3 ± 1.5	25.7 ± 2.1	32.4 ± 5.8	11.1 ± 3.0
14	5.7	Protected	Absent	Sand	16.7 ± 1.2	13.3 ± 3.8	39.4 ± 8.1	6.0 ± 2.6
15	3.1	Protected	Absent	Sand	20.0 ± 2.1	17.3 ± 4.0	23.8 ± 3.7	21.1 ± 5.5
16	3.7	Open	Present	Sand/cobble	15.7 ± 1.8	18.0 ± 6.1	37.7 ± 7.6	39.9 ± 33.8
17	9.2	Protected	Present	Shell/cobble	20.3 ± 1.8	25.0 ± 4.6	22.3 ± 11.1	56.0 ± 23.8
18	4.8	Protected	Absent	Shell/cobble	16.3 ± 1.2	21.0 ± 5.6	22.5 ± 10.1	53.0 ± 27.7

Percentage slope indicates the slope of the beach from the edge of the strandline to the tidal mid-point. Exposure refers to whether sites were located in a protected cove or were open to wave exposure. Spartina refers to whether there was a bed of *Spartina alterniflora* in front, which can reduce wave pressure. Mean species richness and cover values (± SE) are for 1998, 2008 and 2009.

RESULTS

Historical resurveys of strandline plant communities showed a variety of changes in richness, cover and occurrence of species over time. The mean richness and percent cover of either natives or exotics did not significantly change across sites over the 10- and 11-year survey periods (Table 1; Table 2). However, there was a significant increase in total species cover from 1998 to 2009 (Table 2). Similarly, there were no significant changes in the regional species pool for either native or exotic species over the 10- and 11-year periods (Table 2). In contrast, relative differences in mean changes in richness between natives and exotics were significant over 10 and 11 years, while relative differences in mean cover between natives and exotics were significant over the 10, but not the 11-year period (Table 2). The number of sites that experienced increases in the ratios of exotic-to-native richness and exotic-to-native cover was significantly greater than the number expected by chance over the 10 (Fig. 2a,b) and 11-year periods (Fig. S1). The changes in richness ratios across sites are related to absolute changes in richness, where fewer than half the sites saw a decrease in exotics, but more than half saw a decrease in natives (Fig. 2c). In contrast, no clear pattern is apparent in the absolute changes in native and exotic cover at sites (Fig. 2d). Comparisons across sites between resurvey years (2008 and 2009) showed that mean richness and percent cover did not significantly change for either native or exotic species, nor were there significant differences in the relative change of natives and exotics (Table 2). There were also no significant changes between resurvey years (2008 and 2009) in the ratio of exotic-to-native richness and exotic-to-native cover across sites (Fig. S1c,d).

Species that were outliers, i.e., winners and losers, relative to mean changes in site occupancy and cover were common, varied in identity between resurvey years, and had mixed impacts on the significance of observed changes in the exotic-to-native ratios of richness and cover. Using several approaches, we identified species that were outliers (Appendix S1). For any given methodology for identifying outliers, the identity of these species showed strong turnover between resurvey years (Table 3). Differences observed in the frequency of sites with increases in exotic-to-native richness ratios (Fig. 2a) were still significant after excluding outlier species identified using any of the methods for detecting outliers across sites, but were not significant after excluding outliers identified using within site methods (Appendix S2). In contrast, differences observed in the frequency of sites with increases in exotic-to-native cover ratios were never significant after excluding species identified as outliers using any of the methods for detecting outliers (Appendix S2).

We found that species richness across sites was autocorrelated through time. This was true for native species, which showed positive relationships between site richness between 1998–2008 and between 2008–2009 (Appendix S3). This was also true for exotic species and for total richness (natives plus exotics; Appendix S3). There were no significant relationships between native and exotic species richness across sites in any of the three survey years. Neither native nor exotic species richness at sites in 1998 predicted changes in exotic-to-native ratios of richness or cover (Appendix S3).

