

## ARTICLE

# Vegetation zones as indicators of denitrification potential in salt marshes

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**Abstract**

Salt marsh vegetation zones shift in response to large-scale environmental changes such as sea-level rise (SLR) and restoration activities, but it is unclear if they are good indicators of soil nitrogen removal. Our goal was to characterize the relationship between denitrification potential and salt marsh vegetation zones in tidally restored and tidally unrestricted coastal marshes, and to use vegetation zones to extrapolate how SLR may influence high marsh denitrification at the landscape scale. We conducted denitrification enzyme activity assays on sediment collected from three vegetation zones expected to shift in distribution due to SLR and tidal flow restoration across 20 salt marshes in Connecticut, USA ( $n = 60$  sampling plots) during the summer of 2017. We found lower denitrification potential in short-form *Spartina alterniflora* zones (mean, 95% CI: 4, 3–6 mg N h<sup>-1</sup> m<sup>-2</sup>) than in *S. patens* (25, 15–36 mg N h<sup>-1</sup> m<sup>-2</sup>) and *Phragmites australis* (56, 16–96 mg N h<sup>-1</sup> m<sup>-2</sup>) zones. Vegetation zone was the single best predictor and explained 52% of the variation in denitrification potential; incorporating restoration status and soil characteristics (soil salinity, moisture, and ammonium) did not improve model fit. Because denitrification potential did not differ between tidally restored and unrestricted marshes, we suggest landscape-scale changes in denitrification after tidal restoration are likely to be associated with shifts in vegetation, rather than differences driven by restoration status. Sea-level-rise-induced hydrologic changes are widely observed to shift high marsh dominated by *S. patens* to short-form *S. alterniflora*. To explore the implications of this shift in dominant high marsh vegetation, we paired our measured mean denitrification potential rates with projections of high marsh loss from SLR. We found that, under low and medium SLR scenarios, predicted losses of denitrification potential due to replacement of *S. patens* by short-form *S. alterniflora* were substantially larger than losses due to reduced high marsh land area alone. Our results suggest that changes in vegetation zones can serve as

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landscape-scale predictors of the response of denitrification rates to rapid changes occurring in salt marshes.

#### KEYWORDS

denitrification, nitrogen, *Phragmites*, salt marsh, sea level rise, *Spartina*, tidal restoration

## INTRODUCTION

Coastal salt marshes globally are undergoing unprecedented levels of change, driven by their vulnerability to accelerating sea-level rise (SLR) in tandem with local disturbances (Kirwan & Megonigal, 2013). The effects of SLR have been particularly pronounced in the northeastern and mid-Atlantic United States, where SLR is three to four times the global average and is outpacing sediment accretion rates in many salt marshes (Crosby et al., 2016; Sallenger et al., 2012; Watson et al., 2017). The resulting increase in sea-level and tidal range has led to shifts in salt marsh vegetation communities (Smith, 2015; Valiela et al., 2018), which in turn could alter the provision of various salt marsh ecosystem services, including coastal nitrogen cycling (Barbier et al., 2011; Craft et al., 2009; Hinshaw et al., 2017).

Denitrification, the microbial reduction of nitrate to dinitrogen gas, is one of the major pathways of nitrogen removal in salt marshes (Tobias & Neubauer, 2009), plays an important role in intercepting land-derived nitrogen loads (Velinsky et al., 2017; White & Howes, 1994), and is a highly valued ecosystem service that mitigates eutrophication of coastal waters (Barbier et al., 2011; Valiela & Cole, 2002). Denitrification is an anerobic microbially mediated process that is higher under flooded, reducing redox conditions common in salt marshes (Tobias & Neubauer, 2009). However, denitrification rates are highly variable, making it difficult to quantify across broad spatial scales (Groffman et al., 2009). In salt marshes, tidal flow interacts with local topography to create dynamic and heterogeneous soil moisture and redox conditions (Bertness, 1991; Pennings & Callaway, 1992) that control patterns of denitrification across the landscape (Yang & Silver, 2016). Nitrogen inputs (Gardner & White, 2010; Peng et al., 2016), variation in seasonal flooding dynamics (Bai et al., 2017), and salinity (Marks et al., 2016) can also impart important controls on spatial patterning of denitrification in salt marshes. For our understanding of coastal nitrogen cycling to keep pace with rapidly changing salt marshes, methods for scaling up salt marsh denitrification rates to regional scales are needed.

