

Anthropogenic modification of New England salt marsh landscapes

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Salt marshes play a critical role in the ecology and geology of wave-protected shorelines in the Western Atlantic, but as many as 80% of the marshes that once occurred in New England have already been lost to human development. Here we present data that suggest that the remaining salt marshes in southern New England are being rapidly degraded by shoreline development and eutrophication. On the seaward border of these marshes, nitrogen eutrophication stimulated by local shoreline development is shifting the competitive balance among marsh plants by releasing plants from nutrient competition. This shift is leading to the displacement of natural high marsh plants by low marsh cordgrass. On the terrestrial border of these same marshes, shoreline development is also precipitating the invasion of the common reed, *Phragmites*, by means of nitrogen eutrophication caused by the removal of the woody vegetation buffer between terrestrial and salt marsh communities. As a consequence of these human impacts, traditional salt marsh plant communities and the plants and animals that are dependent on these habitats are being displaced by monocultures of weedy species.

Elucidating the causes and consequences of human modification of natural ecosystems is one of the most pressing ecological issues of our times (1). Although the direct impacts of habitat destruction are usually obvious, the indirect effects of many human activities, such as nitrogen loading, have been more difficult to detect, but are likely just as pervasive and critical to understand (2). In this paper, we show how a mechanistic understanding of the organization of salt marsh communities reveals that these ecologically and economically important habitats (3) are currently being dramatically degraded by localized shoreline development and human-induced nitrogen enrichment.

Salt marshes have attracted the attention of scientists because their simple structure makes them amenable for studying the mechanisms that generate ecosystem and community patterns (4–6). New England salt marsh plant communities have a striking vertical zonation (Fig. 1) that has long interested researchers (7, 8). The cordgrass *Spartina alterniflora* dominates low marsh elevations that are flooded daily by tides as a dense, clonally propagated monoculture. On the seaward border of the high marsh, cordgrass is replaced by marsh hay, *Spartina patens*, whereas the terrestrial border of the high marsh is dominated by a monoculture of the black rush, *Juncus gerardi*. A band of the shrub *Iva frutescens* typically demarcates the terrestrial border of these marshes. A number of less-abundant halophytic forbs commonly coexist with the high-marsh dominants (9).

This striking spatial segregation of plants in salt marshes is the product of both plant competition and the strong, physical gradients characteristic of these habitats. Physical stress on plants in salt marshes (e.g., water-logging and salinity) generally decreases with increasing tidal height (10, 11), and there is an inverse relationship between the competitive ability and stress tolerance of marsh plants (12, 13). Consequently, the low elevation borders of these marsh plants are set by physical stress, whereas the high elevation borders are set by plant competition. As a result, competitively superior plants dominate high marsh habitats, whereas stress-tolerant plants dominate low marsh

areas. We have recently shown, however, that the competitive hierarchy that has historically led to the zonation of these plants is controlled by below-ground competition for nutrients (14, 15). With fertilization, *S. alterniflora* competitively displaces *S. patens*, which in turn competitively displaces *J. gerardi* (15). This total reversal in competitive relations is predicted by plant competition theory (16), and is likely caused by high nutrient availability shifting competition from below-ground competition for nutrients when nitrogen is limiting, to above-ground competition for light when nitrogen is not limiting (15). When nutrients are limiting, plants with dense, below-ground biomass of nutrient-harvesting roots are competitively dominant, whereas when nutrients are in excess, plants that allocate more of their biomass to light-harvesting leaves prevail.

This recently elucidated mechanistic understanding of marsh plant communities allows us to predict how they will respond to increased nitrogen loading. Salt marshes are nitrogen limited systems (17, 18), and global nitrogen supplies have more than doubled over the last century since the invention of artificial fertilizers (2). Our findings lead us to predict that increased nitrogen levels will result in plants traditionally restricted by interspecific competition to lower marsh habitats invading higher marsh elevations (14, 15).

