

Coastal eutrophication as a driver of salt marsh loss

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Salt marshes are highly productive coastal wetlands that provide important ecosystem services such as storm protection for coastal cities, nutrient removal and carbon sequestration. Despite protective measures, however, worldwide losses of these ecosystems have accelerated in recent decades¹. Here we present data from a nine-year whole-ecosystem nutrient-enrichment experiment. Our study demonstrates that nutrient enrichment, a global problem for coastal ecosystems^{2–4}, can be a driver of salt marsh loss. We show that nutrient levels commonly associated with coastal eutrophication increased above-ground leaf biomass, decreased the dense, below-ground biomass of bank-stabilizing roots, and increased microbial decomposition of organic matter. Alterations in these key ecosystem properties reduced geomorphic stability, resulting in creek-bank collapse with significant areas of creek-bank marsh converted to unvegetated mud. This pattern of marsh loss parallels observations for anthropogenically nutrient-enriched marshes worldwide, with creek-edge and bay-edge marsh evolving into mudflats and wider creeks^{5–7}. Our work suggests that current nutrient loading rates to many coastal ecosystems have overwhelmed the capacity of marshes to remove nitrogen without deleterious effects. Projected increases in nitrogen flux to the coast, related to increased fertilizer use required to feed an expanding human population, may rapidly result in a coastal landscape with less marsh, which would reduce the capacity of coastal regions to provide important ecological and economic services.

An accelerated global nitrogen cycle^{1–3} has greatly increased the flow of reactive nitrogen (primarily as NO_3^-) from land to coastal marine ecosystems, causing harmful algal blooms, hypoxia and fisheries losses^{5,8}. Salt marshes occupy a critical interface between the land and the sea, where they provide important ecological and economic services, such as nutrient removal, storm protection for coastal cities and carbon sequestration, and habitats for numerous species of fish, birds and invertebrates. It is thought that salt marshes can protect coastal bays by removing land-derived nutrients^{9,10}, a conclusion based on measures of whole-system nutrient budgets^{11,12} and plot-level experiments in which added nutrients were transformed into greater above-ground plant production (primarily cordgrass *Spartina* spp.) or denitrified⁴. Globally between a quarter and half of the area of the world's tidal marshes has been lost, and although multiple factors (sea-level rise, development, loss of sediment supply) are known to contribute to marsh loss¹, in some locations the drivers remain unexplained. Understanding the mechanisms underlying the continued loss of this ecologically and economically important ecosystem is a global priority.

Here we present an ecosystem-level experimental approach to understanding how the intertwined responses of plant biomass allocation, microbial decomposition, and geomorphic stability to coastal nutrient enrichment may drive salt marsh loss. For nine years (2004–2012) we have enriched multiple whole-ecosystem marsh landscapes to nutrient levels that correspond to moderately-to-highly eutrophic waters by adding dissolved nutrients to flooding tidal water¹³. Approximately 50%–60% of the added NO_3^- was processed (assimilated or denitrified)

in the nutrient-enriched systems; the remainder was exported in ebbing tidal water¹². The large scale of this experiment, which included creeks, mudflats, tall-form smooth cordgrass (*Spartina alterniflora*) at the creek-channel edge and saltmeadow cordgrass (*S. patens*) in the high marsh, has revealed interactions that would not be apparent from plot-level experiments in individual habitats.

Nutrient enrichment may invoke a series of positive feedbacks by altering ecosystem processes that affect below-ground dynamics and creek-bank stability, leaving marshes more susceptible to the erosive forces of storms and sea-level rise and gravitational slumping. In less than a decade, a cascade of changes induced by nutrient enrichment resulted in loss of low marsh along the creek-bank edge (Fig. 1a–f) and a corresponding loss of ecosystem function. Smooth cordgrass along the creek-bank edge responded to nutrient enrichment with increased above-ground biomass expressed as heavier, taller shoots (Fig. 2a), lower structural compounds (decrease of about half in foliar lignin), and increased N content (Table 1), with response ratios comparable to plot-level nutrient-enrichment experiments^{4,14}. Increased plant height coupled with less structural tissue caused more extensive areas of smooth cordgrass to fall over (lodge)—a well-known response to over-fertilizing grasses¹⁵. Using permanent transects and high-precision global positioning system (GPS) mapping across the elevation gradient, we found no evidence (D.S.J., R.S.W. and L.A.D., manuscript in preparation) for the hypothesized shift in the up-elevation boundary between *S. alterniflora* and *S. patens* in response to nutrients¹⁵. In nutrient-enriched marshes, smooth cordgrass allocated less photosynthate to nutrient-gathering roots and storage rhizomes, resulting in a third less total below-ground biomass and a lower root:shoot ratio (Fig. 2b, c). Two smooth cordgrass growth attributes, a highly plastic above-ground/below-ground allocation¹⁶ and foliar uptake of NO_3^- (ref. 17), contribute to the reductions in total below-ground biomass observed in nutrient-enriched marshes.

