
Shoreline Development Drives Invasion of *Phragmites australis* and the Loss of Plant Diversity on New England Salt Marshes

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Abstract: *The reed Phragmites australis Cav. is aggressively invading salt marshes along the Atlantic Coast of North America. We examined the interactive role of habitat alteration (i.e., shoreline development) in driving this invasion and its consequences for plant richness in New England salt marshes. We surveyed 22 salt marshes in Narragansett Bay, Rhode Island, and quantified shoreline development, Phragmites cover, soil salinity, and nitrogen availability. Shoreline development, operationally defined as removal of the woody vegetation bordering marshes, explained >90% of intermarsh variation in Phragmites cover. Shoreline development was also significantly correlated with reduced soil salinities and increased nitrogen availability, suggesting that removing woody vegetation bordering marshes increases nitrogen availability and decreases soil salinities, thus facilitating Phragmites invasion. Soil salinity (64%) and nitrogen availability (56%) alone explained a large proportion of variation in Phragmites cover, but together they explained 80% of the variation in Phragmites invasion success. Both univariate and aggregate (multidimensional scaling) analyses of plant community composition revealed that Phragmites dominance in developed salt marshes resulted in an almost three-fold decrease in plant species richness. Our findings illustrate the importance of maintaining integrity of habitat borders in conserving natural communities and provide an example of the critical role that local conservation can play in preserving these systems. In addition, our findings provide ecologists and natural resource managers with a mechanistic understanding of how human habitat alteration in one vegetation community can interact with species introductions in adjacent communities (i.e., flow-on or adjacency effects) to hasten ecosystem degradation.*

Key Words: adjacency effects, cross-ecosystem linkages, eutrophication, habitat degradation, human and shoreline development, invasive species, *Phragmites australis*, salt marshes

El Desarrollo Costero Impulsa la Invasión de *Phragmites australis* y la Pérdida de Diversidad de Plantas en Marismas de Nueva Inglaterra

Resumen: *El carrizo, Phragmites australis Cav., está invadiendo marismas agresivamente a lo largo de la costa Atlántica d Norte América. Examinamos el papel interactivo de la alteración de hábitat (i.e., desarrollo costero) en el impulso de esta invasión y sus consecuencias sobre la riqueza de especies en marismas de Nueva Inglaterra. Muestreamos 22 marismas en la Bahía Narrangasett, Rhode Island, y cuantificamos el desarrollo costero, la cobertura de Phragmites, la salinidad del suelo y la disponibilidad de nitrógeno. El desarrollo costero, definido operativamente como la remoción de la vegetación leñosa que bordea a las marismas, explicó > 90% de la variación intermarismas de la cobertura de Phragmites. El desarrollo costero también estuvo significativamente correlacionado con reducción de salinidad del suelo e incremento de la disponibilidad de nitrógeno, lo que sugiere que la remoción de la vegetación leñosa circundante a las marismas incrementa la disponibilidad de nitrógeno y disminuye la salinidad facilitando la invasión de Phragmites. Solas, la salinidad del suelo (64%) y disponibilidad de nitrógeno (56%) explicaron una gran proporción de la variación en el*

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éxito invasor de *Phragmites*, pero en conjunto explicaron 80% de la variación en el éxito de invasión de *Phragmites*. Tanto el análisis univariado como agregado (escalamiento multidimensional) de la composición de la comunidad de plantas revelaron que la dominancia de *Phragmites* en marismas desarrolladas resultó en un decremento de casi el triple en la riqueza de especies de plantas. Nuestros hallazgos ilustran la importancia de mantener la integridad de los bordes de hábitat en la conservación de comunidades naturales y proporciona un ejemplo del papel crítico que puede tener la conservación local en la preservación de comunidades naturales. Adicionalmente, nuestros hallazgos proporcionan a ecologistas y gestores de recursos naturales un entendimiento mecanicista de cómo puede interactuar la alteración de hábitat por humanos en una comunidad vegetal con la introducción de especies en comunidades adyacentes (i.e., efectos de flujo o adyacencia) para acelerar la degradación del ecosistema.

Palabras Clave: degradación de hábitat, desarrollo humano y costero, efectos de adyacencia, especies invasoras, eutrofización, interrelaciones ecosistémicas, marismas, *Phragmites australis*

Introduction

Species introductions and habitat alteration are two of the most important threats to global biodiversity and ecosystem structure and function (Mack et al. 2000; Steneck & Carlton 2001). Many researchers have demonstrated biodiversity and ecosystem function loss due to introduction of exotic species (Mack 1996; Lovel 1997; Ruiz et al. 1999; Mack et al. 2000; Mooney & Hobbs 2000). Likewise, destruction and alteration of native populations and habitats by development (Farnsworth & Ellison 1997; Lens et al. 2002), nonpoint- and point-source pollution (Valiela et al. 1985; Vitousek et al. 1997), eutrophication (Grigg 1984; Bertness et al. 2002), and overharvesting of exploited populations (Estes & Palmisano 1974; Watling & Norse 1998; Silliman & Bertness 2002) are all serious threats to natural communities. Moreover, many of these human impacts may interact with species introductions to accelerate the success and speed of species invasions and concomitant habitat degradation (Dukes & Mooney 1999). For example, human disturbances to natural systems may increase the invasion success of weedy exotic species (Beyers 2000; Stackowicz et al. 2002), and over-exploitation of harvested populations may reduce population sizes and create opportunities for successful invasion (Stackowicz et al. 1999). These links between anthropogenic effects on communities and invasion success and the mechanisms underlying them, however, have only recently been explored.

