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Changing Salt Marsh Vegetation: Implications For Denitrification

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Changing Salt Marsh Vegetation: Implications for Denitrification

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Changing Salt Marsh Vegetation: Implications for Denitrification

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ABSTRACT

Salt marsh vegetation zones are good indicators of soil conditions and will shift in response to large-scale changes to their environment such as sea-level rise and restoration activities. The goal of our study was to characterize the relationship between soil denitrification potential and salt marsh vegetation zones in tidally restored and unrestricted coastal marshes, and to use vegetation zones to predict how sea-level rise may influence landscape-scale denitrification. We conducted denitrification enzyme activity assays (DEA) on sediment collected from 20 salt marshes across Connecticut and found denitrification potential to be 7 and 17 times lower in short-form *Spartina alterniflora* zones compared to zones dominated by *Spartina patens* and *Phragmites australis* respectively. Denitrification potential was not significantly different between tidally restored and unrestricted coastal marshes, thus landscape-scale changes in denitrification after tidal restoration are likely to be associated with shifts in vegetation rather than differences driven by restoration status. Based on sea-level rise model projections, the replacement of *S. patens* by short-form *S. alterniflora* is expected to be widespread across Connecticut, decreasing statewide potential denitrification from the low-to-high marsh transitional zone by at least 500 kg-N/ hr by 2085. Our results suggest that vegetation zones can serve as predictors of landscape-scale denitrification rates and their response to rapid changes occurring in salt marshes.

INTRODUCTION

Coastal salt marshes globally are undergoing unprecedented levels of change, driven heavily by their vulnerability to accelerating sea-level rise (SLR) in tandem with local disturbances (Kirwan and Megonigal 2013). The effects of SLR have been particularly pronounced on the northeastern extent of the North American Atlantic coast, where SLR three to four times the global average is outpacing sediment accretion rates in many salt marshes (Sallenger et al. 2012; Crosby et al. 2016; Watson et al. 2017). The resulting increase in sea-level and tidal range has led to shifts in salt marsh vegetation communities (Smith 2014; Valiela et al. 2018), which in turn are expected to alter the provision of various salt marsh ecosystem services (Craft et al. 2009; Barbier et al. 2011). Among the affected ecosystem services, there is a need to understand how coastal nitrogen cycling will be influenced by SLR and the associated shifts in salt marsh vegetation.

Denitrification, the microbial reduction of nitrate to dinitrogen gas, is one of the major pathways of nitrogen removal in salt marshes and plays an important role in intercepting land-derived nitrogen loads (White and Howes 1994; Velinsky et al. 2017). Given its role in making salt marshes substantial nitrogen sinks, denitrification is a highly-valued ecosystem service that helps prevent eutrophication in coastal waters (Valiela and Cole 2002; Barbier et al. 2011). However, denitrification is difficult to quantify due its high spatial and temporal variation (Groffman et al. 1999), which is further compounded in salt marshes where tidal influence interacts with topography to create dynamic and heterogeneous soil conditions across the landscape (Bertness 1991; Pennings and Callaway 1992). For our understanding of coastal nitrogen cycling to keep pace with rapidly changing salt marshes, there is a need to develop methods for spatially scaling salt marsh denitrification. In that regard, salt marsh vegetation zones that reflect the hydrologic mosaic of salt marshes are strong candidates for serving as denitrification indicators.

Salt marsh vegetation communities are distributed along hydrological and salinity gradients, forming vertically stratified zones determined by elevation and tidal flooding regimes (Bertness 1991). In addition to closely tracking even small changes in elevation and hydrology, vegetation often also reinforces differential conditions through plant-soil feedbacks like rhizosphere oxidation and microbial symbioses (Howes et al. 1981; Burke et al. 2002). Given this close relationship, salt marsh vegetation zones have been shown to be good indicators of soil characteristics and functions (Wigand et al. 2004; Moffett and Gorelick 2016; Yang and Silver 2016). With the accelerating pace of global coastal change, extending this vegetation-centric understanding to denitrification could help overcome its high spatial variation and improve denitrification scaling in salt marshes.

While denitrification in salt marshes has been measured widely and frequently (Caffrey et al. 2007), explicit comparisons of denitrification rates across vegetation zones are relatively limited. A meta-analysis by Alldred and Baines (2016) suggested that dominant vegetation can be a good indicator of denitrification across wetland types and measurement methods. Indeed, evidence from New England salt marshes supports the hypothesis that denitrification differs among vegetation zones (Kaplan et al. 1979; Windham and Meyerson 2003; Wigand et al. 2004; Dollhopf et al. 2005). However, these studies quantified different combinations of zones, usually at single sites, and used different methods to measure denitrification. Therefore, a generalized understanding of the relationship between vegetation zones and denitrification will require not only a wide geographic sampling distribution, but also explicit comparisons of multiple zones using similar measurement protocols.

To characterize the relationship between vegetation zones and denitrification, we conducted a field survey spanning 20 salt marshes across the Connecticut coast. We compared the denitrification potential of three important vegetation zones in southern New England salt marshes: short-form *Spartina alterniflora* (smooth cordgrass), *Spartina patens* (saltmeadow cordgrass), and *Phragmites australis* (common reed). We focused on these specific vegetation zones not only for representativeness of their respective habitats, but also because they are among the key vegetation zones involved in changes to New England salt marshes (Warren and Niering 1993; Donnelly and Bertness 2001; Smith 2013, 2014).