The continuous availability of high NO_3^- in the water and more decomposable marsh grass detritus (due to higher N content and lower lignin) increased decomposition rates (Table 1). Whole-ecosystem nitrate removal was 40 times higher in the nutrient-enriched marsh and was primarily attributable to microbial use of the added NO_3^- to decompose organic matter¹². Potential denitrification—an indicator of anaerobic microbial decomposition using nitrate as an electron acceptor with the end product being N_2 gas—increased 1.7-fold in creek bank sediments, while litter respiration—a measure of aerobic microbial decomposition—almost doubled (1.9-fold). Denitrification is the highest energy-yielding decomposition process in anoxic marsh sediments and is favoured in the presence of high nitrate⁵. Accelerated decomposition increased the fraction of fine detrital organic matter, with 65% of the cores from nutrient-enriched creeks having a higher percentage of fine organic matter. As a result, the fine-grained, less-consolidated creek banks retained more water at low tide (Fig. 2d).

The combination of fewer roots and rhizomes, drag by tidal currents on lodged plants, more decomposed organic matter and higher water content undermines the structural integrity of the creek bank such that the effects of standard physical forces become enhanced. Loss of roots

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Reference

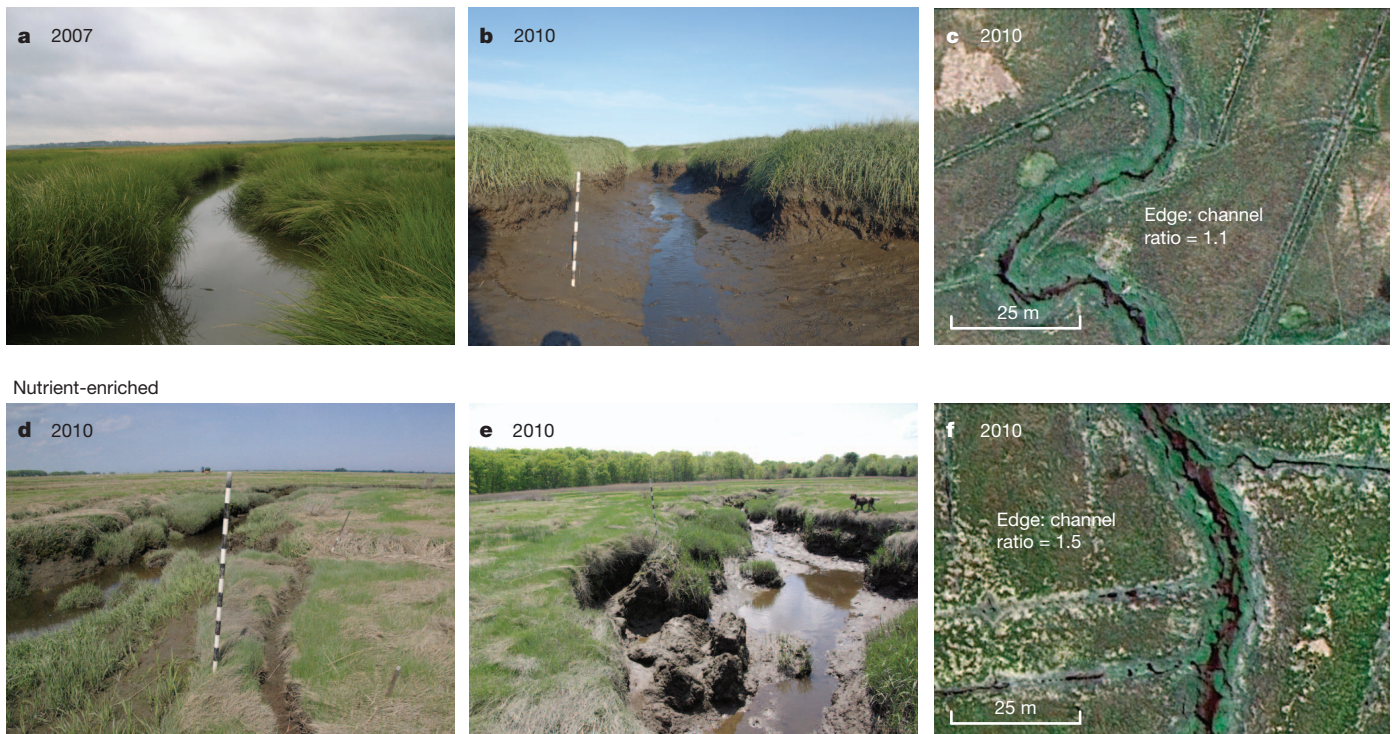


Figure 1 | Comparison photos of the marshes from the ecosystem nutrient-enrichment experiment. a–c, Reference. d–f, Nutrient-enriched. Photo credits: a, b, d and e, L.A.D.; c and f, Google Earth (19 June 2010 image, copyright 2012 Google).