A great amount of scientific work over the past decade has focused on studying the introduction of exotic species into natural communities (reviews in Carlton 1996; Mack et al. 2000; Steneck & Carlton 2001). Most research on invasive species has focused on documenting how common invasions by exotic species are (Carlton 1992), identifying routes and agents of the spread of exotic species (Carlton & Geller 1993; Callaway & Aschoug 2000; Callaway et al. 2003), investigating biological controls (Van Driesche & Bellows 1996; Strong & Pemberton 2000), and quantifying effects of successful invasions on native populations and communities (Grosholz et al. 2000; Mack et al. 2000;

Byers & Goldwasser 2001). Although these are important topics, they do not contribute significantly to developing a predictive understanding of how human disturbance interacts with species introductions to affect invasion success. Much less research (e.g., McIntyre & Lavorel 1994a; McIntyre & Lavorel 1994b; Grosholz 1996; Kiesecker et al. 2001; Rouget et al. 2001; Fine 2002; Stackowitz et al. 2002) has focused on developing this predictive understanding, which is desperately needed by conservation biologists and natural resource managers.

Atlantic coast salt marshes from southern Maine to Chesapeake Bay (U.S.A.) are currently being dramatically altered by an invasive plant, the common reed *Phragmites australis*. This large (2–4 m tall), clonal reed has occurred in Atlantic marshes for at least 10,000 years, but historically was not a numerically dominant marsh species. Over the past 50 years, however, *Phragmites* has expanded into lower elevations and become a dominant species. Saltonstall (2002) has recently shown that introduction of an exotic genotype (i.e., a cryptic invasion) in the 1950s has partially fueled the spread of *Phragmites* throughout its original range. This intense and rapid invasion has been particularly well studied in freshwater and brackish tidal wetlands in the North American middle Atlantic, where *Phragmites* has spread at the expense of displacing other wetland plants (Chambers et al. 1999 and references therein, 2003). Until recently, *Phragmites* was thought to be limited from invading salt marshes by high soil salinities (Chambers et al. 1999), but through clonal integration *Phragmites* can now invade marshes exposed to full-strength seawater (Amesberry et al. 2000; Minchinton & Bertness 2003) and is aggressively invading New England salt marshes, which are often exposed to anthropogenic disturbance (Bertness et al. 2002; Minchinton & Bertness 2003).

We examined how human habitat alteration has affected the invasion success of *Phragmites* in salt marshes of Narragansett Bay, Rhode Island (U.S.A.). In particular we considered the interactive roles of shoreline development, nutrient enrichment, and salinity reduction in facilitating the spread of *Phragmites*. We used a correlative

landscape-level approach, with hypotheses and choice of independent variables based on previous manipulative experiments (Levine et al. 1998; Edelkraut et al. 2000; Emery et al. 2001; Minchinton & Bertness 2003) that provided a mechanistic understanding of how variation in soil salinity and nitrogen availability alters competitive outcomes among salt marsh plants on small spatial scales (square meters). Our approach thus minimizes the “circular causation” and/or “fishing trip” problems associated with purely correlative studies (Sokal & Rohlf 2000) because we have demonstrated a priori through experimentation important community structuring variables that have the potential to be major community drivers at landscape levels.

Increasing nitrogen supply can dramatically shift the competitive balance among native New England salt marsh plants (Levine et al. 1998; Emery et al. 2001). Increased nitrogen availability shifts competitive dominance from plants that are good nutrient competitors to those that are good light competitors. This suggests that the striking plant zonation of New England salt marshes described early in the twentieth century (Miller & Egler 1950; Redfield 1972) was driven by competition for nitrogen and that the highly eutrophic contemporary New England landscapes are being taken over by cordgrass (*Spartina alterniflora* Loisel), a dominant competitor for light (Levine et al. 1998; Bertness et al. 2002). In a previous study (Bertness et al. 2002), we found that shoreline development explains over 90% of intermarsh variation in the extent to which *Phragmites* has invaded marshes and that nitrogen availability—locally elevated by shoreline development—may be a major driver of *Phragmites* invasion. Problems with this initial work were that our surveys did not consider the potential role played by reduced salinity in facilitating *Phragmites* invasion and were not originally designed to look at *Phragmites*. High salinities have long been thought to limit the spread of *Phragmites* (Chambers et al. 1999 and references therein), and by removing the woody vegetation intercepting and utilizing freshwater runoff to marshes, shoreline development may increase freshwater input to marshes, lowering marsh salinities and encouraging *Phragmites* invasion. Thus, shoreline development may enhance *Phragmites* spread via both increased nutrient input and reduced salinity. Here we used broad-scale surveys to provide a mechanistic understanding of how habitat alteration by humans has interacted with introduction of the non-native *Phragmites* genotype (Saltonstall 2002) to drive its spread, rate of expansion, and impacts on the diversity of native plant species.