Salt marsh vegetation zones, which both reflect and influence the mosaic of soil conditions in salt marshes, are strong candidates for serving as indicators of

denitrification at broad spatial scales. Salt marsh vegetation zones are distributed along hydrological and salinity gradients, forming vertically stratified zones determined by elevation and tidal flooding regimes (Bertness, 1991). In southern New England salt marshes, monotypic stands of the tall form of *Spartina alterniflora* (>30 cm tall) typically dominate low elevation marsh and flank tidal creeks, with short-form *S. alterniflora* (<30 cm tall) extending into higher elevation marsh where the less flood- and salinity-tolerant *S. patens* has historically dominated (Bertness, 1991; Niering & Warren, 1980). In recent decades, large areas of *S. patens* have been replaced by short-form *S. alterniflora* as sea levels have risen (Raposa et al., 2017; Smith, 2015; Warren & Niering, 1993). Plant–soil feedbacks, such as rhizosphere oxidation and microbial symbioses, can reinforce differential soil conditions among salt marsh vegetation zones (Burke et al., 2002; Howes et al., 1981). For example, a positive feedback between plant growth and sediment oxidation is well known for *S. alterniflora* (Mendelssohn et al., 1981). Given that plant communities both track and influence local soil conditions, salt marsh vegetation zones have been shown to be good indicators of soil conditions, including soil oxygenation and porewater chemistry (Dollhopf et al., 2005; Moffett & Gorelick, 2016; Yang & Silver, 2016), yet how denitrification rates are related to salt marsh vegetation zones has not been broadly characterized.

Across geophysical regions, wetland types, and measurement methods, dominant vegetation can be a good predictor of denitrification rates (as suggested by a recent meta-analysis; Alldred & Baines, 2016). Evidence from New England salt marshes further supports the prediction that denitrification differs among vegetation zones, with the highest rates measured in low marsh dominated by tall-form *S. alterniflora* and lower rates in high marsh dominated by short-form *S. alterniflora*, *S. patens*, or *Distichlis spicata* (Kaplan et al., 1979; Wigand et al., 2004). However, prior studies of denitrification in salt marshes are limited in spatial scope and have not systematically sampled vegetation zones or used consistent methods to measure denitrification. Broadening our understanding of the relationships between vegetation zones and denitrification requires a wider geographic sampling distribution, direct comparisons of multiple vegetation zones using the same measurement protocols, and a more nuanced consideration of high marsh zones dominated by species expected to shift with SLR.

In New England salt marshes, in addition to SLR, invasive species and wetland management also alter the distribution of vegetation zones, with the potential to change spatial patterns of denitrification. On the landward side of salt marshes, the brackish-marsh–upland boundary has experienced widespread invasion by *Phragmites australis*, with coastal land development and tidal restrictions exacerbating the extent of the invasion (Minchinton & Bertness, 2003; Roman et al., 1984; Silliman & Bertness, 2004). Invasion of *P. australis* is associated with loss of native salt marsh vegetation and the species that depend on it, making it a key target for restoration and management (Elphick et al., 2015; Keller, 2000; Warren et al., 2001). Tidal flow restoration by the removal or modification of structural tidal restrictions like roads or dikes is commonly used to replace *P. australis* with native salt marsh vegetation (Smith & Warren, 2012). In brackish and fresh tidal wetlands, *P. australis*-dominated soils have been associated with higher denitrification potential than native or recently restored soils, representing a possible tradeoff during restoration (Alldred et al., 2016; Findlay et al., 2003; Windham & Meyerson, 2003). Furthermore, although *S. patens*-dominated high marsh is often the reference for restoration, *S. alterniflora* often comes to dominate (Elphick et al., 2015), creating uncertainty in the response of ecosystem function post restoration. The invasion of *P. australis* and associated tidal flow management represent yet another way in which vegetation zones are shifting in salt marshes, with potential implications for denitrification.

Our goal was to characterize the relationship between denitrification potential and dominant salt marsh vegetation zones that are undergoing distribution shifts due to SLR and tidal flow restoration. We conducted a field survey spanning 20 salt marshes across 130 km of coastline during the summer and compared the denitrification potential of three widespread vegetation zones in southern New England salt marshes: short-form *S. alterniflora*, *S. patens*, and *P. australis*. Collectively, these zones dominate the higher elevation portions of New England salt marshes and shifts in their relative abundance are anticipated with SLR and *P. australis* management (Donnelly & Bertness, 2001; Smith, 2013, 2015; Warren & Niering, 1993). In this study, we measure laboratory rates of denitrification potential as an index of the denitrifier population in soils. Denitrification potential is generally reflective of long term in situ denitrification rates (Groffman & Tiedje, 1989) that respond to soil conditions, which both influence and are influenced by salt marsh vegetation. We opted to use denitrification potential laboratory assays to compare relative rates across many sites ( $n = 20$  coastal wetlands, three vegetation zones per wetland) in this study. Our specific objectives were to compare potential denitrification rates (1) among dominant salt marsh vegetation zones and (2) between