In southern New England salt marshes, monotypic stands of *S. alterniflora* have historically dominated the low marsh, with its tall-form flanking tidal creeks and its short-form extending into parts of the high marsh (Niering and Warren 1980, Nixon 1982, Bertness 1991). Meanwhile, *S. patens* is one of the most common plant species in the less frequently-flooded high marsh (Niering and Warren 1980; Nixon 1982; Bertness 1991). In recent decades, large areas of *S. patens* have been replaced by short-form *S. alterniflora* as a result of SLR (Warren and Niering 1993; Smith 2014; Raposa et al. 2017). Despite this pattern of replacement being widely observed, its effects on salt marsh denitrification rates have not been characterized.

On the landward side of the salt marsh, the brackish marsh-upland boundary has experienced widespread invasion of *P. australis*, facilitated by coastal land development and man-made tidal restrictions (Roman et al. 1984; Minchinton and Bertness 2003; Silliman and Bertness 2004). Invasion of *P. australis* has been associated with dramatic losses of habitat for a multitude of wetland plant and animal species, making it a key target for restoration and management (Keller 2000; Warren et al. 2001; Elphick et al. 2015). In New England salt marshes, tidal flow restoration, the removal or modification of structural tidal restrictions like roads or dikes, has been a common method to remove *P. australis* and restore native salt marsh vegetation (Smith and Warren 2012). However, *P. australis*-dominated soils have been associated with higher denitrification potential than native or recently-restored soils in brackish and fresh tidal wetlands, representing a possible tradeoff during restoration (Findlay et al. 2003; Windham and Meyerson 2003; Alldred et al. 2016). To address this possible effect of tidal restoration on soil denitrification, our study sought to characterize the difference in soil denitrification between tidally restored and unrestricted salt marshes.

Our goal was to capture the range of potential denitrification rates across the salt marsh vegetation continuum in tidally restored and unrestricted salt marshes. We explicitly designed our survey with a broad geographic distribution (n = 20 coastal salt marshes across approx. 130 km of coastline) to maximize the generalizability of our findings. Our specific objectives were to compare potential denitrification rates between (1) dominant salt marsh vegetation zones and (2) tidally restored and unrestricted salt marshes, and (3) estimate how SLR may influence potential denitrification rates at the landscape scale. To assess the effect of SLR-driven replacement of high marsh with low marsh on denitrification rates on the landscape-scale, we scaled our measured rates using a published Connecticut-specific application of the Sea-level Affecting Marshes Model (SLAMM; Clough et al. 2016).

METHODS

Site selection

To obtain soil samples from each vegetation zone, we conducted a field survey across 20 salt marshes along the Connecticut (USA) coast during Aug 10-23, 2017 (Figure 1). All sites were chosen based on the presence of all three vegetation zones of interest (*S. alterniflora*, *S. patens*, *P. australis*) as indicated by published maps (Correll et al. 2019) and confirmed by ground-truthing. Our sites were categorized into 10 tidally-restored sites and 10 unrestricted sites. We defined 'unrestricted sites' as those that have not been subject to tidal restriction or subsequent tidal flow restoration throughout their documented history. 'Tidally restored sites' are salt marshes that have received tidal flow restoration at some point in the last 50 years through the removal or modification of tidally-restricting structures like tidal gates, culverts, etc.

At each site, we selected areas within each vegetation zone on the condition that they were within 100 m of the same tidal creek to increase the likelihood that they received a similar source, timing, and amplitude of flooding. To improve representativeness of our sampling, we set up three plots within each vegetation zone, each at least 5 m from the others (Figure 2). All biomass and soil samples collected from each zone were aggregated from the three plots.

Sample collection and processing

At each plot, we set up 1 x 1 m quadrats to estimate percent live plant and litter cover. Each quadrat was divided into 16 subplots (each 25 x 25 cm), from which we randomly selected one where we clipped live aboveground plant biomass at the sediment surface. In the same subplot, we collected soil cores down to 10 cm depth (196 cm^2 volume) to quantify belowground plant biomass. The cores were subsequently washed through a 2 mm sieve, dried at 65 °C for 72 hours and then weighed. In two other randomly selected subplots, we collected two additional soil cores to use for bulk density and soil chemistry analyses. All soil samples used for soil chemistry were transported to the lab on ice, sieved through a 2 mm sieve, then stored at 4 °C until analysis. Bulk density and volumetric soil moisture content were determined by drying soil cores and sieved sediment respectively at 105 °C.

Denitrification potential

We used denitrification enzyme activity assays (DEA) with the acetylene inhibition method to quantify the denitrification potential of our soils (Groffman et al. 1999). In 125 ml glass flasks with air-tight seals, we mixed 5 g of homogenized soil with 10 ml of DEA solution containing chloramphenicol, excess carbon, and excess nitrogen (3.6 mg KNO_3, 2.5 mg glucose, and 0.625 mg chloramphenicol per g wet soil). Prior to incubation, we flushed each flask with N_2 gas to induce anoxic conditions, then replaced 10 ml of headspace gas with acetylene gas to inhibit the reduction of N_2O to N_2. By removing carbon and nitrogen limitations and inducing anoxic conditions, the procedure quantified the denitrification potential of our soils, with all the gaseous products expressed exclusively as N_2O. Discrete gas samples were drawn at four time points: approximately 0, 30, 60, and 90 minutes after incubations began. We measured the N_2O concentration of the gas samples using a Clarus 580 gas chromatograph with an electron capture detector (PerkinElmer, Shelton, CT). Samples were delivered with a TurboMatrix 40 Trap Headspace Autosampler (PerkinElmer, Shelton, CT).