Methods

We surveyed 22 salt marshes in Narragansett Bay, Rhode Island. All marshes were located in the middle to lower bay, where they are routinely exposed to nearly full-

strength seawater (25–30 parts per thousand) and have not been heavily affected by human disturbances such as diking or filling. Average rainfall in Narragansett Bay marshes over the past 20 years has been approximately 8.12 ± 1.3 cm/month. The climate is temperate, with four distinct seasons, and average monthly temperature for the growing season (May–September) is approximately $19.4 \pm 2.3^\circ$ C. Natural vegetation in these marshes is relatively low-lying (typically <50 cm in height), with around nine species occupying high-marsh habitat (with three dominant plant zones: *Juncus gerrardi* Loisel, *Spartina patens* Aiton, and *Iva frutescens* L.), whereas the low marsh is dominated by *Spartina alterniflora*, the salt marsh cordgrass (Bertness 1999). We chose sites with a wide range of nutrient inputs: island marshes with little shoreline development and little potential for localized nutrient enrichment, and marshes adjacent to golf courses, farms, and housing developments, where the potential for nutrient loading is high. Larger marshes with >300 m of shoreline were subdivided into two site replicates if natural breaks occurred along the marsh shoreline that justified splitting them into separate sites. We avoided sites with evidence of freshwater seeps or creeks draining onto the high marsh.

In July 2002 we took photographs of 100–200 m (in 50-m sections) of the terrestrial border of each marsh. We analyzed these photographs by measuring the length of shoreline at each site invaded by *Phragmites* and the length of the terrestrial border of each marsh that had been modified by humans. We scored borders as invaded by *Phragmites* only if *Phragmites* was the dominant feature of the border (>90% cover along high-marsh border) and had displaced or was in the process of actively displacing typical high-marsh vegetation. *Phragmites* stands were considered to be actively displacing vegetation if >10 runners, >2 m in length were observed moving into the marsh matrix from the *Phragmites* stand. Borders where *Phragmites* was present but low in density and mixed with other vegetation were not considered invaded by *Phragmites*. Thus, our operational definition of a border dominated by *Phragmites* was conservative. We also used the photographs of each marsh to quantify the length of the terrestrial border of each marsh that was modified by humans. We considered a border unmodified only if it abutted a naturally forested strip of woody vegetation that was >10 m wide. Marshes bordered by lawns, farms, roads, or any type of human modification were considered developed.

We used total aboveground nitrogen in cordgrass (*Spartina alterniflora*) tissue per unit area as a site-specific indicator of relative nitrogen availability. Cordgrass production is nitrogen-limited and responded to increased nitrogen availability with increased aboveground growth and elevated tissue nitrogen levels, making this a good site-specific measure of nitrogen availability (Silliman & Zieman 2001; Bertness et al. 2002). Because cordgrass production is also influenced by elevation, at each

site we estimated nitrogen availability (N in aboveground plant biomass) in the terrestrial border of the *S. alterniflora* zone. Because nitrogen availability decreases with increasing elevation in zones dominated by *Spartina alterniflora* (Mendelssohn 1979) and because *S. alterniflora* invades higher marsh elevations at high nutrient levels (Bertness et al. 2002), our measure of nitrogen availability among marshes is conservative.

We quantified variation in nitrogen availability at each site in August 2002. Aboveground cordgrass biomass was cut at ground level in eight randomly located 0.25×0.25 m quadrats on the terrestrial border of the *S. alterniflora* zone at each site. Plant samples were cleaned of all dirt and dead tissue and were then dried at 40° C and weighed. To determine plant nitrogen content for each quadrat sampled, we randomly pooled three dried stems from each sample, ground them up, and analyzed them for nitrogen content using standard techniques (Osgood & Zieman 1993; Bertness et al. 2002). We then calculated total aboveground nitrogen for each quadrat by multiplying cordgrass biomass (g/m^2) by stem nitrogen levels (%) for each replicate quadrat. Because herbivore damage to cordgrass was minimal at our sites ($<3\%$ of leaf surface area), our method for measuring relative nitrogen availability was not confounded by strong and/or variable top-down effects (Silliman & Bortolus 2003). In addition, there was no difference between marsh soil salinities or sulfide concentrations in areas where we measured plant nitrogen availability (i.e., terrestrial border of the *S. alterniflora* zone; $p > 0.48$, one-way analysis of variance [ANOVA], both cases), which would have confounded our attempts to independently relate shoreline development to marsh nitrogen levels (Bradley & Morris 1991; Bertness et al. 2002).

We did not use total nitrogen in aboveground plant tissue at the *Phragmites*-terrestrial border as a proxy for marsh nitrogen availability because salinities varied greatly among these areas, confounding our attempts to independently relate marsh shoreline development to marsh nitrogen levels, and because this border interface was not available for all marshes (i.e., many undeveloped habitats).

We quantified soil salinity at the high-marsh border of each site (above and more landward than the area where plant nitrogen availability was measured) during slack tides in July 2002. We measured soil salinities at the high-marsh border because this is the marsh area being actively invaded by *Phragmites* and the one most susceptible to reduction of soil salinities by increased freshwater input due to shoreline development. Reduction of marsh salinity by freshwater runoff in New England marshes is generally restricted to irregularly flooded high-marsh habitats where *Phragmites* is invading, whereas increases in nitrogen availability due to runoff tend to extend throughout the entire marsh (Bertness et al. 2002; B.R.S. and M.D.B.,

personal observations). The effects of lowering salinity are likely limited to the irregularly flooded high marsh because low-marsh habitats are flooded twice daily by full-strength seawater, which probably negates the diluting effects of freshwater runoff on soil salt levels. In our marsh survey, soil salinities in the low marsh did not differ among sites. We measured soil salinity at the high-marsh border every 10 m along a 100-m transect line by cutting a $2 \times 2 \times 2$ cm plug of sediment from the substrate with a knife and squeezing the pore water on a salinity refractometer (Bertness et al. 1992). We used the mean of these 10 measurements for each site as a site-specific estimate of salinity. We also quantified the rate at which *Phragmites* is invading Narragansett Bay salt marshes and the impact that *Phragmites* is having on plant species richness of the salt marsh.