We found no evidence to support the contention that differences in disturbance among our sites were important in mediating any of the patterns we observed. Our four proxies for disturbance across sites (a qualitative index, site slope,

Table 2 Changes in plant richness and percentage cover across the region and across sites. We determined that mean changes in exotic richness and cover increased significantly relative to native richness and cover in three out of four long-term comparisons, such that differences in mean changes in richness between natives and exotics were significant over 10 and 11 years ($n = 18$, $t = 2.03$, $d = 34$, $P < 0.003$; $n = 18$, $t = 2.03$, $d = 34$, $P < 0.003$), while differences in mean cover between natives and exotics were significant over the 10 ($n = 18$, $t = 2.03$, d.f. = 34, $P < 0.04$), but not the 11-year period. Inter-annual trends from 2008 to 2009 showed no significant differences between mean changes in exotic richness and cover or mean changes in native richness and cover ($n = 18$, $t = 0.96$, d.f. = 34, $P = 0.48$, $n = 18$, $t = 0.97$, d.f. = 34, $P = 0.52$)

	1998	2008	2009	Δ 98–08	Δ 98–09	Δ 08–09
Total native richness across sites	59	63	55	4	−4	−8
Total exotic richness across sites	77	79	81	2	4	2
Mean native richness per site	18.22	15.83	17.22	−2.39	−1	1.39
Mean exotic richness per site	18	19.5	23.4	1.5	5.4	3.9
Mean native cover per site	30.24	28.99	42.8	−1.25	12.56	13.81
Mean exotic cover per site	25.65	36.88	46	11.23	20.35	9.12

variance in vegetation cover and mean vegetation cover) were not correlated with species richness, cover, exotic-to-native ratios, or their change over time. Of the 142 tests we conducted utilizing both linear and quadratic regression, we found only five significant relationships. However, after applying a Bonferonni correction for multiple comparisons, these relationships were no longer significant.

Our literature surveys revealed that the mean date of first known occurrence in southern New England for the exotic species found in our surveys was 1855, with a range of dates for individual species from 1785 to 1919 (Appendix S4). There was no significant relationship between first known date of occurrence for exotics species in southern New England and their change in site occupancy or cover over the 10- or 11-year periods.

We found that mean annual precipitation in Rhode Island from 1971 to 2010 was 49.17″ inches with a standard deviation 6.71″ and mean annual temperature was 10.16 °C with a standard deviation of 0.24 °C. Precipitation and temperature values across survey years were as follows: 1998) 57.52″, 11.44 °C; 2008) 58.13″, 10.44 °C; 2009) 54.88″, 9.89 °C. These data show that annual precipitation and annual temperatures from all surveys years were within two standard deviations of mean values. Finally, we determined that mean annual temperatures have significantly increased across Rhode Island from 1895 to 2009 ($F_{1,115} = 103.7$, $P < 0.0001$).

DISCUSSION

We examined changes in native and exotic diversity over 10- and 11-year time periods in the historically invaded strandline plant communities of Narragansett Bay and found that exotic dominance increased over those time periods, both with respect to the ratios of exotic-to-native species richness and cover, as well as for the relative difference in mean native and mean exotic richness and cover (Table 2, Fig. 2a–d, Fig. S1a, c). The robustness of this signal of increasing exotic dominance over time is strengthened when considered in the context of the strandline plant system, which is highly dynamic. Indeed, we found that there was high turnover in the identity of outlier species between resurvey years (Table 3), and there is high turnover in the overall composition of species at sites (M. J. Heard and D. F. Sax, in prep.). While levels of native and exotic richness at particular sites were maintained over time, historic levels of species richness had no effect on increases in exotic cover over time (Appendix S3). Further, although strandlines are heavily influenced by winter storms and wave stress, we determined that the increases in exotic dominance we observed were not driven by differences in disturbance among sites.

These findings demonstrate that the strandline plant communities of Narragansett Bay are still in flux and support the conclusion that increases in exotic dominance may be one of the principle outcomes of historical invasions (Strayer *et al.*, 2006). Furthermore, the preferential maintenance of exotic species via increases in exotic richness and cover relative to natives may have consequences for local communities as increases in exotic dominance could create a rising extinction debt for natives that will be paid over time (Kuussaari *et al.*, 2009; Jackson & Sax, 2010). However, given that native richness did not significantly decrease across sites during our study (Table 2), the possibility of an extinction debt in this system remains unclear.