and rhizomes (which bind sediments and provide drainage macropores) and loss of large organic matter particles (which form air pockets that can help drain creek banks) both contribute to increased creek-bank water content¹⁸. The higher pore water pressure in the bank reduces the frictional shear strength of the soil and increases the sliding force by adding weight to the creek bank¹⁹. At low water, the weight of the saturated bank exceeds the cohesive forces holding it together, the top of the bank cracks and creek-bank sections slide downward by gravitational slumping¹⁸. The structural failure of the creek edge implies that tidal forces, which under non-eutrophic conditions can be withstood, overcome the lowered cohesive strength of the nutrient-enriched bank habitat. Cracks developed over time with nutrient enrichment (Fig. 2d), and after seven years of enrichment, there were more (threefold) and longer (4.5-fold) fractures at the top of the bank parallel to the creek (Table 1) and large blocks of low marsh slumped into the creek (Fig. 2e). Without the buttressing edge of low marsh, high-marsh turf sheared from the sediment at the base of the active rooting layer creating ‘toupees’ that slid down slope into creek channels (Supplementary Fig. 1), tripling the area of bare mud over time (Table 1). The average width of the band of tall *S. alterniflora* along the creek edge decreased from approximately 3 m to approximately 2 m wide and became highly reticulated (Fig. 1c versus Fig. 1f; Fig. 2e) in nutrient-enriched systems. High-resolution measurements of channel cross-sections between the fifth and eighth years of enrichment indicate that the maximum erosion rate of creek banks was 0.2 m³ per year per metre of channel length. Loss of marsh along creek channel edges contrasts sharply with models that suggest that higher above-ground plant biomass in response to nutrients would in turn trap more sediment and stabilize marsh edges relative to sea-level rise²⁰. Slumping and cracking leads to a positive feedback, with increased infiltration by nutrient-rich water into sediments, which stimulate microbial decomposition of peat and further weakens sediments. As nutrient-enriched creek banks collapse and retreat, channels widen, increasing the unvegetated intertidal area at the expense of vegetated marsh.

The generality of our whole-ecosystem experiment is supported by extensive process work in small marsh fertilization plots and in anthropogenically nutrient-enriched estuaries. From Louisiana to Nova Scotia, nutrient enrichment has been shown consistently to increase above-ground plant biomass^{14,16}, mainly to decrease but sometimes not to change below-ground biomass^{16,21–24} and to increase decomposition^{22,25}. The decomposition response might be expected to be stronger in Northern marshes with a high percentage of organic matter, but because the organic content of our creek-bank marsh is in the middle of the range for Atlantic coast marshes (Methods), we expect our decomposition response is typical. The combination of root loss and increased decomposition can decrease soil strength²⁶. The development of cracks that lead to marsh loss has been approximately linear over the initial nine-years; however, this is a process that will play out over decades. Much uncertainty remains about whether this process of marsh loss is self-limiting, because creek banks may eventually be stabilized by the decrease in slope steepness from slumps, or self-reinforcing owing to fractures facilitating the seepage of nutrient-enriched water into the bank and stimulating decomposition. Other local environmental factors (such as tidal range, temperature and sediment deposition) may modify the effects of nutrients on ecosystem processes. Therefore, understanding the whole-ecosystem response to nutrient loading across broad environmental gradients and longer timescales requires more experimental ecosystem-level studies.

Many salt marshes may be at risk, because nutrient fluxes to the coast have increased worldwide, with the largest increases in N flux occurring at coastlines with large areas of intertidal marshland in the temperate zones of eastern North America, Europe and eastern China (Fig. 3a). A recent survey²⁷ documented 415 eutrophic coastal systems of concern worldwide, and found that only 13 systems were in recovery. There is evidence that salt-marsh loss in Europe⁵ and along the Atlantic coast of the United States^{6,7} may be driven, in part, by anthropogenic nutrient enrichment. Along Long Island Sound, Connecticut, USA, coincident with increased total N in runoff, several marshes lost 27%–54% of their low marsh (Fig. 3b), but very little high marsh, resulting