We calculated potential denitrification rates as the linear rate of accumulated headspace N_2O-N over time per g dry soil. Minimum detectable concentration difference (MDCD) was determined following Yates et al. (2006) and potential denitrification rates were considered above detection only if at least two time points had higher detectable concentrations than the concentration at time zero. Four potential denitrification rates were below detection and were removed from analyses. When N_2O accumulation saturated the headspace (i.e., $R^2 < 0.90$ of the linear regression of N_2O concentration over time for all four time points), we calculated potential denitrification rates from the time of linear accumulation by excluding the 90 and/or 60 minute time points.

Rates of N_2O accumulation were converted to rates of denitrification potential per m^2 using bulk density and belowground biomass data. We calculated the mass of dry soil per soil core by subtracting dried belowground biomass from dried soil cores, which we then multiplied by denitrification potential per g dry soil. Given that each soil core had an area of 19.6 cm^2, we extrapolated denitrification potential from each soil core to m^2.

Soil Chemistry:

To measure sediment pH and electrical conductivity (EC), we added 10 g of sieved and homogenized soil to 50 ml of DI water, and shook the solution at 160 rpm for 10 minutes. After letting the sediment settle for 10 minutes, we measured pH and EC of the soil solution using an Orion Star A215 Benchtop pH/ Conductivity Meter (Thermo Fisher Scientific, Waltham, MA).

To extract ammonium (NH_4^+) and nitrate (NO_3^-), we mixed 2.5 g of soil with 25 ml of 2M KCl, shook the solution at 200 rpm for 30 minutes, centrifuged at 2500 rpm for 5 minutes, and filtered the supernatant through Whatman 589/1 filters (adapted from Keeney and Nelson 1982). We measured KCl-extractable NH_4^+ using the phenate method (APHA 1999) and KCl-extractable NO_3^- using cadmium reduction (APHA 1999) on a SmartChem® 200 discrete analyzer (Westco Scientific Instruments, Brookfield, CT). All but six NO_3^- measurements were below our detection limit of 0.18 mg N L^{-1}, hence NO_3^- was excluded from all statistical analyses.

We measured water-extractable chloride (Cl^-) and sulfate (SO_4^{2-}) by mixing 2.5 g of homogenized soil sample with 25 ml DI water, shaking at 200 rpm for 30 minutes, and centrifuging at 2500 rpm for 5 minutes. The supernatant was filtered through Whatman GF/F filters and analyzed for Cl^- and SO_4^{2-} concentrations with a Dionex Ion Chromatography System (ICS 1100; Thermo Fisher Scientific, Waltham, MA).

We quantified the %C and %N of aboveground biomass and sieved soil samples. We cut all samples into small pieces (all dimensions <1 cm), then ground them in a ball mill at 400 rpm for 20-40 minutes. We placed subsamples into aluminum tin rolls (8-10 mg for plant biomass and 10-15 mg for sediment). Each sample was analyzed for %C and %N with a Costech ECS 4010 CHNSO Analyzer (Costech Analytical Technologies, Valencia, CA).

Statistical analyses

We conducted our statistical analyses in R version 3.5.1 (R Core Team 2019) and the R Studio Interface version 1.1.383 (R Studio Team 2019). We checked the homogeneity of variances of potential denitrification rate data with the Levene's Test (R function 'leveneTest'). After checking the normality of continuous data using Shapiro-Wilk tests (R function 'shapiro.test'), we log-transformed potential denitrification rates to meet the assumption of normality.

To explore the predictors of denitrification potential, we conducted model selection on linear mixed effects models with the R function 'lme4'. We included tidal restoration status and vegetation zone as fixed effects. Due to constraints in sample size, we limited our continuous variables to the three most representative and biologically relevant factors: pH, EC, and sediment %N. EC was used as a proxy for soil moisture content, Cl^-, SO_4^{2-}, belowground biomass and bulk density (all $R^2 > 0.5$ except soil moisture content). Aboveground biomass, %C, and %N were excluded from analyses due to having low direct biological relevance to denitrification rates. Sediment %N was used in place of belowground %N and NH_4^+ as it encompassed both variables. We included sampling site as a random effect in all models. We set up all 32 possible linear mixed effects models (site as random effect, two categorical variables, and three continuous variables), and used Akaike Information Criterion (AIC) to select the best models for predicting denitrification potential. We also used a two-way ANOVA to determine differences in denitrification potential and soil chemistry among vegetation zones and restoration status, followed by post-hoc Tukey tests.

SLAMM Scaling

We obtained the estimated rate of SLR-driven high marsh conversion to low marsh from SLAMM projections applied to the Connecticut coast by Clough et al. (2016; https://www.ct.gov/deep/cwp/view.asp?a=2698&q=322898). The major variables used in the initial model included elevation, wetland cover, sediment accretion rates, and tide ranges, while the updated 2016 version that we used added marsh collapse, tidal muting resulting from tidal flow restrictions, and SLR scenarios derived from Horton et al. (2015). From the resulting land cover spatial maps, we identified areas classified as irregularly-flooded marsh (high marsh) by 2025 that were projected to be replaced by regularly-flooded marsh (low marsh) by 2055 and 2085. We limited our analysis to the “medium” to “high-medium”, and “high” SLR scenarios (914 mm, 1270 mm, and 1905 mm SLR by 2100 respectively) because they produced high marsh loss rates similar to historical trends in Long Island salt marshes (Cameron Engineering and Associates 2015). We calculated changes to denitrification potential by multiplying the total area of conversion across the state by the average difference in denitrification potential between the *S. patens* (high marsh) and short-form *S. alterniflora* zones (low marsh).