One intriguing finding of our study is that specific manifestations of increasing exotic dominance can be generated by different mechanisms. The strength of increasing exotic-to-native richness ratios was influenced by the presence of outlier species, but was also apparent in the absence of these winner and loser species – at least when calculating outliers based on across-site comparisons. This was true whether outliers were identified based on one or two standard deviations from mean changes in either site occupancy or total cover (Appendix S2). This finding indicates that the cumulative, incremental changes among many species can drive patterns of increasing exotic dominance. This contrasts with the much more common evidence in the literature of the role that a single invading species can play in changing systems (Lodge, 1993; Wiser *et al.*, 1998; Sanders *et al.*, 2003). In this context, our finding that changes in exotic-to-native cover ratios were driven by changes in outlier species is not surprising. Still, the finding is noteworthy because it shows that large changes in a few species, as well as small changes among many species can drive different aspects of increasing exotic dominance in invaded

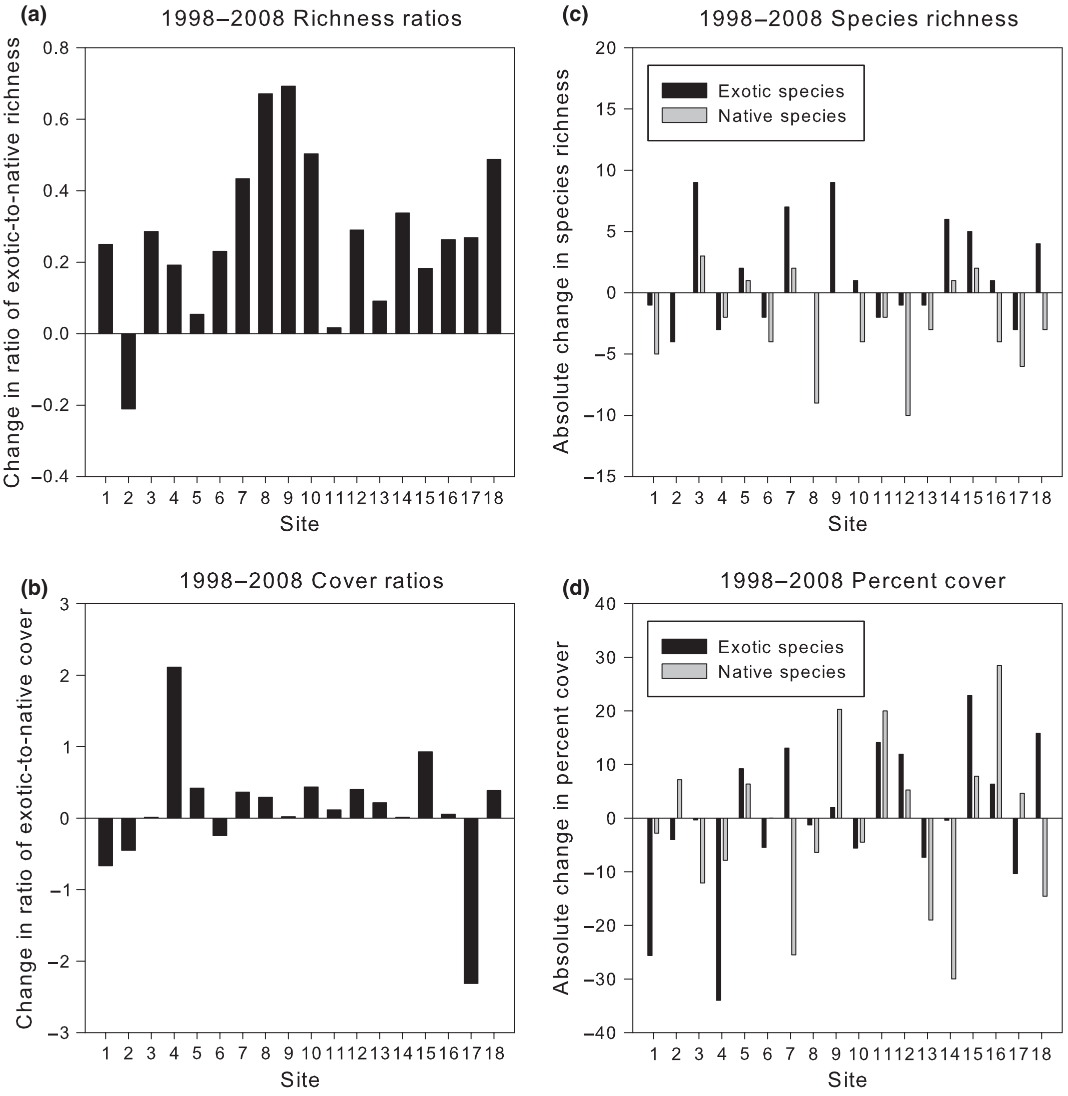

Figure 2 Changes in the ratio of exotic-to-native richness and cover, as well as absolute changes in species richness and cover from 1998 to 2008. (a) Exotic-to-native richness ratios increased at 17 of 18 sites between 1998 and 2008 ($\chi^2 = 14.22$, $P < 0.0002$). (b) Exotic-to-native cover ratios increased at 14 of 18 sites between 1998 and 2008 ($\chi^2 = 5.56$, $P < 0.02$). (c, d) Absolute changes in species richness and percent cover from 1998 to 2008.