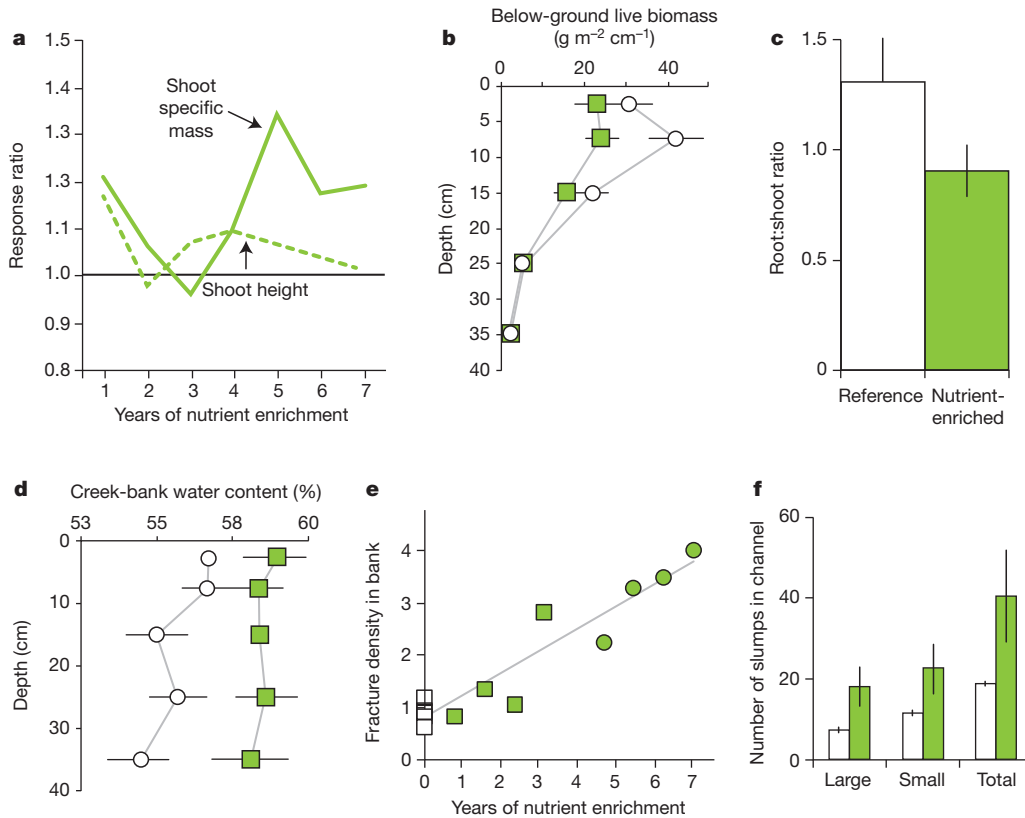


Figure 2 | Ecosystem attributes of reference and nutrient-enriched salt marshes after up to 7 years of nutrient enrichment. a–c, Plant attributes. a, Annual response ratio (nutrient-enriched/reference) for above-ground shoot attributes. Responses were comparable to other marsh nutrient-enrichment studies along the North American Atlantic coast and, as is typical in marshes, the strength was variable from year to year (green indicates average values of fertilized marshes greater than reference marshes, $n = 6$ per year; solid green line is shoot specific mass; dashed green line is shoot height; points above the response-ratio of 1.0 (horizontal black line) indicate increased growth in response to fertilization in that year). b, Below-ground root and rhizome biomass in reference (open circles) and nutrient-enriched (solid green squares)

marshes (2010; $n = 20$ per treatment). c, The above-ground to below-ground plant biomass ratio ($n = 20$ per treatment). d–f, Creek-bank geotechnical and geomorphic attributes. d, Vertical profile of percentage water content in reference (open circles) and nutrient-enriched (solid green squares) marsh creek-bank sediments with depth (2010; $n = 20$ per treatment). e, Fracture density in high marsh plotted against years of nutrient enrichment. Annual means are shown for reference (open squares), the start of enrichment in 2009 (solid squares) and the start of enrichment in 2004 (solid circles). f, Number of low-marsh creek-bank slumps in the channel in reference (open bars) and nutrient-enriched (solid green bars) marshes (2010; $n = 2$). Values are all mean \pm standard error.

Table 1 | Response of salt marsh ecosystem properties to chronic nutrient enrichment

Ecosystem properties	Response ratio	Mean (standard error)		P-value
		Reference	Nutrient	
Vascular plants				
Shoot height (cm)*	1.1	146 (3)	154 (2)	0.04
Shoot mass (g)*	1.2	6.18 (0.28)	7.18 (0.18)	0.01
Shoot specific mass (g cm^{-1})*	1.1	0.042 (0.002)	0.046 (0.001)	0.02
Lodging (%)		0 (0)	41 (2)	<0.001
Foliar N (%)*	1.1	1.43 (0.08)	1.54 (0.09)	<0.001
Lignin (%)***	0.6	30 (7.5)	17 (1.6)	0.07
Below-ground biomass (g m^{-2})	0.7	579 (60)	387 (64)	0.08
Creek geomorphology and sediment geotechnical properties				
Fracture density (number per 50 m of creek edge)**	3	1.1 (0.2)	3.3 (0.7)	<0.001
Amount of creek bank with fractures (%)**	4.5	6.6 (0.7)	29.5 (2.6)	<0.001
Fracture length (m)**	4.5	3.3 (0.4)	14.7 (1.7)	0.002
Exposed mud area (%)**	3	7.5 (1.7)	22.8 (4.6)	0.004
Total number of slumps in channel per creek	2.1	19.0 (1.0)	40.5 (11.5)	0.07
Fine organic matter (%)	1.7	16.1 (1.9)	26.7 (4.5)	0.17
Water content (%)	1.04	56.2 (0.4)	58.5 (0.1)	0.02
Channel width/depth ratio	1.3	3.02 (0.11)	3.86 (0.02)	<0.001
Microbial decomposition processes				
Plant litter respiration ($\text{CO}_2 \text{ g}^{-1} \text{ s}^{-1}$)	1.9	1.29 (0.12)	2.49 (0.33)	0.04
Potential denitrification in creekbank sediment ($\text{nmol g}^{-1} \text{ h}^{-1}$)***	1.7	40.7 (7.9)	70.8 (6.3)	0.01

A response ratio (nutrient-enrichment/reference) greater than one indicates a positive response to nutrient enrichment. P-values indicate the effect of nutrient enrichment on response variables; see 'Statistical summary' in Methods. Means (\pm s.e.m., standard error of the mean) were calculated from the data averaged by creek each year ($N = 2$ for nutrient-enriched and $N = 2$ for reference, except where noted). *Means (\pm s.e.m.) calculated from data averaged by creek and pooled across seven years of data. **Means (\pm s.e.m.) calculated from long-term nutrient-enriched and reference data averaged by creek and pooled across two years (2009 and 2010) of data. ***Data averaged across subplots within creeks ($N = 1$ per treatment).