To quantify the rate of *Phragmites* invasion, in July 2001 we marked the borders of *Phragmites* stands invading the zones of *Iva frutescens* (terrestrial border of the high marsh), *Spartina patens* (seaward border of the high marsh) and *Spartina alterniflora* (low marsh) at as many of the sites listed above as possible. Borders were marked with flags every 2 m for 10–20 m. We revisited the sites in July 2002 and measured border movement at each flag. Not all borders existed at all sites, and the flags were lost at some sites, limiting the number of marsh borders we were able to use for quantifying border movement. Because large, discrete stands of *Phragmites* were uncommon at sites with low nutrient availability, we were unable to use these data to examine intermarsh differences in the rate of *Phragmites* invasion. In spite of these problems, we had seven movement estimates for each border type.

To quantify the impact of *Phragmites* invasion on plant species richness, we ran 5 30-m transect lines through the *Iva frutescens* zone (terrestrial marsh border) of 10 marshes with dense *Phragmites* cover and 10 marshes without *Phragmites* cover. We used the *Iva* zone for this survey because it is the marsh area that is initially colonized and most commonly dominated by *Phragmites* and is the area of New England salt marshes with the highest plant species diversity (Hacker & Bertness 1999). Along each line transect at 3-m intervals, we recorded the percent cover of plant species in a 1-m^2 quadrat ($n = 10/\text{line transect}$). The quadrat was divided into 100 equal units, and species presence was noted for each unit and values summed for total percent cover.

We used multidimensional scaling (MDS) analysis to examine the relationship between plant species richness and shoreline development. For analysis, mean percent cover for each species in the high marsh was determined for each of our 22 marshes with survey methods described above. The matrix used for MDS analysis then contained the mean percent cover values for 14 plant species for each marsh ($n = 22$ marshes) and the

corresponding category of shoreline development for those particular marshes.

We used linear-regression models to relate the percentage of shoreline developed to *Phragmites* dominance on the border, to marsh nitrogen availability, and to marsh soil salinities. A multiple-regression model was used to relate the combined effects of marsh nitrogen availability and soil salinities to *Phragmites* dominance on the border. In all cases, more than one value for a single response variable was recorded for each marsh (e.g., for plant nitrogen availability, $n = 8/\text{marsh}$). For statistical analyses, therefore, we used the mean of multiple values for each measured variable as a single datum per marsh. Each marsh was considered one replicate. For each variable, percent border developed, salinity, and nitrogen availability, sample size equaled 22. Differences in plant richness (effect of *Phragmites* dominance in high marsh), plant percent cover (effect of *Phragmites* dominance in high marsh), and *Phragmites* expansion rate (effect of marsh zone) were determined with a one-way ANOVA followed by Tukey's post hoc test. Data used for one-way ANOVAs exhibited homogeneity of variance and were normally distributed or were log-transformed for analysis. Transformations produced data that met ANOVA assumptions.

To further assess the impacts of shoreline development, we used an aggregate analysis measure (Micheli et al. 1999), MDS, to examine patterns of species composition among marshes with different degrees of shoreline development. Multidimensional scaling constructs a two-dimensional ordination in a manner that best represents relationships among samples in a similarity matrix (Field et al. 1982; Clarke & Warwick 2001). In ordination plots, relative distance among points reflects dissimilarity of species composition of marsh sites (i.e., closer points represent sites with more similar species composition). Prior to MDS analysis, we categorized sites based on their degree of marsh development: high (>75%), moderate (25–75%), and low (<25%). Similarity matrices were calculated with the Bray-Curtis similarity index (Bray & Curtis 1957). Analysis of similarities (ANOSIM; Clarke & Warwick 1994), a nonparametric analog of multiple analysis of variance (MANOVA), was used to test for differences in species composition according to connectivity category. When ANOSIM revealed significant differences, we performed similarity percentage analysis (Clarke & Warwick 1994) to identify the species accounting for the differences.

Results

Border development was significantly correlated ($p < 0.01$) with percentage of marsh border dominated by *Phragmites*, soil salinity at the border, and nitrogen availability (Fig. 1). Percent border development explained