We examined the hypothesis that nitrogen supply is currently affecting plant species distributions across New England marsh landscapes by surveying 14 salt marshes in Narragansett Bay, Rhode Island.[†] We tested the specific hypothesis that at sites with high nitrogen availability, the cordgrass *S. alterniflora* is invading high marsh habitats, displacing the marsh hay, *S. patens*. To do this, we choose sites with a wide range of nutrient inputs, island marshes with little development and little potential for localized nutrient enrichment, and marshes adjacent to golf courses, farms, and housing developments where the potential for nutrient loading was high. At each site we established a tidal height benchmark by using a surveyor's level and corrected National Oceanographic and Atmospheric Administration tide predictions. We visited each site repeatedly (2–4 times), ground truthing the benchmarks to actual water levels and tidal data until our benchmarks were accurate to ± 2 cm. We then used these benchmarks to measure the elevation of 10 random locations on undisturbed *S. alterniflora*/*S. patens* borders at each site. [We chose this border because it is the most labile border in this community (4) and typically is the most discrete and

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[†]The salt marshes used were all located in middle to lower Bay locations, where they were routinely exposed to nearly full-strength seawater (25–30 parts per thousand) and had not been directly impacted by human disturbances such as diking or filling. The marshes used were Nag Creek West and East, Coggs Hall Cove, and North Point on Prudence Island, RI; Rumstick Point, Barrington Country Club, Nayatt Point, Rhode Island School of Design Marsh, and Smith's Cove in Barrington, RI; Colt State Park and North Farm in Bristol, RI; East Greenwich Country Club and Goddard Park in East Greenwich, RI; and Common Fence Point in Portsmouth, RI.

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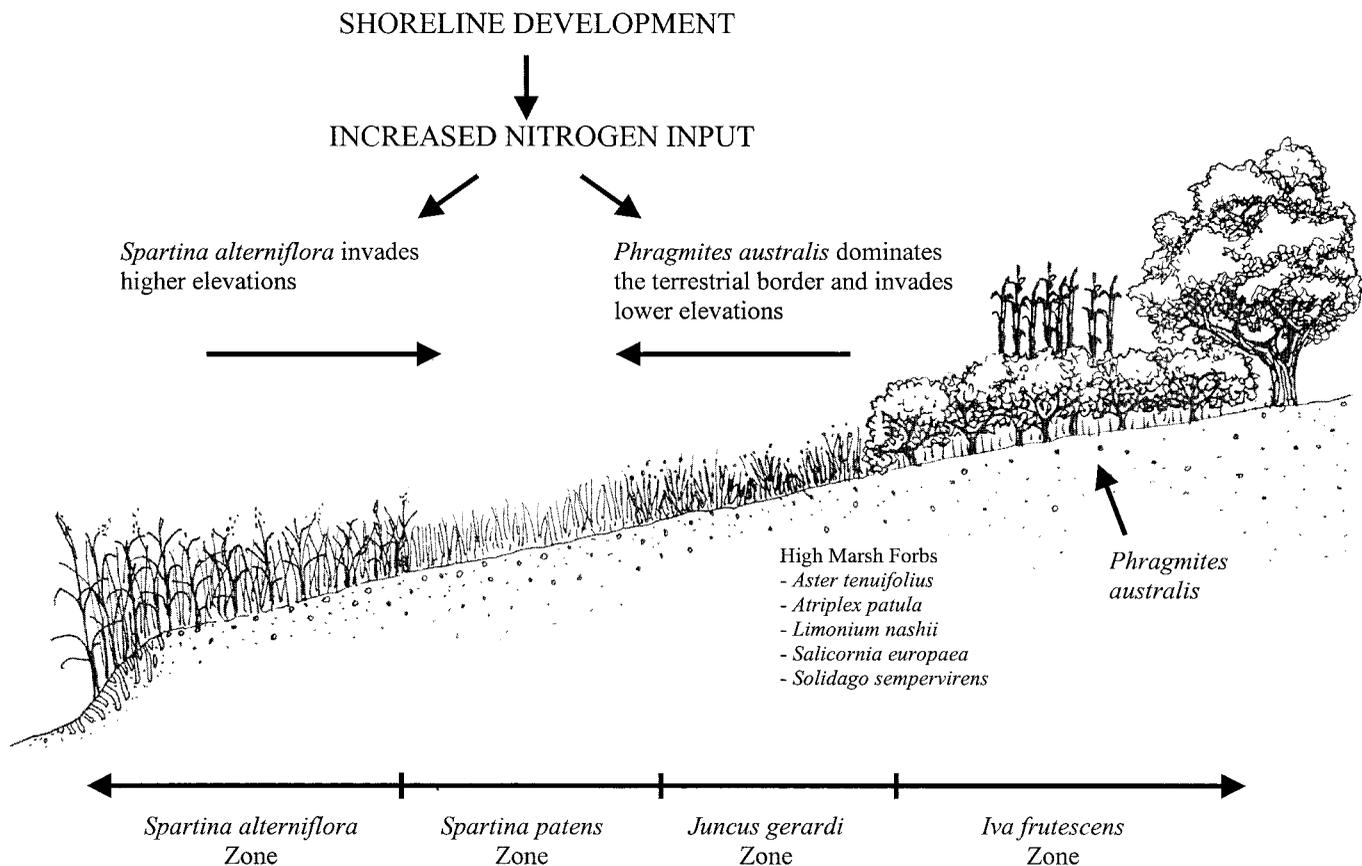


Fig. 1. Cross section of a southern New England salt marsh illustrating the major vegetation zones and general results of this paper.

unambiguous vegetation interface in New England salt marshes (13).]