communities through time. Finally, it is worth noting that outliers generated by our within-site comparisons provide an overly conservative indication of the influence of outlier species, because this method generates such a long list of outliers when summed across sites that they must have a strong influence on observed dynamics almost by definition.

We also found that native species richness was not significantly correlated with the patterns of increase in exotic dominance we observed across sites (Appendix S3). This finding is significant for three main reasons. First, it suggests that natives are not precluding exotics from establishing in strandline plant communities over time. Second, it supports the hypothesis that many communities may not be saturated with species (Sax *et al.*, 2007; Stohlgren *et al.*, 2008). Third, it is consistent with empirical studies that show that exotics often increase in dominance in areas of high native diversity (Stohlgren *et al.*, 1999; Fridley *et al.*, 2007; Sax *et al.*, 2007).

Levels of native and exotic richness and cover were maintained over time at individual sites (Table 1; Table 2 Appendix S3) with one exception. We found that there was a significant increase in mean total cover from 1998 to 2009. While we are unable to evaluate whether this change was due to changes in growth rates over time, we did not find any evidence to support the contention that disturbance was driving this trend, as the proxies that we measured were not correlated with species richness, cover, or their changes over time. These findings are somewhat surprising as strandline communities are highly prone to disturbance from storms that can alter shoreline topography and bury plant communities (van der Valk, 1974; Ehrenfeld, 1990; Bruno *et al.*, 2004) and we expected to find some signature of disturbance

Table 3 Shared winners & losers

Method	Native losers	Native winners	Exotic losers	Exotic winners
Site Occupancy – 2 SD	20% (*n* = 5)	100% (*n* = 1)	67% (*n* = 3)	13% (*n* = 8)
Site Occupancy – 1 SD	36% (*n* = 11)	22% (*n* = 9)	21% (*n* = 14)	32% (*n* = 19)
Cover Across Sites – 2 SD	50% (*n* = 4)	N/A	0% (*n* = 3)	0% (*n* = 5)
Cover Across Sites – 1 SD	60% (*n* = 5)	0% (*n* = 1)	67% (*n* = 9)	33% (*n* = 3)
Cover Within Sites – 2 SD	70% (*n* = 10)	0% (*n* = 6)	73% (*n* = 15)	50% (*n* = 6)
Cover Within Sites – 1 SD	76% (*n* = 17)	45% (*n* = 11)	63% (*n* = 24)	33% (*n* = 15)

Percentages indicate the number of species of winners and losers (i.e. two types of outliers) shared between the two resurvey periods (1998–2008 and 1998–2009) for each of the methodologies used to identify outlier species. Outliers, i.e. species more than two or more than one standard deviation from the mean, were determined based on changes in site occupancy across sites, total cover across sites and total cover within sites (see Methods for a full description). The total number of winner and loser species found for both survey periods are listed in parentheses. N/A refers to there being no native winners.

on these systems. Our lack of evidence for the importance of disturbance in these systems could be attributed to one of several explanations. First, the proxies for disturbance that we used may have been too course-scaled to identify meaningful patterns. While this is conceivable it would only seem to be a likely explanation if the signature of differences in disturbance in this system is small, as the proxies we used (e.g., site slope) are known to relate strongly to patterns of wave disturbance at shoreline sites (Bruno, 2000; Riis & Hawes, 2003; van de Koppel *et al.*, 2005). Second, although there is likely to be meaningful variation in disturbance among sites, as some are on exposed coastlines and others in protected coves, it is conceivable that the total range of variation in disturbance is small enough, relative to variation in disturbance across different habitat types, that the impacts of differences in disturbance among our sites do not lead to detectible patterns. Third, the differences in disturbance among sites could be important in some ways, but are simply swamped out by the strength of increasing exotic dominance through time, suggesting that invaders are the drivers of change rather than passengers (Didham *et al.*, 2005; MacDougall & Turkington, 2005). More work that explicitly aimed to characterize disturbance at these sites would be needed to distinguish among these possibilities.