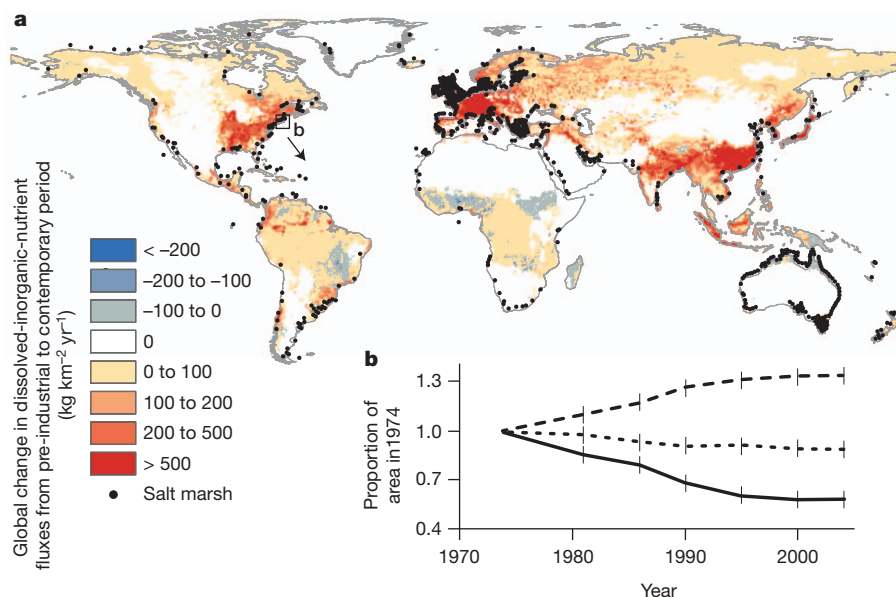


Figure 3 | The global relationship between nutrient loading and salt-marsh distribution and loss. **a**, The spatial distribution of the ramping up of anthropogenic nitrogen loading (dissolved inorganic nutrient (DIN) fluxes) from continents to coastal oceans from the pre-industrial period (1800s) to the contemporary period compared to global locations of salt marshes.

in wider creeks and increased mudflat area over the last three decades⁷. In Jamaica Bay, New York, USA, the rate of creek and open-bay-edge marsh loss in the 1990s was almost double that of the previous four decades ($134 \text{ km}^2 \text{ yr}^{-1}$ versus $72 \text{ km}^2 \text{ yr}^{-1}$) and the timing corresponds to an increase in total nitrogen loading (up to $80 \mu\text{M}$ open-bay total dissolved N) from sewage inputs⁶. Jamaica Bay marshes also have reduced root and rhizome mass and more degraded sediment²⁴, similar to our experimentally nutrient-enriched marshes.

The loss of creek-channel marsh banks is particularly significant because it is the most productive marsh zone and a critical area for regulating (C storage and N removal) and provisioning (fisheries) ecosystem services. Below-ground plant productivity disproportionately contributes to detrital organic matter in a wide variety of ecosystems²⁸, suggesting that the measured reduction in below-ground allocation may decrease the C storage potential of marshes. Marshes along creek channel edges are hotspots for denitrification with rates of N removal fivefold to tenfold higher than mudflats²⁹, suggesting that marsh conversion to mudflat decreases the ability of the coastal landscape to remove N from tidal waters. Considerable research shows the importance of the creek marsh edges in providing shelter and food to juvenile fish and shrimp^{30,31}, so the loss of marsh-edge habitat may ultimately negatively affect fisheries production.

Simultaneous increases in nutrient loading and in sea-level rise may result in synergistic marsh loss greater than the effects of either stressor alone. For example, the higher wave energy and flow velocities associated with sea level rise³² when combined with decreased creek-bank stability induced by nutrient enrichment may accelerate erosion and creek-bank loss. The drowning of high marsh due to sea-level rise and loss of creek-edge marsh due to eutrophication, especially when exacerbated by upland development that limits the ability of marshes to move inland, may lead to a coastal landscape with a dramatically reduced capacity to provide important ecological and economic services. N flux to the coastal zone has already increased at least tenfold over pre-industrial levels and is projected to continue to increase as we ramp up fertilizer use to produce food for the expanding human population over the next few decades^{1,27}. The potential deterioration of coastal marshes due to eutrophication adds an unanticipated dimension to the challenge of managing nitrogen while meeting food production in the twenty-first century.

b, Conversion of low marsh to mudflat in six nutrient-enriched Long Island Sound estuaries¹⁰ (see box in **a** indicating location of **b**). Substantial loss of low marsh (solid line), smaller loss of high marsh (dotted line) and increase in mudflat (dashed line) area over time correlates with increased nutrients from sewage treatment plants and runoff from land. Values are mean \pm standard error.

METHODS SUMMARY

We enriched primary tidal creeks in Plum Island Estuary, Massachusetts, USA, to nutrient levels corresponding to moderately-to-highly eutrophic coastal waters by adding N and P to the twice-daily flooding tides for nine years (2004–2012) during the growing season (about 120 days, 15 May–15 September), enriching about $30,000 \text{ m}^2$ of marsh per experimental primary creek system ($N = 2$ enrichment started in 2004, $N = 1$ started in 2009, reference $N = 2-6$)¹³. Initial measurements (1998–2003) found few differences among tidal creeks¹³, and other potential drivers did not differ among treatment marshes or do not occur in the Plum Island Estuary (Supplementary Information).

To detect changes in plant biomass allocation, the height, dry weight, and quality (percentage N, lignin content) of *Spartina alterniflora* above-ground shoots were measured and below-ground cores were analysed for live roots and rhizome biomass. Cores were also analysed for sediment geotechnical properties (water content, percentage organic matter and particle size). To determine changes in creek geomorphology, fractures in the vegetated marsh platform were enumerated along 250–300 m of creek banks and point-intercept transects indicated the presence or absence of vegetation in the creek bank. Creek-bank blocks that had slumped into tidal creeks were enumerated and creek width, depth and erosion measured over time using a 'total station' and high-precision GPS surveys. Microbial decomposition was measured as potential denitrification in the creek bank and microbial respiration of surface litter.