Because cordgrass production is limited by nitrogen and responds to increased nitrogen availability with increased above-ground growth and elevated tissue nitrogen levels, we used total above-ground nitrogen in cordgrass tissue per unit area as a site-specific indicator of nitrogen availability (19). Cordgrass production is also influenced by elevation, so we estimated nitrogen availability (N in above-ground plant biomass) at a specific elevation at each site, the terrestrial border of the *S. alterniflora* zone. Because nitrogen availability decreases with increasing marsh elevation[†] and we were testing the prediction that nitrogen availability would be greatest at the highest *S. alterniflora*/*S. patens* borders, our measure of nitrogen availability among marshes is biased against our hypothesis and thus is a conservative estimate.[‡]

Total above-ground nitrogen showed a strong, positive relationship with the tidal elevation of the *S. alterniflora*/*S. patens* border (Fig. 2A). Nitrogen variation among marshes explained nearly 40% of the variation in the elevation of this border; borders with high nutrient levels were nearly half a meter higher than at those with the lowest total nutrients.

The alternative hypothesis that these results can be explained by site variation in physical variables can be rejected. Site-specific nitrogen availability was not significantly correlated with any of

the physicochemical factors that are widely believed to regulate plant nutrient availability in marshes (i.e., porewater ammonium and sulfide concentrations, salinity, redox potential, and tidal range; ref. 20).[§] Thus, the strong relationship observed among these sites between site-specific nitrogen availability and low/high marsh border height occurs independent of the prominent physical factors already known to influence cordgrass production.

What is responsible for the observed site variation in nitrogen availability? Because recent mechanistic studies have documented a strong positive relationship between shoreline development and the nitrogen eutrophication of adjacent near-shore waters (21, 22), we tested the hypothesis that our site-specific differences in nitrogen availability were caused by site differences in shoreline development. To quantify shoreline development, we took photographs of the terrestrial border of each marsh and quantified the length of the terrestrial border of each marsh that had human modification. We considered a border unmodified only if it was abutted by a naturally forested strip of

[§]To test whether site-specific N availability (N in above-ground plant biomass) was correlated with any of the physicochemical factors that are widely believed to regulate plant nutrient availability in marshes, we measured porewater ammonium (19, 20), redox potential (19, 20), salinity (19, 20), and S^{2-} concentrations (19, 20) at the low/high marsh border of all sites by using standard protocols. At each biomass sampling station ($n = 8$ for each marsh), one porewater lysimeter was placed in the substrate at a depth of 10 cm. All porewater variables were then measured in August. In all cases, there was no significant correlation between marsh-specific nitrogen availability and the measured physicochemical variable (independent variable = ammonium: $y = 0.9167x + 0.7282$, $r^2 = 0.023$, $P > 0.60$; independent variable = redox potential: $y = 0.0003x + 1.4015$, $r^2 = 0.0075$, $P > 0.70$; independent variable = salinity: $y = 0.0389x + 0.1853$, $r^2 = 0.065$, $P > 0.40$; independent variable = S^{2-} : $y = -9E-05x + 1.5405$, $r^2 = 0.0173$, $P > 0.60$). All sites were located within Narragansett Bay and experienced similar tidal ranges.

[†]We quantified variation in nitrogen availability at each site in August 2000. Above-ground cordgrass biomass was cut at ground level in 8 randomly located 0.25×0.25 m quadrats on the terrestrial border of the *S. alterniflora* zone at each site and then dried at 40°C and weighed. Plant tissue nitrogen concentrations were determined by using standard techniques (20). Total above-ground nitrogen for each quadrat was calculated by multiplying cordgrass biomass (g/m^2) times tissues nitrogen levels (%).