Our study cannot determine whether the increases in exotic dominance we observed from 1998 to 2009 are (1) part of an ongoing pattern of increasing dominance that began when exotics established across sites, (2) due to delayed impacts of invasions that have only been recently realized, but were set in motion following initial invasion events, or (3) resulting from change in environmental conditions that was not caused by exotics, but which favours them. Previous work has suggested that exotic establishment may be followed by a lag-period before exotics can increase population sizes or expand to all suitable habitats (Crooks, 2005; Caley *et al.*, 2008). We found no relationship between the date of exotic establishment in southern New England and changes in site occupancy or cover over time within strandline communities; however, given our lack of knowledge of the precise date that individual invasions occurred, lack of evidence for a trend is not a strong support for or against the potential importance of delayed impacts following invasions. Previous work on invasions has shown that increases in temperature may selectively favour increases in exotic dominance over time (Rahel & Olden, 2008; Vila *et al.*, 2009). In Rhode Island there has been a significant increase in mean annual temperatures within the last century (1895–2009), which could favour exotic dominance. Ultimately, barring additional evidence it is not possible to know the precise mechanism of increasing exotic dominance through time at these sites.

While the patterns of change observed in our study are conclusive, it is possible that the changes observed were influenced by atypical conditions that differentially favoured natives or exotics in one of our survey years or by some type of strong interannual variation. Potential atypical conditions could include anomalous climatic conditions or unusual disturbance events (Cleland *et al.*, 2004; Adler & Levine, 2007). For disturbance events to be important in driving the dynamics we observed they would need to have occurred synchronously across all or most of our study sites, which are spread out across a broad geographic area (Fig. 1). This seems unlikely, particularly as the key regular source of disturbance in these systems, i.e., winter storms were not recorded to be atypical across our sites, either within our survey years or the years immediately preceding them (NOAA (National Satellite & Information Service), 2012b). A detailed climatic analysis is beyond the scope of our study, but a simple evaluation of temperature and precipitation records also showed that none of our survey years were more than two standard deviations from mean values from 1971 to 2010. While we have limited data to evaluate the strength of interannual variation in biotic response to environmental conditions, in our two resurvey years (2008–2009) we found that exotic-to-native ratios, mean richness and cover for native and exotic species, and the relative differences in mean changes in richness and cover between natives and exotics showed no significant changes. Collectively, these findings reduce concern that trends observed over the 10- and 11-year survey periods were driven by interannual variation in climatic conditions or disturbance.

Our resurveys in 2008 and 2009 were performed on permanently marked plots, but the original survey conducted in

1998 was not permanently marked, such that the starting points of our transects in the resurvey years were likely to be off by several meters from the original survey. While it is conceivable that limited spatial imprecision between the survey and resurveys could influence our findings, it is extremely unlikely to be important relative to the measures of community change that we have analysed in this study. This is because there is no likely expectation that spatial imprecision would consistently favour an increased presence of exotics at each of our sites. For example, the increase in exotic-to-native richness we observed at 17 of 18 resurveyed sites is extremely unlikely to be due to small changes in the starting points of the transects examined at each site, which should on average favour natives and exotics equally.

To date, we have lacked the empirical or theoretical foundation to predict how the consequences of species invasions are likely to be exhibited in historically invaded communities (Strayer *et al.*, 2006). Here we have shown that the long-term consequences of invasions in the historically invaded strandline plant communities of Narragansett Bay have resulted in increasing exotic dominance over the past decade, that native species richness did not preclude increases in exotic dominance, that disturbance may not be driving increases in exotic dominance and that observed changes have been driven by the proliferation of a small number of specific winners and losers, as well as by smaller, incremental shifts among many species. Collectively, these findings highlight the dynamic nature of historically invaded communities and suggest that the long-term impacts of invasions may play an important, but previously uncharacterized role in determining community composition over time.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Identity of winners and losers from 1998 to 2008 and 1998 to 2009.

Appendix S2 Summary of outlier analyses to identify winners and losers.

Appendix S3 Linear regression table for changes in native and exotic richness over time.

Appendix S4 First known presence dates in southern New England for exotic species.

Figure S1 Change in ratios of exotic-to-native richness and cover between 1998–2009 and between 2008–2009.

BIOSKETCHES

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