Full Methods and any associated references are available in the online version of the paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions L.A.D., D.S.J., R.S.W., B.J.P. & J.W.F. designed the experiment and participated in sampling and data analysis. S.F. participated in geomorphic and geotechnical evaluation. W.M.W. estimated global N loading to coastal saltmarshes. L.A.D. and D.S.J. wrote the initial manuscript. All authors contributed to and approved the manuscript.

Author Information The data reported in this paper are archived in the Plum Island PIE-LTER database. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to L.A.D. (ldeegan@mbl.edu).

METHODS

Site description. Our study was conducted in primary tidal creeks^{12,13,33,34} in the Plum Island Estuary in northeastern Massachusetts (42° 45' N; 70° 52' W). The Plum Island Estuary is a salt-marsh-dominated system that is currently unaffected by nutrient enrichment¹³. The system has twice-daily tides (mean tide range 2.9 m; 20–33 p.s.u.). Of the total estuarine area of 59.8 km², approximately 39.8 km² is vegetated wetlands, most of which is classic *Spartina* salt marsh^{35,36}. *Spartina alterniflora* (tall-form smooth cordgrass: 130–200 cm in height, approximately 1,100 g m⁻² yr⁻¹ above-ground production) forms a twice-daily flooded 2–3-m-wide low marsh band along tidal creek channels. *Spartina patens* (saltmeadow cordgrass: 20–50 cm in height, approximately 600 g m⁻² yr⁻¹ above-ground production) dominates the high marsh platform and is flooded by around 25% of high tides. On creek banks and bayfronts *S. alterniflora* occupies the top half of the mean tide range. *S. alterniflora* stems trap inorganic sediment, building steep creek channel banks of cohesive sediment (around 15% organic matter, with the mineral component composed of 58% silt, 25% clay and 16% sand), while below-ground roots and rhizomes (80% of root biomass in the top 20 cm, with some rhizomes over 1 m in depth) provide fibrous material that binds sediment and stabilizes the marsh edge^{37–39}. The percentage of organic C in the sediments of our creek-bank marshes (7% organic C; 15% organic matter) is in the middle of the range for salt marshes along the Atlantic and Gulf coasts of North America (~1–28% organic C, with most marshes in the 6–15% range)⁴⁰. *S. patens* contributes to marsh elevation principally by below-ground biomass (80% of roots and rhizomes are in the top 10 cm) accumulation in the form of peat.

Nutrient-enrichment experiment. Our experiment differs from others in four important ways. (1) Nitrogen was added as nitrate (NO₃⁻), the form that dominates land-derived N, contributing to coastal eutrophication and that is used directly as an electron acceptor in decomposition processes. (2) Nutrients were added directly to flooding tidal water to mimic the most important way in which anthropogenic nutrient loading is delivered to tidal marshes. Dissolved nutrients carried in water will interact and reach parts of the ecosystem differently from dry fertilizer. Previous plot-level salt-marsh nutrient-enrichment studies⁴¹ used dry fertilizer (typically urea or NH₄NO₃) sprinkled approximately bi-weekly to monthly on the surface of small plots (typically <5 m²) and were generally not conducted in tall, creek-bank *S. alterniflora* environments. Tidal water is the primary vector for N delivery to coastal marshes, suggesting that if mode (dissolved in water versus dry surface application) and type of N (NO₃⁻ versus NH₄⁺) are important in determining ecosystem response to nutrient enrichment, previous experiments may not be sufficient for determining how salt marshes respond to coastal nutrient enrichment. (3) We conducted a long-term (nutrient enrichment began in 2004) ecosystem manipulation experiment in which marsh landscapes were nutrient-enriched to levels corresponding to moderate to highly eutrophic coastal waters^{42–44}. Our NO₃⁻ enrichment target of 70–100 µM NO₃⁻ (added as NaNO₃) was 15 times the Plum Island background (<5 µM NO₃⁻) and the PO₄⁻ (added as NaH₂PO₄) target of 5–7 µM was 5 times the background (~1 µM PO₄³⁻). This was approximately a 15:1 N:P ratio in flooding creek water. (4) We conducted an ecosystem-level experiment consisting of experimental marsh units ($n = 6$; 3 reference and 3 nutrient-enriched) comprised of first-order creeks (about 300 m long and 15 m wide at the mouth, tapering to 2 m near terminus) and about 30,000 m² of cordgrass marsh area, thus allowing us to examine interacting habitats in the marsh ecosystem (creek channels, mudflats, creek-bank low marsh, and high marsh) and examine the response of plants, animals, biogeochemical processes and landscape-level geomorphic processes. Other factors did not differ among treatment creeks (Supplementary Information). Analysis of baseline characteristics before experimental manipulation (1998–2003) found little difference among the experimental marsh systems¹³. The primary comparisons are among two long-term (7 years by the end of 2010) nutrient-enriched (N1, N2) marshes and two reference (R1, R2) marshes that have been intensively monitored. To provide a time series of geomorphic change, we include data from a third nutrient-enrichment marsh (N3) that was started in 2009.

Measurements. This is a multi-year nutrient enrichment experiment, and not all response variables reported here were measured in each year. Some responses to enrichment were unanticipated (for example, rapid geomorphic changes) and so measurements were not taken before manipulation and sometimes only a single season of data is available. The nature of the different data sets with different time series of collections necessitated various statistical analyses (detailed below).