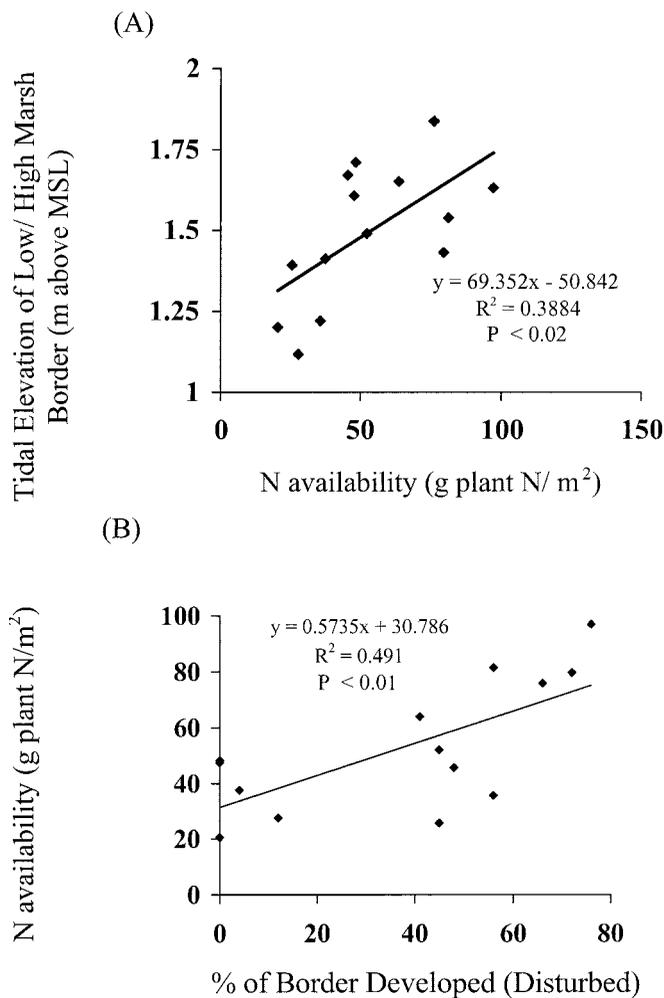


Fig. 2. Relationship between plant nitrogen availability and the tidal elevation of the *S. alterniflora*/*S. patens* border (A) and shoreline development (terrestrial border disturbance) and plant nitrogen availability (B) at 15 salt marshes in Narragansett Bay, RI. MSL, mean sea level.

woody vegetation >10 m wide. Marshes bordered by lawns, farms, roads, or any type of human modification were considered developed. Variation in shoreline development among our study sites explained 50% of the variation in nitrogen availability (Fig. 2B). These data reveal that localized near-shore human activities, rather than diffuse, nonpoint sources of nitrogen, are largely responsible for local increases in marsh nitrogen availability that trigger the expansion of cordgrass from its traditional low-marsh reaches into the high marsh.

Although these data reveal that the structure of New England marshes is being altered by an anthropogenic nitrogen-driven invasion of cordgrass on their seaward border, the terrestrial borders of these same marshes are also being threatened by an aggressive invasion of the reed *Phragmites australis*. This large (2–4 m tall), clonal reed has been a member of New England marshes for at least 10,000 years, but historically it was not a numerically dominant species (4). Over the past century, however, *Phragmites* has expanded to lower elevations and become a dominant species. This has been well studied in freshwater and brackish tidal wetlands in the North American middle Atlantic, where the spread of *Phragmites* at the expense of displacing other wetland plants has been suggested to be driven by human modification of wetlands (23, 24).