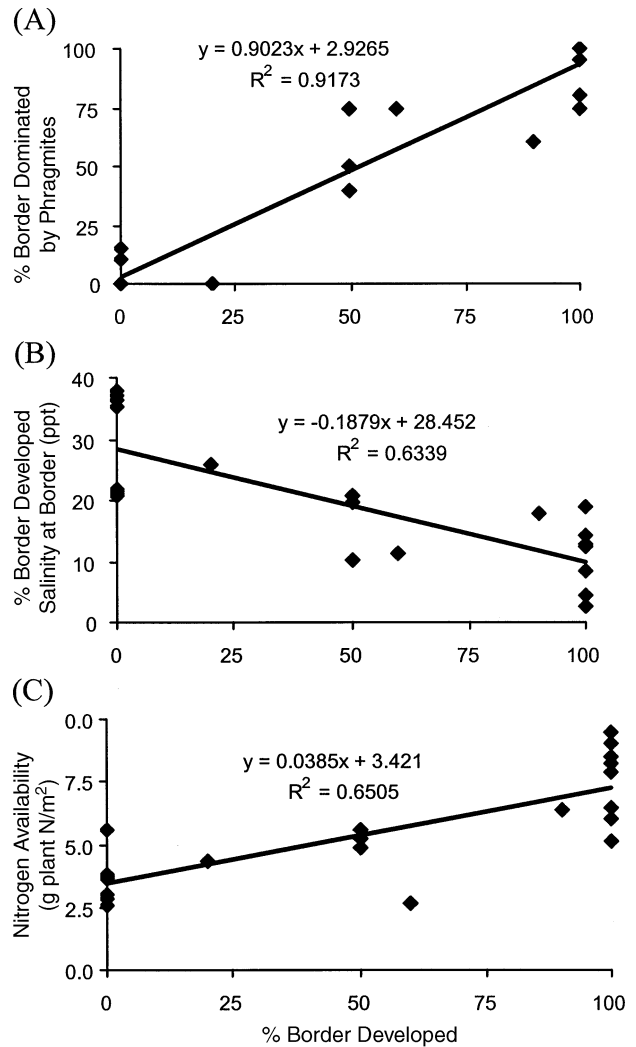


Figure 1. Least-squares linear model of percentage of marsh border developed, and (a) percentage of border dominated by *Phragmites*, (b) marsh soil salinities in the high marsh, and (c) marsh plant nitrogen availability ($n = 22$ marshes; there appears to be <22 data points because there were multiple data points with the same or similar values).

92% of intermarsh variation in percent of border dominated by *Phragmites* (Fig. 1a). As we found in our earlier survey of Narragansett Bay marshes (Bertness et al. 2001), marshes with <25% border development had minimal (<25%) *Phragmites*, whereas marshes with >50% border development typically had >75% of their border dominated by *Phragmites*. Border development also explained 63% of intermarsh variation in high-marsh soil salinity ($p < 0.01$; Fig. 1b) and explained 65% of intermarsh variation in nitrogen availability ($p < 0.01$; Fig. 1c). Border development decreased marsh soil salinity and increased marsh nitrogen availability.

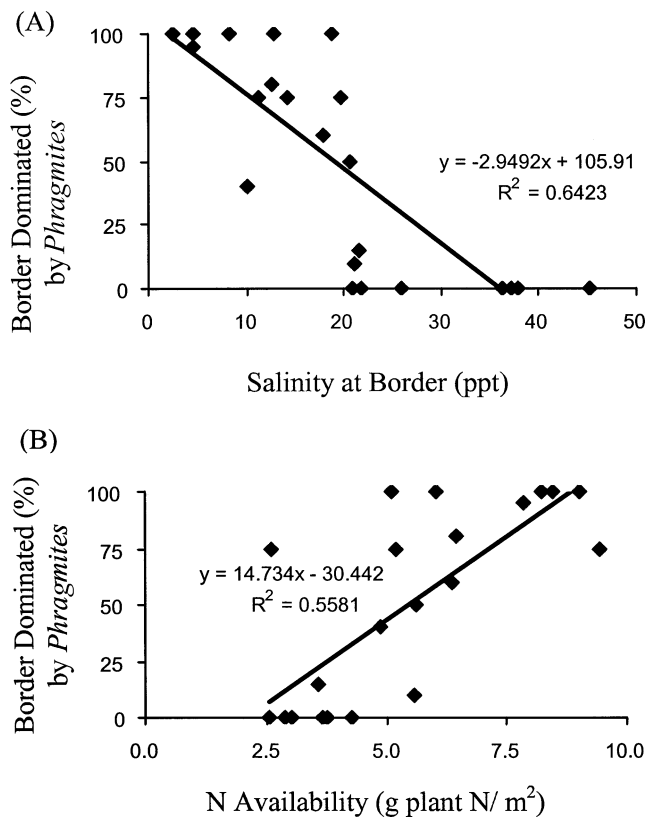


Figure 2. Least-squares linear model of (a) marsh soil salinities in the high marsh and percentage of border dominated by *Phragmites* and (b) marsh plant nitrogen availability and percentage of border dominated by *Phragmites* ($n = 22$; there appears to be <22 data points because there were multiple data points with the same or similar values).

Both soil salinity and nitrogen availability of marsh were significantly ($p < 0.01$) correlated with percentage of marsh border dominated by *Phragmites* (Fig. 2). Soil salinity at the border explained 64% of intermarsh variation in the dominance of *Phragmites* (Fig. 2a), whereas nitrogen availability explained 56% of intermarsh variation in the dominance of *Phragmites* (Fig. 2b). We used multiple regression to examine the combined effects of soil salinity and nitrogen availability on *Phragmites* invasion. Border soil salinity and nitrogen availability together explained 80% of intermarsh variation in *Phragmites* dominance ($r^2 = 0.796$; $p < 0.001$; $df = 2$; $MS = 15269$; $F = 38.49$).