RESULTS

Our model selection suggested that vegetation zone was the single best predictor of denitrification potential (Table 1). Potential denitrification rates were significantly different among vegetation zones ($F_{2,44} = 23.56$, $p < 0.001$; Figure 3). There was no difference in denitrification potential between tidally-restored and unrestricted sites ($F_{1,44} = 0.521$, $p = 0.474$), or the interaction between vegetation zone and restoration status ($F_{2,44} = 1.7$, $p = 0.194$). The short-form *S. alterniflora* zone had the lowest potential denitrification rate per m^2, averaging 7 times lower than the *S. patens* zone ($p = 0.009$) and 17 times lower than the *P. australis* zone ($p = 0.002$; Table 2). Due to differences in bulk densities across zones, expressing denitrification potential per g dry soil changed the magnitude but not the significance or direction of differences between zones ($F_{2,52} = 8.91$, $p = 0.005$; Figure 4).

P. australis was associated with significantly lower EC ($F_{2,57} = 23.02$, $p < 0.001$) and soil moisture content ($F_{2,57} = 6.328$, $p = 0.003$) than both short-form *S. alterniflora* and *S. patens* (Table 3), but no difference was observed for either variable between the two *Spartina* zones. No difference was observed among zones for pH ($F_{2,57} = 0.506$, $p = 0.61$) and sediment %N ($F_{2,57} = 0.737$, $p = 0.483$; Table 3).

SLAMM projections suggest that across the CT coast in 2025, there will be approximately 40 km^2 of high marsh (irregularly flooded marsh) and 11 km^2 of low marsh (regularly-flooded marsh). From 2025 to 2055, conversion from high to low marsh affected 11% to 70% of the total marsh area depending on SLR scenario, leading to a loss of denitrification potential ranging from 100 to 617 kg-N/ hr across the coast (Table 4). By 2085, the medium SLR scenario led to 47% conversion of total marsh and a loss of 541 kg-N/ hr. In the high SLR scenario, almost all high marsh was converted to either low marsh or open water by 2085.The comparison of 2025 and 2085 in the high SLR scenario is underestimated because much of the high marsh was converted to open water instead of low marsh.

DISCUSSION

Vegetation zones in salt marshes are good indicators of soil conditions like flooding frequency and salinity since they reflect the capacity of dominant plant species to be competitive in narrow ranges of environmental conditions (Bertness 1991, Mitsch and Gosselink 2015). Similarly, we found that (1) vegetation zone was the sole significant indicator of denitrification potential and was more important for predicting denitrification potential than pH, EC, sediment %N, and restoration status. We also found (2) no significant difference in potential denitrification rates between tidally-restored and unrestricted salt marshes. Given that denitrification potential is more closely correlated with vegetation than restoration status, our results emphasize a need for *S. patens* revegetation to uphold nitrogen removal rates following *P. australis* decline. Finally, scaling denitrification potential with vegetation zone shifts suggested that (3) SLR-driven replacement of *S. patens* with short-form *S. alterniflora* could represent substantial losses to salt marsh denitrification potential.

Vegetation zones as indicators of denitrification

Vegetation zone was the best indicator of denitrification potential compared to restoration status, EC, pH, and sediment %N. Although there is evidence that some of these other variables can influence denitrification rates (Simek and Cooper 2002; Santoro 2010), our results suggest that vegetations zones in southern New England salt marshes supersede them in predicting denitrification potential. Sediment %N and pH were neither different among vegetation zones nor correlated with denitrification potential; although EC was different among vegetation zones, it also did not predict denitrification potential. Our results highlight the importance of dominant vegetation in predicting denitrification with *S. patens* and *P. australis* being associated with higher denitrification potential than short-form *S. alterniflora*. In their meta-analysis, Alldred and Baines (2016) found that high variability within vegetation types could limit their ability to predict denitrification; our results suggest that with a uniform methodology, dominant salt marsh vegetation can reliably predict denitrification and is a better predictor of denitrification than soil physiochemical properties. Our measured rates of denitrification potential in the short-form *S. alterniflora* zone (mean 3.5 mg-N/ hr/ m^2) were similar to those reported by Dollhopf et al. (2005; mean 3.25 mg-N/ hr/ m^2) and Hill et al. (2018; mean 2.7 mg-N/ hr/ m^2). Denitrification potential in the *S. patens* and *P. australis* zones were lower but within the same order of magnitude as other studies (Windham and Meyerson 2003; Wigand et al. 2004).

Tidal restoration and P. australis

Denitrification potential was not significantly different between tidally restored and unrestricted salt marshes, suggesting that denitrification potential cannot be predicted by tidal restoration status alone. Rather, restoration-driven shifts in vegetation may be better indicators of landscape-scale changes to denitrification. On average across all sites, denitrification potential was higher in the *P. australis* zone than in the short-form *S. alterniflora* zone, but we found no difference compared to the *S. patens* zone. Given the lack of evidence for a difference between *S. patens* and *P. australis* denitrification potential, successful colonization of former-*P. australis* habitat by *S. patens* may not alter the level of nitrogen removal capacity, which has been a concern associated with *P. australis* removal in wetland systems (Findlay et al. 2003; Kiviat 2013). Conversely, should tidally-restored areas be recolonized predominantly by low marsh plant species, as has been reported in Connecticut salt marshes (Elphick et al. 2015), then the landscape-scale denitrification potential may decrease.