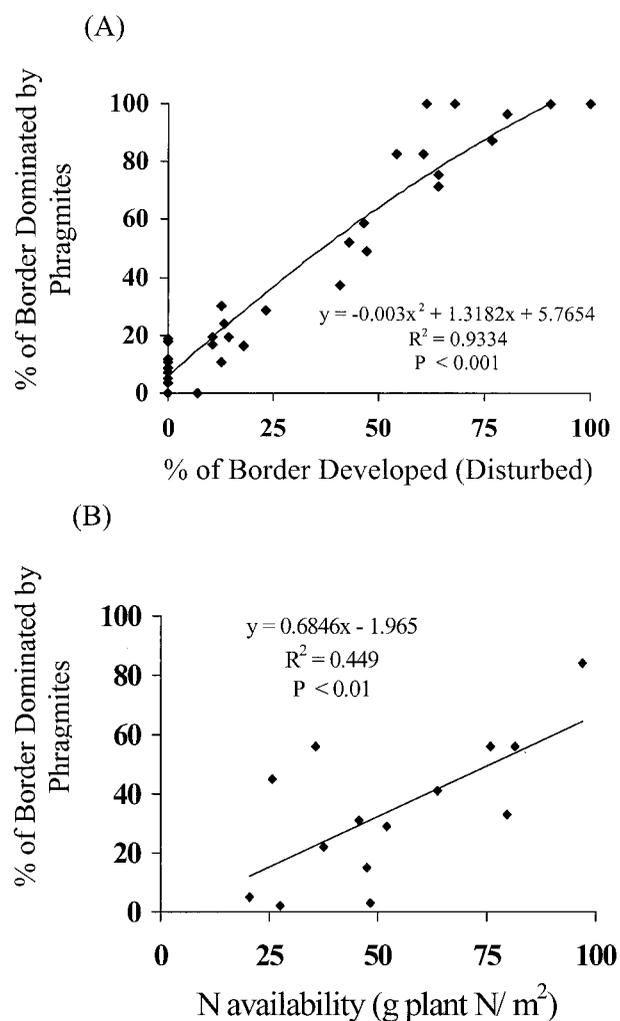


Fig. 3. Relationship between shoreline development (A) and plant nitrogen availability (B) and the dominance of the terrestrial border of Narragansett Bay salt marshes by dense stands of *P. australis*.

Until recently, *Phragmites* was thought to be limited from invading salt marshes by high soil salinities (23). Recent work in southern New England, however, has shown that through clonal integration *Phragmites* can invade marshes exposed to full-strength seawater (25). To test the hypothesis that shoreline development is stimulating the current expansion of *Phragmites* into New England salt marshes, we surveyed 30 marshes in Narragansett Bay exposed to full-strength seawater for *Phragmites* dominance and shoreline development.[†] Among sites, local shoreline development explains over 90% of the *Phragmites* expansion into the salt marshes of Narragansett Bay (Fig. 3A). Pristine salt marshes without developed shorelines typically have less than 15% of their terrestrial border dominated by *Phrag-*

[†]The surveyed marshes were all exposed to full strength seawater, 25–30 parts per thousand, and included the marshes used for the eutrophication/border elevation survey (see † footnote). In September 2000, we took photographs of 200–300 m (in 50-m sections) of the terrestrial border of each marsh. We analyzed these photographs by measuring the length of the shoreline at each site that had been invaded by *Phragmites* and the length of the terrestrial border of each marsh that had human modification. We scored borders as invaded by *Phragmites* only if *Phragmites* was the dominant feature of the border, and had displaced or was in the process of actively displacing typical high marsh vegetation. Borders where *Phragmites* was present, but in low densities mixed with other vegetation, were not considered invaded by *Phragmites*. Thus our operational definition of a *Phragmites*-dominated border was conservative.

mites. In contrast, marshes with more than 50% of their border developed had most of their terrestrial border invaded by *Phragmites*. Because *Phragmites* has a tall, dense above-ground canopy, it is a dominant competitor for light (23, 25), and nutrient enrichment associated with shoreline development may be responsible for giving *Phragmites* the competitive advantage over traditional high-marsh vegetation under high-nitrogen conditions. To determine how much of the strong influence of shoreline development on *Phragmites* invasion can be attributed to increasing nitrogen supplies, we examined the relationship between our site-specific estimate of nitrogen availability and *Phragmites* dominance at our 14 original study sites.[†] Among marsh variation in nitrogen availability explained 45% of site variation in the dominance of *Phragmites* (Fig. 3B).

Together, these results reveal that nitrogen eutrophication precipitated by shoreline development, acting at surprisingly local spatial scales, is driving the expansion of cordgrass and *Phragmites* across New England salt marshes. This expansion is leading to traditional New England salt marsh landscapes, including formerly dominant plants and numerous less abundant forbs, being displaced by simple, species-poor monocultures of

weedy species, reducing plant species richness 5-fold.[‡] These findings illustrate how a mechanistic understanding of natural communities can predict anthropogenic impacts on natural ecosystems and reveal that local shoreline management is critical for marsh conservation.

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[‡]Inspection of borders heavily invaded by *Phragmites* reveal that it was spreading at rates of 1–1.5 m/year and had already or was in the process of displacing established stands of *I. frutescens*, *J. gerardi*, and *S. patens*. Moreover, all of the forbs (*Atriplex patula*, *Salicornia europaea*, *Limonium nashii*, *Solidago sempervirens*, and *Aster tenuifolius*) that commonly live in high-marsh stands of *J. gerardi* or *S. patens* (9) are displaced by *Phragmites* once it has invaded the high marsh (23, 24). Thus, in heavily developed marshes dominated by only cordgrass and *Phragmites*, as predicted by our results, plant species richness would conservatively be estimated to drop from 10 common species to 2 common species.

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