The invasion rate of *Phragmites* decreased with decreasing marsh elevation, as there was a significant effect of marsh zone on rate of invasion ($p < 0.01$, ANOVA; Fig. 3). All pair-wise comparisons between marsh zones of mean expansion rate were significantly different at $p < 0.05$ (Tukey's post hoc). In the *Iva frutescens* zone at the terrestrial marsh border, *Phragmites* expansion was nearly 70 cm/year. In the *Spartina patens* zone on the

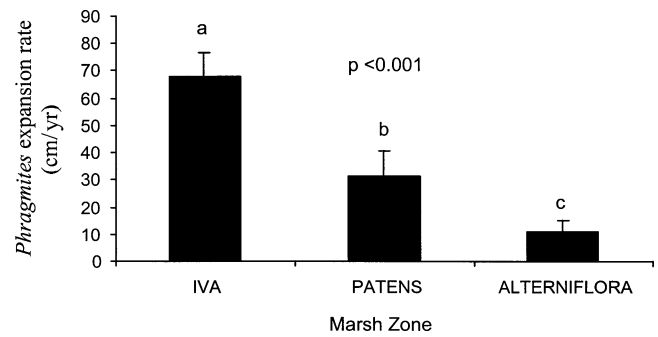


Figure 3. Expansion rate of *Phragmites* in salt marshes of Narragansett Bay, Rhode Island, as a function of marsh zone ($n = 7$ for each zone). Error bars are ± 1 SE.

seaward border of the high marsh, *Phragmites* invasion was only 30 cm/year, whereas in the *Spartina alterniflora* zone in the low marsh, *Phragmites* invasion was just over 10 cm/year. We recognize that invasion rates measured over longer periods than one year (e.g., 10 years) are necessary and would provide better resolution. Such data do not exist for Narragansett Bay salt marshes, however, and these results provide an important baseline reference and insight into potential patterns of *Phragmites* invasion rates over longer time periods.

Our quantification of percent plant cover in high marshes with and without dense *Phragmites* stands (Fig. 4) revealed that high marshes that had not been invaded by *Phragmites* had nearly three times the plant species richness (mean = 6 ± 0.12 species/marsh) of marshes that had been invaded by *Phragmites* (mean = 2 ± 0.29 species/marsh). These differences were reflected in the MDS ordination, in which there is clear separation in ordination space among marsh sites with high, moderate, and low development ($R = 0.774$, $p < 0.001$; Fig. 5). In high marshes not invaded by *Phragmites*, 14 species

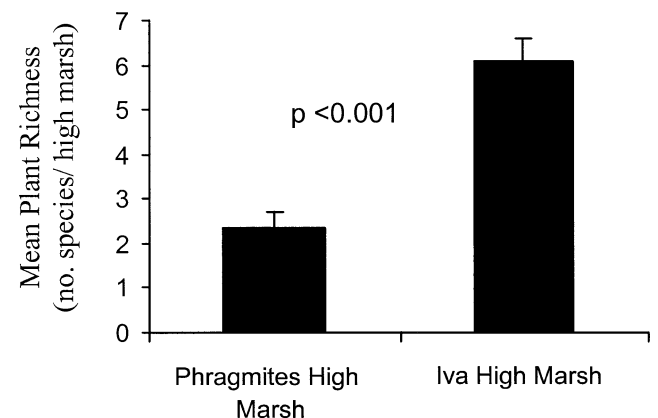


Figure 4. Effect of dominance of *Phragmites* in high marsh on salt marsh plant richness ($n = 10$). Error bars are ± 1 SE.

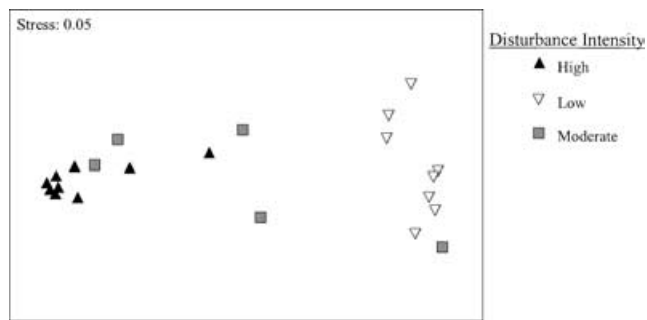


Figure 5. Results of multidimensional scaling (MDS) determining patterns of species composition among marshes with different degrees of shoreline development: high (>75%), moderate (25–75%), and low (<25%) (analysis of similarities, $R = 0.774$, $p < 0.001$). The MDS ordination shows that with higher development there is a more homogenous and less diverse marsh plant community (i.e., sites with high levels of development are closely aligned, whereas sites of low development are spread farther apart).

of plants were found: *Juncus gerardi*, *Spartina patens*, *Distichilus spicata* L., *Iva frutescens*, *Limonium nasbii* Walt., *Atriplex patula* L., *Solidago sempervirens* L., *Juncus balticus* Willd., *Salicornia virginica* L., *Salicornia europea* L., *Aster subulatus* Michx., *Spartina cynaroides* L., *Triglochin maritime* L., and *Triticum* sp. By contrast, in *Phragmites* dominated high marshes, only 4 species managed to persist: *Juncus gerardi*, *Spartina patens*, *Distichilus spicata*, and *Iva frutescens*. Their abundance within *Phragmites* stands, however, was greatly reduced (on average, a 94% reduction in percent cover; Fig. 6). In the most robust portions of *Phragmites* clones, not even these common high-marsh plants survived, and *Phragmites* understory consisted only of *Phragmites* litter. In expanding *Phragmites* clones, we often found dead *Iva frutescens* skeletons. In our survey of high-marsh borders that had not been densely colonized by *Phragmites*, we found eight plant species that were absent in areas dominated by *Phragmites*. Thus, high-marsh habitats were nearly three times more diverse in terms of species richness before *Phragmites* invaded than after.