Our results contrast with a study by Windham and Meyerson (2003) that found higher denitrification potential in *P. australis* than *S. patens,* with the difference possibly due to the larger range of habitats occupied by *P. australis* in our study corresponding with greater range of denitrification potentials (Chambers 1997; Findlay et al. 2003). Furthermore, our study did not have sufficient data to address the effect of time since restoration, which has been shown to be positively correlated with denitrification potential in brackish wetlands in Connecticut (Doroski et al. 2019). However, the differences we found in denitrification rates across vegetation zones highlight the possible role of vegetation in driving the trajectory of denitrification in restored sites.

Sea-level rise and high marsh change

With short-form *S. alterniflora* occupying the upper range of the low marsh and *S. patens* representing the seaward boundary of the high marsh, the two zones are often found adjacent or intermixed with each other. Despite their proximity, our results showed that short-form *S. alterniflora* was associated with significantly lower denitrification potential than *S. patens,* which is reflective of their different thresholds of suitable soil conditions (Bertness 1991). As SLR alters the hydrology of salt marshes, *S. patens* zones are disappearing from the lower ends of their historical range due to increases in flooding frequency, with its former habitat often being colonized by the more inundation- and salinity-resistant short-form *S. alterniflora* (Pezeshki and Delaune 1993; Donnelly and Bertness 2001; Smith 2014).

Our scaling results suggest that as *S. patens* is replaced by short-form *S. alterniflora*, the denitrification potential of salt marshes could decrease significantly (Table 2). Like other recent studies, we found high variation in the rate of high to low marsh conversion across wetlands, with a subset of particularly vulnerable salt marshes driving statewide average rates of change (Figure 5, Cameron Engineering and Associates 2015, Smith 2014). The SLAMM projections we used may have underestimated the rate of *S. patens* loss and replacement as we did not account for marsh dieback and disturbance events which have been shown to facilitate this process (Raposa et al. 2017). Moreover, we also did not account for areas of the high marsh that are already occupied by short-form *S. alterniflora*, so the projected denitrification losses may already be underway.

While our results showed that the replacement of *S. patens* by short-form *S. alterniflora* could have substantial consequences for soil denitrification potential, this pattern of change is ultimately limited to the low-to-high marsh boundary. Extending our understanding of the effects of SLR-driven vegetation change on denitrification beyond the low-to-high marsh boundary will require characterization of other major vegetation zones, especially tall-form *S. alterniflora*. Studies in New England have shown that tall-form *S. alterniflora* is associated with higher denitrification rates than both short-form *S. alterniflora* (Kaplan et al. 1979; Dollhopf et al. 2005) and *S. patens* zones (Wigand et al. 2004). The primary habitat of tall-form *S. alterniflora*, creek banks, has been associated with higher nitrogen retention than the marsh interior, an effect attributed to better soil aeration, more frequent tidal flushing, and higher nutrient inputs (Howes and Goehringer 1994; Anderson et al. 1997; Gribsholt et al. 2005). With SLR-driven expansions of the low marsh, it is possible that increased tall-form *S. alterniflora* cover may compensate for the loss of denitrification from the replacement of *S. patens* with short-form *S. alterniflora*. This would align with the hypothesis by Larsen et al. (2010) that SLR will increase the relative contribution of creek bank habitats to nitrogen retention relative to the marsh interior.

CONCLUSIONS

Our results show that salt marsh vegetation zones are good indicators of denitrification potential and that the influence of tidal restoration on denitrification should be tracked through vegetation response. Furthermore, we found the SLR-driven replacement of *S. patens* with short-form *S. alterniflora* could lead to decreases in landscape-scale denitrification in the high-to-low marsh boundary. As salt marshes globally experience rapid vegetation change, establishing links between vegetation zones and soil processes could improve our understanding of how ecosystem function is responding to these changes.

TABLES

Table 1. Model selection of linear mixed effects models. The ten models with the lowest Akaike Information Criterion (AIC) are included with number of variables (K), difference in AIC compared to the top model (Δ AIC), and conditional R^2 (cond. R^2).

Variables:	K	AIC	Δ AIC	cond. R^2
Vegetation zone	1	70.28	0	0.61
Vegetation zone, restoration status	2	73.73	3.45	0.60
Vegetation zone, sediment %N	2	74.06	3.78	0.59
Vegetation zone, pH	2	74.33	4.05	0.64
Vegetation zone EC	2	75.37	5.09	0.60
Vegetation zone, restoration status, sediment %N	3	77.44	7.16	0.65
Vegetation zone, sediment %N, EC	3	77.65	7.37	0.6
Vegetation zone, restoration status, pH	3	77.74	7.46	0.59
Vegetation zone, sediment %N, EC	3	78.10	7.82	0.59
Vegetation zone, restoration status, EC	3	78.89	8.61	0.63

Table 2. Potential denitrification rates (95% confidence intervals) by vegetation zone.

Vegetation Zone	Mean denitrification potential	
	ng-N/ hr/ g dry soil	mg-N/ hr/ m^2
short *S. alterniflora*	58 – 122	2 – 5
S. patens	241 – 507	15.4 – 35
P. australis	256 – 1413	17 – 101

Table 3. EC (1:5 soil-to-water ratio), gravimetric soil moisture content, pH, and sediment %N (mean ± S.E.) by vegetation zone (total n = 60 for all variables). Distinct symbols denote significant difference by vegetation zone ($p < 0.05$).