Above-ground plant responses. Above-ground measurements of creek-bank *S. alterniflora* were taken in creeks R1, R2 and N1, N2 in years 1–7 of nutrient enrichment. Individual plant shoot length (cm), shoot mass (g dry weight) and shoot-specific mass (g dry weight cm⁻¹) of creek-bank *S. alterniflora* were measured at the end of the growing season (mid-August) on individual shoots (18–25) at three sites within each creek ($n = 54$ –75 shoots per treatment creek per year). Each shoot was individually washed to remove sediments, measured for length,

dried at 80 °C to a constant mass and weighed. Leaf tissue from 3–5 leaves from each site was ground and analysed for percentage nitrogen using a PerkinElmer 2400 Series II CHNS/O analyser ($n = 4$ –8 per creek per year).

In year 5 of nutrient enrichment, lignin (as a percentage of the ash-free organic content) was determined on composite samples of 3–5 shoots from three sites within creeks R1 and N1 as acid-insoluble fractions using a two-stage digestion in sulphuric acid⁴⁵.

Plant lodging was surveyed at the end of the season after peak production in N1, N2, R1, R2 and four additional reference creeks in nutrient treatment year 4 ($N = 2$ for nutrient enrichment and $N = 6$ for reference). Surveys were completed on 10-m sections every 50 m from the 0-m mark to 300 m landward. Each section classified into a lodging class (0–5, 5–15, 25–50 and >50% of plants in the area lodged) for a sampling effort of $n = 16$ –26 sections per creek.

Below-ground responses. Below-ground biomass, organic matter and water content were determined by coring ($n = 10$ per creek, 10 cm diameter, taken to a depth of about 0.5 m; creeks R1, R2, N1, N2) in treatment year 7 (2010). Cores were sliced into sections (0–5, 5–10, 10–20, 20–30, 30–40 cm), sub-samples were taken for determination of percentage water (a small syringe core in each section), and the remaining material was separated by sieving into two size classes of dead organic matter (large >3 mm; fine <3 mm and >1 mm) and live below-ground biomass (roots and rhizomes). Sediment geotechnical properties (percentage water was determined as mass loss after drying a known volume of sediment at 105 °C for 24 h; percentage fine organic matter was taken to be detritus greater than 1 mm but less than 3 mm in size) were determined on cores taken for below-ground plant biomass. For statistical analysis (see 'Statistical Summary' below), we focused on the top 20 cm of the cores.

Microbial decomposition processes. Total microbial production in surficial sediments was 54% higher⁴⁶ (years 1 and 2) and potential denitrification on the high *S. patens* marsh was higher⁴⁷ (year 3) than in the reference systems. To determine whether microbial denitrification was also increased in creek banks, potential denitrification⁴⁸ was measured on sediment slurries—at the surface (0–5 cm) and deep (5–10 cm)—from creek-bank cores from three sites in creeks R1 and N1 in year 5 of nutrient enrichment ($n = 3$ per depth per creek).

To determine whether plant litter decomposition was accelerated, in year 7 plant litter respiration was measured. Respiration was measured from decomposing litter from litterbags (15 g dry weight of *S. patens*; 1 mm mesh size) placed flush on the high-marsh (*S. patens*) surface in nutrient enrichment (N1, N2) and reference (R1, R2) creeks. Nutrient enrichment stimulated detritivore snail densities³⁴ and therefore to account for the effect of detritivore density on decomposition, litterbags were manipulated to have snail densities of 0, 1, 2, 4 or 8 times the reference creek densities ($n = 5$ –8 litterbags per creek). After 5 weeks, microbial respiration (CO₂ g⁻¹ s⁻¹) of 2–3 g of litter from the litterbags was measured using a LI-6200 Portable Photosynthesis System.

Creek-bank fracture density and vegetation loss. These measurements were taken during the growing season in creeks R1, R2 and N1, N2 in years 6 and 7 of nutrient enrichment. Fractures, defined as a visible break in the high marsh (*S. patens*-dominated) turf that parallels the creek channel (Supplementary Fig. 1) within 3 m of the *S. alterniflora*/*S. patens* border were measured early in the growing season before cordgrass growth obscured these features. Both sides of each creek were sampled for fractures in contiguous 50-m segments from the 0-m mark to 200-m landward. The number of fractures and their characteristics (length, width and depth of fracture) were recorded within each segment. In these same segments, percentage exposed sediment (mud) area was determined by point-intercept transects in the middle of the growing season, when the grass canopy was fully developed, at 1-m increments. The soil surface 1-m perpendicular and creekward of the *S. alterniflora*/*S. patens* border was scored as 'vegetated' (with *S. alterniflora* culms within a 30-cm-diameter circle of the point) or as 'bare mud' (without *S. alterniflora*). The fraction of points unvegetated within each 50-m segment was considered a single observation. For fracture density, fracture length, percentage fractured and percentage exposed mud, each 50-m segment (4 per channel side, 2 sides) was considered an individual observation, thus providing $n = 8$ observations per creek per year. This was also done for the third enriched and reference creeks (R3, N3) in years 1–4 of enrichment.