Discussion

Our results show that shoreline development facilitates invasion of *Phragmites* in New England salt marshes by increasing nutrient availability and decreasing soil salinities. These findings suggest that maintaining the integrity of natural habitat borders may be critical in preserving native communities and stress that local conservation efforts may be extremely important.

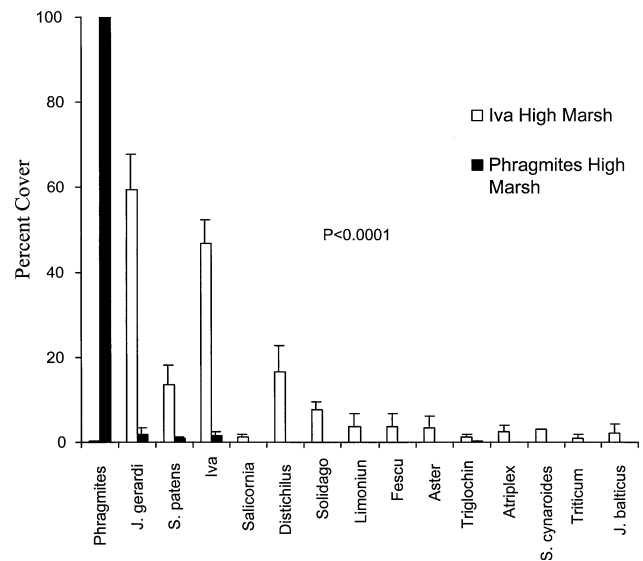


Figure 6. Effect of dominance of *Phragmites* in high marsh on percent cover of salt marsh plants ($n = 10$). Error bars are ± 1 SE.

Facilitation of *Phragmites* Expansion by Shoreline Development

Maritime forest, brush, and grassland communities are critical buffers to eutrophication of estuaries, because they intercept heavy loads of terrestrial runoff rich in nitrogen (McClelland et al. 1997; McClelland & Valiela 1998 and references therein; Valiela et al 2000; Mitch & Gosselink 2000). Removal of forested buffer zones on the border of the Chesapeake Bay, Virginia, has been linked to increased nitrogen loading in adjacent seagrasses and concomitant community die-off due to overgrowth by fast-growing leafy algae (Orth & Moore 1983). In New England salt marshes, small-scale experiments (1 m^2) manipulating nitrogen levels and presence of upland vegetation suggest that both increased nitrogen loading and upland plant removal are critical for successful *Phragmites* expansion (Minchinton & Bertness 2003). Local removal of upland plants allows greater uptake of nitrogen by *Phragmites*, and increased nitrogen availability shifted plant competition in adjacent vegetated plots from belowground for nitrogen to aboveground for light, allowing the much taller *Phragmites* (>3 m tall) to out-compete neighboring marsh vegetation (0.5–1 m tall) (Minchinton & Bertness 2003). The widespread removal of forested buffer zone on the borders of New England salt marshes (Bertness et al. 2002) suggests that these experimental results could be operating on a much larger scale.

The results of our extensive survey of 22 Narragansett Bay marshes demonstrate that there is an extremely strong relationship between shoreline development and expansion of *Phragmites* in southern New England salt marshes. We found that shoreline development explained

91% of intermarsh variation in *Phragmites* cover. This is particularly impressive because of our simple definition of shoreline development: removal of woody vegetation bordering pristine marshes. Because most marshes in Narragansett Bay with developed borders are abutted by golf courses, farms, or housing developments, runoff on these marshes will be rich in fertilizers. Border development decreased soil salinity at the high marsh-terrestrial border and increased nitrogen availability into low-marsh habitats, likely because, without a woody vegetation border, nitrogen-rich freshwater runoff drains directly into the marsh rather than being intercepted and utilized by the woody vegetation (McClelland et al. 1997; McClelland & Valiela 1998). Decreased salinity in the high marsh likely facilitates initial seedling establishment of the low salt-tolerant *Phragmites* (Chambers et al. 1999, 2003) on marsh borders, and increased soil nitrogen availability throughout the marsh (Figs. 1 & 2, Bertness et al. 2002) likely precipitating its clonal expansion into marsh interior by shifting plant competition aboveground for light (Emery et al. 2001; Minchinton & Bertness 2003). The immediate effect of this human-facilitated invasion is a predictable shift in community composition (Fig. 5), a three-fold decrease in marsh plant richness (Fig. 6) and, we predict, eventual local extinction of all high-marsh plant species via competitive overgrowth by *Phragmites*, with only the more powerful aboveground competitor, *Spartina alterniflora*, remaining on the seaward edge of marshes, where porewater salinities are highest and *Phragmites* expansion rates greatly reduced.

Because we employed a correlational method to examine the effects of *Phragmites* invasion on marsh plant richness, our results could be confounded by a priori site conditions, such as disturbance, that had naturally reduced plant richness before invasion. However, given that (1) in almost all *Phragmites*-dominated high marshes surveyed, we frequently found skeletons of the natural high marsh dominant (*Iva frutescens*); (2) disturbances in these marshes occurred on a much smaller scale than *Phragmites* invasions (Bertness 1999), and (3) small-scale experiments have shown that *Phragmites* competitively excludes marsh plants in *undisturbed* assemblages under high-nutrient and low-salinity conditions (Minchinton & Bertness 2003), it is most likely that *Phragmites* invasion and not past, natural disturbance events resulted in observed differences in plant diversity.