Variable	Vegetation Zone		
	short *S. alterniflora*	*S. patens*	*P. australis*
EC (mS)	7.9 ± 0.28 ^{a}	6.99 ± 0.26 ^{a}	4.8 ± 0.42 ^{b}
Soil moisture content (%)	686.61 ± 76.65 ^{a}	578.32 ± 71.09 ^{a}	316.11 ± 79.22 ^{b}
pH	6.55 ± 0.15 ^{a}	6.71 ± 0.08 ^{a}	6.66 ± 0.11 ^{a}
Sediment %N (%)	1.17 ± 0.09 ^{a}	1.08 ± 0.09 ^{a}	0.97 ± 0.15 ^{a}

Table 4. Predicted rate of high to low marsh conversion and subsequent change to denitrification potential based on SLAMM projections for the Connecticut coast. Med, med-high, and high SLR scenarios represent 914, 1270, and 1905 mm of SLR by 2100 respectively. All estimations of changes by 2055 and 2085 were obtained by comparing against predicted conditions in 2025.

SLR scenario	Change from high to low marsh (km^2)		% of initial marsh area affected		Loss to denitrification potential (kg-N/ hr)	
	Year		*Year*		*Year*	
	2055	2085	2055	2085	2055	2085
Med	4.6	24.8	11.2	46.9	100.8	541.3
Med-High	10.7	32.1	26.2	60.9	233.9	700.2
High	28.3	19.2	70.2	36.4	617.7	419.6

FIGURES

Figure 1. Sampling locations in salt marshes across the Connecticut coast. To the extent possible, sites were selected to represent the geographic distribution of salt marshes along the coast.

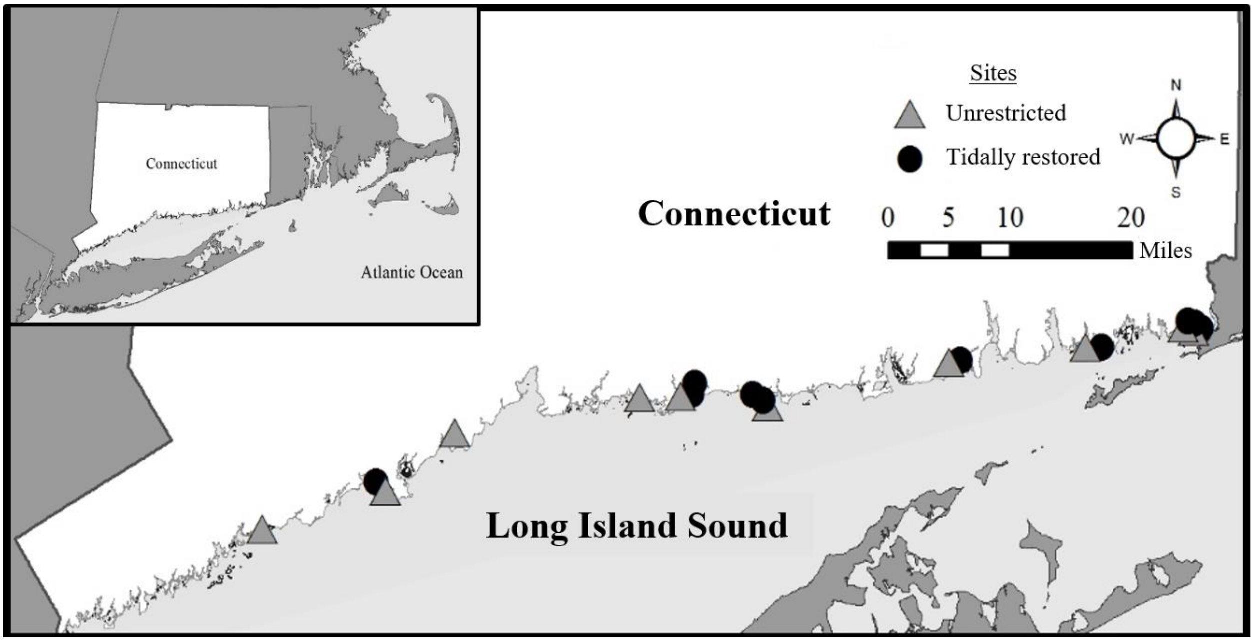


Figure 2. Field sampling design of vegetation zone selection and sampling plots. At each site, we identified three vegetation zones of interest: short-form *S. alterniflora*, *S. patens*, and *P. australis*. In zones dominated by each species, we established three sampling plots from which samples for that zone were aggregated.