Creek-bank and channel structure. High-resolution total station surveys of reference (R1, R2) and nutrient-enriched creek channels (N1, N2) and banks were performed in years 5 (2008) and 8 (2011) of the nutrient-enrichment experiment. We initially measured 43 cross-sections in enriched creeks and 38 in the reference channels, with 10–20 points per cross-section, depending on the morphological complexity of the cross-section. Twenty-six cross-sections in the nutrient-enriched creek channels and 27 in the reference channels were reoccupied after three years, whereas in the remaining cross-sections the control poles were lost. Erosion was computed for each cross-section as the areal difference between the year 5 and year 8 surveys.

In year 7 of nutrient enrichment slumped sections of creek bank were enumerated in creek channels (R1, R2 and N1, N2). At low tide, large and small slumped sections of creek bank were enumerated in 50-m reaches starting from the 0-m mark up to 200–250 m. Large sections were defined as peat blocks that were separated away from the low marsh area by at least 0.25 m horizontally and at least 0.25 m lower than the mean elevation of the low marsh. Large peat blocks were at least 1 m either in height, length or width, with small blocks being at least 0.25 m in height. Height was defined as the distance from the bottom of the peat block to the highest point of the block. Ninety per cent of the large peat blocks had live *S. alterniflora* shoots and were 1.1 m wide and 2.1 m long on average. Small creek-bank sections were defined as low-marsh peat chunks that were <1 m in height, width and length, but at least 0.25 m in at least one of these dimensions. Small slumps were generally unvegetated, had visibly eroded perimeters and were found in the deepest part of the channel. The total count of slumps per creek was considered a sample and thus within treatment area sampling replication was $n = 1$ per creek.

Global nutrient loading to salt marshes. We used an existing global river network N removal model^{49,50} to estimate global increase in N loading to coastal oceans from the pre-industrial period (1800s) to the contemporary period (2000s) compared to the locations of salt marshes⁵¹.

Statistical summary. Analyses were performed on data primarily from the long-term nutrient-enrichment creeks and the paired reference creeks. Data collection from creeks often entailed sampling several subplots within experimental creeks (see 'Measurements' section above). Except where noted, data were averaged across subplots within each creek before analysis⁵² and statistical analyses were performed at the creek level (nutrient enrichment $n = 2$, reference $n = 2$). All data were checked for assumptions of normality and homoscedasticity and transformed to meet assumptions⁵³. The large spatial scale of the experiment necessitated low replication, which can reduce statistical power, so results were considered significant at $\alpha \leq 0.10$, as is typical in a complex large-scale ecosystem experiment where background variability is generally high and replication low^{54–57}. Our results, however, are robust, because 13 out of 17 tests were significant at $\alpha \leq 0.05$ despite low replication (Table 1). Statistical analyses were performed in R (version 2.15.0).

Repeated measures analysis of variance with between-subject factors (nutrient enrichment) were performed for response variables for which 7 years of data were available: plant shoot height, shoot mass, shoot specific weight (natural $\log X + 1$ transformation), and percentage foliar nitrogen (arcsine-squareroot transformation).

Using 'space for time' substitution, linear regression models were used to analyse data for fracture density (natural $\log X + 1$ transformation), fracture length (natural $\log X + 1$ transformation), percentage of creek bank with fractures (arcsine-squareroot transformation), and percentage non-vegetated exposed mud area (arcsine-squareroot transformation) against the number of years the creek had received nutrient enrichment. Data for fracture density was collected in 2009–2012 and analysis was at the creek level, thus $n = 24$: for year 0, $n = 3$ per year (R1, R2, R3 in 2009–2012); for years 1–4, $n = 1$ per year (N3 in 2009–2012); and for years 6–9, $n = 2$ per year (N1, N2 in 2009–2012). Data for other variables was collected in 2009 and 2010 and analysis was at the creek level, thus $n = 10$: for year 0, $n = 4$ (two years of data from R1, R2); for year 1, $n = 1$ (N3 in 2009); for year 2, $n = 1$ (N3 in 2010); for year 6, $n = 2$ (N1, N2 in 2009); and for year 7, $n = 2$ (N1, N2 in 2010).

One tailed t -tests were performed on the following response variables: percentage water content (arcsine-squareroot transformation), live below-ground biomass, percentage fine organic matter (arcsine-squareroot transformation), slumps per creek ($\log X + 1$ transformation), lodging (percentage of plants lodged; arcsine-squareroot transformation), potential denitrification and percent foliar lignin (arcsine-squareroot transformation). For lodging, t -tests were performed on the percentage of plots within a creek that were scored with >50% plants lodged. For potential denitrification, initial statistical analysis indicated no difference between depths, so data from different depths were pooled in the final analysis ($n = 6$ per creek). Because potential denitrification and percentage foliar lignin were taken only from one creek per treatment (R1 and N1), data were analysed with the subplots as the experimental units. These process measurements

are used as supporting evidence, but cannot be used to extrapolate the results to a wider population of systems because there was no treatment replication at the creek level.

Analysis of covariance was performed on plant litter respiration and channel width/depth ratio. In these analyses the factor was nutrient level—reference ($n = 2$) and nutrient enrichment ($n = 2$). The covariate in the analysis of plant litter respiration was the number of snails in the litterbags. The covariate in the analysis of the channel width/depth ratio was the distance upstream from the beginning of the treatment area (designated as 0 m; a spatial covariate). In both analyses of covariance, the slopes were similar, but the intercepts were different, indicating a difference between treatments at the zero covariate level.

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