Key to long-term maintenance of native biodiversity and ecosystem function is to understand how human habitat alteration interacts with introduced species to precipitate invasions (Kareiva 1996; Dukes & Mooney 1999). Our large-scale survey results, combined with extensive, small-scale experiments elucidating factors regulating marsh plant structure and competitive hierarchies (Bertness 1991a, 1991b; Bertness et al. 1992; Emery et al. 2002; Minchinton & Bertness 2003), provide a mechanistic

understanding of the role played by human development in precipitating invasion of an introduced species (cryptic invasion; Saltonstall 2002). Specifically, our results show that human destruction of terrestrial woody borders along salt marshes drives *Phragmites* invasion by increasing cross-ecosystem delivery of both freshwater and growth-limiting nitrogen.

Unlike studies showing that human habitat alteration increases invasion success within that community by decreasing competition from native plants (Dukes & Mooney 1999), our results show how habitat destruction of border ecosystems, with strong regulatory ties to forcing-factors in adjacent systems, drives invasion success by altering levels of key controlling factors—i.e., porewater salinity and nitrogen—to favor dominance by introduced species. Developing a better understanding of how habitat alteration interacts with species introductions to drive invasion success will then depend on developing predictive models (Hersperger & Forman 2003) of when and where habitat destruction will increase cross-ecosystem linkages (i.e., adjacency effects; Hersperger & Forman 2003) to facilitate invasion in communities not directly altered by human activities. Our results suggest that ecologists must think creatively when investigating mechanisms of invasion in a system and highlight to managers that the integrity of borders between ecosystems must be maintained for successful conservation of the target system.

Mechanisms of Plant Species Invasions in North American Salt Marshes

Over the past 25 years invasive species have dramatically changed North American salt marshes. On the Pacific coast, two cordgrass species, *Spartina alterniflora* from the east coast of North America (which has produced a vigorous hybrid with the native *Spartina foliosa*) and *Spartina anglica* from England, have been introduced. These plants, *S. anglica* and the *Spartina* hybrid, have extensively invaded West Coast mudflats and in the process have displaced not only the infaunal organisms dependent on soft-sediment habitats but also the migratory sea birds that forage in these communities (Sayce 1988; Ayers et al. 1999). The rapid success of invasive Atlantic cordgrasses on the Pacific coast is thought to be largely the result of Pacific marshes not having a native grass capable of living at low intertidal elevations.

By contrast, our research and Saltonstall's (2002) indicates that (1) invasion of *Phragmites* into salt marshes along the northeastern coast of the United States is probably the result of an interaction between introduction of a non-native genotype and habitat alteration by humans and (2) *Phragmites* is actively displacing established marsh plants and not invading an evolutionary void. We hypothesize that the non-native *Phragmites* genotype is

more productive under high nitrogen conditions (Saltonstall 2002), and that extensive removal of the woody buffer along New England coastlines and concomitant elevation of plant nitrogen availability has likely precipitated its invasion. Why *Phragmites* has not extensively invaded southeastern salt marshes (Saltonstall 2002) is an important conservation and ecological question that must be experimentally addressed. Potential reasons include the following: (1) there has not been enough time for the invasive genotype to expand southward from its invasion center in New England (Saltonstall 2002); (2) higher salt concentrations of southern high-marsh soils impede invasion by low salt-tolerant *Phragmites* even when shores are developed and nitrogen loading is high; (3) competition for light from taller and more robust southern high-marsh species under high nitrogen conditions (e.g., *Juncus roemerianus* [black needlerush]) is more intense; (4) development of shoreline may be less extensive in the south.

Implications for Salt Marsh Conservation

Restoration efforts aim to return ecosystems to some approximation of their structural and functional condition before disturbance occurred (Gore 1985; National Research Council 1992; Aronson et al. 1993; Calow 1998). Restoration goals must be ecologically sound but also logistically and economically feasible (Henry & Amoros 1995; Hobbs & Harris 2001). From a management perspective, our results (this study and previous experimental investigations) provide resource managers with a mechanistic understanding of *Phragmites* invasion, which gives them the tools to feasibly and economically limit *Phragmites* expansion. In spite of the perception that *Phragmites* invasion is a spatially large-scale phenomenon, our results reveal that it is controlled locally in salt marshes.

Conserving woody vegetation borders and minimizing disturbance around salt marshes are clearly the best ways to limit *Phragmites* expansion. Our understanding of the function of woody vegetation borders, however, also suggests that limiting the use of fertilizers around marshes and limiting freshwater runoff to marshes will limit the spread of *Phragmites*. For salt marshes already partially invaded, we suggest reestablishment of woody border and removal of established *Phragmites* via cutting and direct application of herbicide. Our study results and those of others (Minchinton & Bertness 2003) show that invasion rates for *Phragmites* in marshes with disturbed borders are approximately 1.5 m/year. If kept in check through a policy of yearly containment, we predict that *Phragmites* invasion can be locally halted and even eradicated. If managers ignore expansion into salt marshes over the next 20 years, however, our results indicate that salt marshes will go the way of nearby fresh tidal marshes, with dominance

of *Phragmites* and local extinction of native plant assemblages.

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