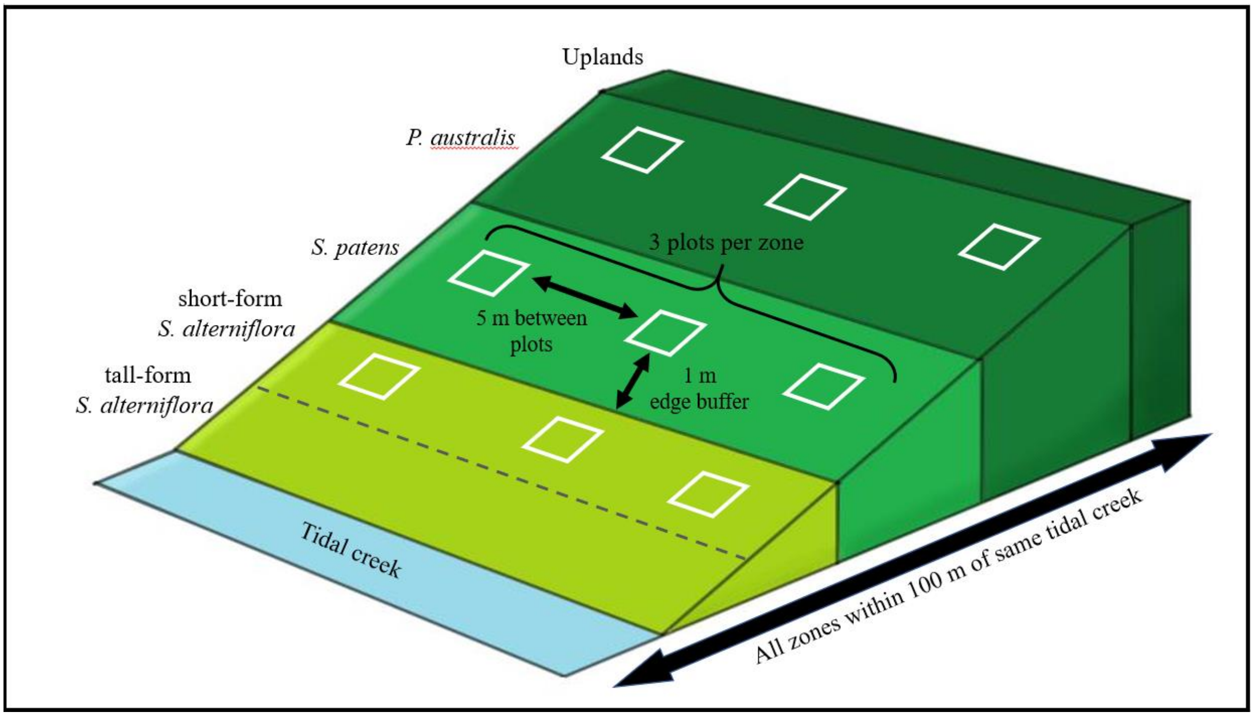


Figure 3. Denitrification potential (per m^2) by restoration status and vegetation zone. Characters denote significant differences among vegetation zones at $p < 0.05$.

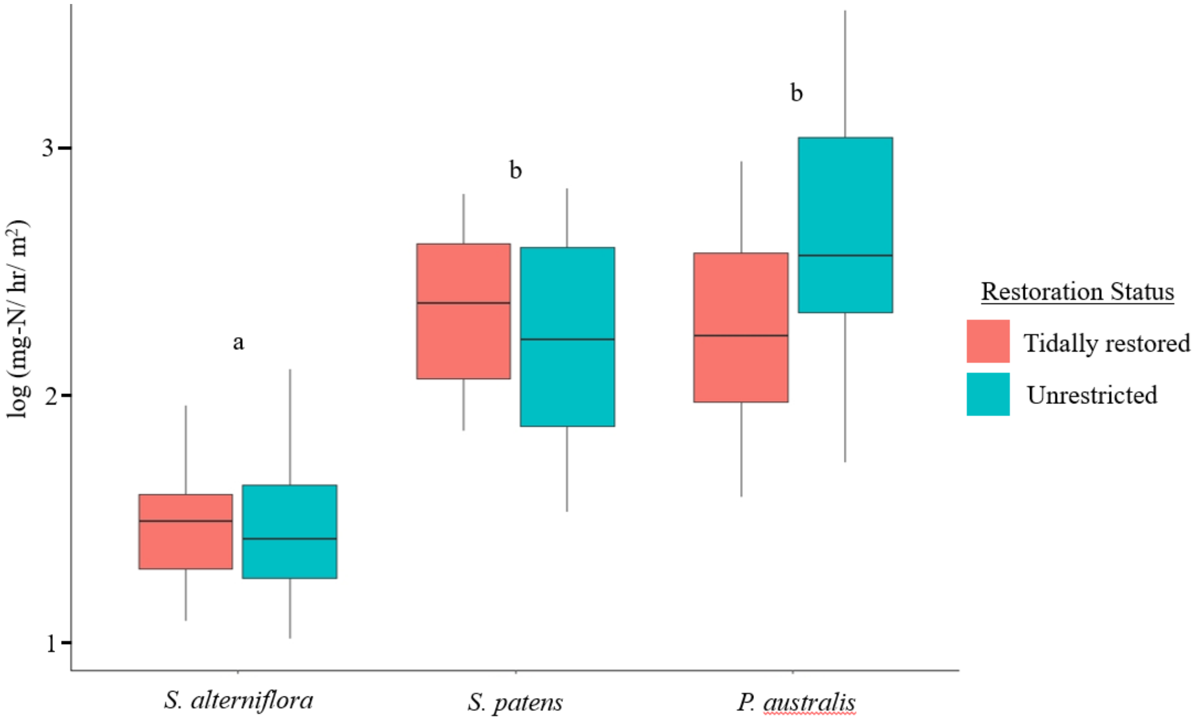


Figure 4. Denitrification potential (per g dry soil) in by restoration status and vegetation zone. Characters denote significant differences among vegetation zones at $p < 0.05$.

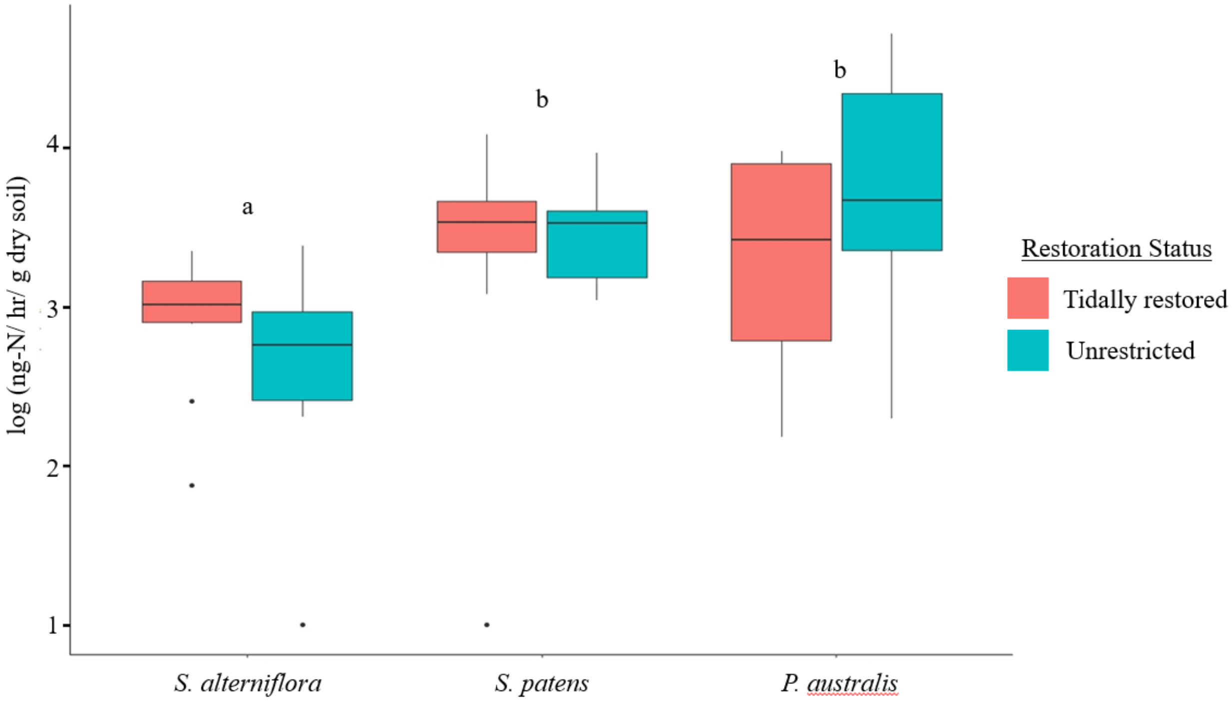
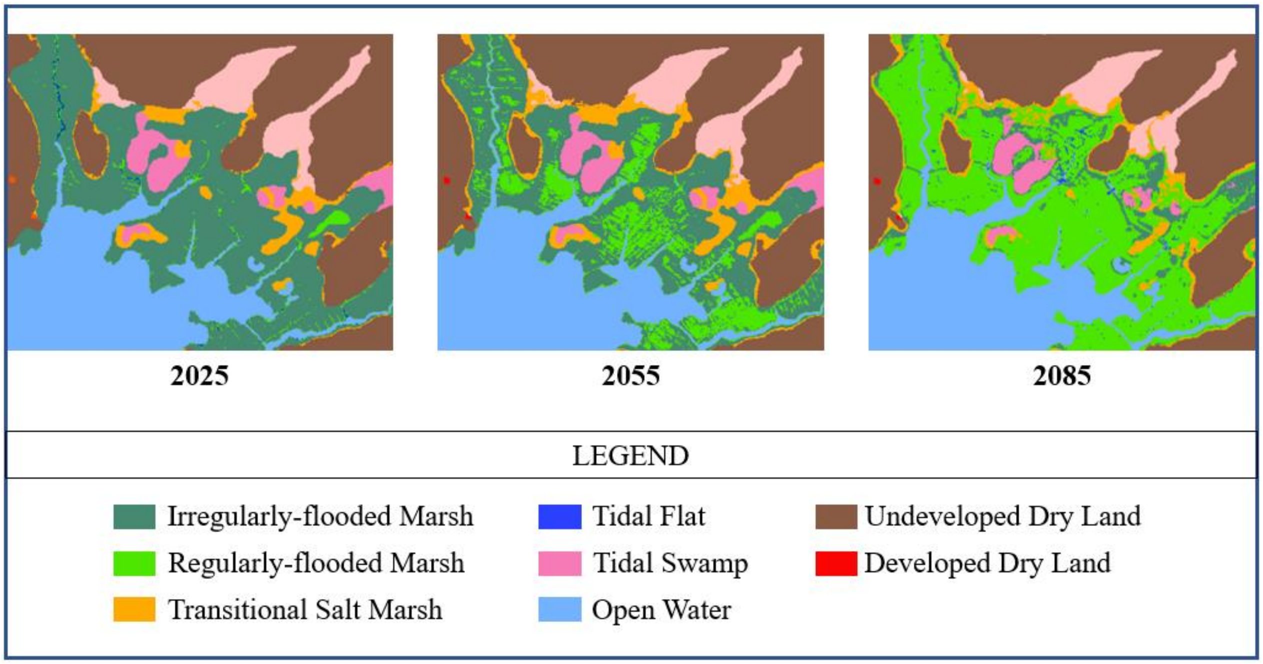


Figure 5. Land cover change to Barn Island Wildlife Management Area, Stonington, CT as predicted by SLAMM application with intermediate rate of SLR (152 mm by 2025, 406 mm by 2055, and 737 mm by 2085). Whole-coast scaling showed that 46% of the statewide salt marsh area will undergo conversion from high to low marsh by 2085, with Barn Island representative of the most vulnerable wetlands facing above-average conversion rates.



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