tidally restored and unrestricted salt marshes, and (3) to estimate how SLR may influence high marsh denitrification rates at the landscape scale. To assess the potential for SLR-driven replacement of *S. patens* with short-form *S. alterniflora* to affect denitrification rates on the landscape-scale, we extrapolated our measured rates to the Connecticut coastline using existing projections of marsh migration with SLR (Clough et al., 2015).

## METHODS

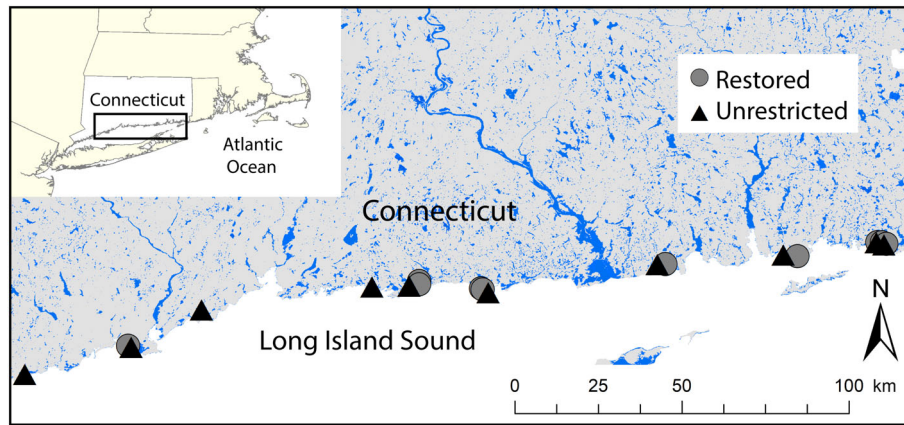
### Site selection

We conducted a field survey across 20 salt marshes along the Connecticut (USA) coast during the summer of 2017 (10 August to 23 August; Figure 1) during which we collected soil samples from short-form *S. alterniflora*, *S. patens*, and *P. australis* vegetation zones in each marsh. Sites were chosen based on the presence of target species as indicated by published maps (Correll et al., 2019) and confirmed by site visits. Ten of our sites lacked human-made tidal restrictions throughout their documented history (unrestricted sites), and 10 had tidal flow restored following the removal or modification of tidally restricting structures (e.g., weir boards, tide gates, culverts) during the previous 50 years (tidally restored sites; Appendix S1: Table S1). We explicitly designed our survey with a wide geographic distribution ( $n = 20$  coastal salt marshes across 130 km of coastline) to maximize the generalizability of our findings.

### Sample collection and processing

We identified vegetation zones for sampling with relative cover of the target species  $>50\%$  in an area  $>35\text{ m}^2$  and within 100 m of the same tidal creek to increase the likelihood that they received a similar source, timing, and amplitude of flooding at each salt marsh study site. Within each vegetation zone at each site, we set up three replicate  $1\text{-m}^2$  plots that were parallel to the nearest tidal creek, at least 5 m from each other, and at least 1 m from the vegetation zone edge. All biomass and soil samples collected from each zone were aggregated from the three plots, and we sampled all plots within 3 h of low tide to control for tidal influence.

At each  $1\text{-m}^2$  plot, we visually estimated percent live plant cover (for all species present), litter cover, and bare ground (0%–100%) to the nearest 1% (Lishawa et al., 2015). Every nine plots, we conducted independent duplicate visual estimates across sampling teams to ensure consistency in our percent cover estimates. Each



**FIGURE 1** Sampling locations of 20 salt marshes (10 restored, black triangles and 10 unrestricted, gray circles) across 130 km of the Connecticut, USA coast

plot was divided into 16  $25 \times 25$  cm subplots. In one randomly selected subplot, we collected a 10 cm deep soil core (5 cm diameter;  $196 \text{ cm}^3$  volume) to quantify belowground plant biomass. The upper 10 cm of soil has the highest root density in wetlands; Santini et al. (2019) found greater than 80% of belowground biomass in natural and restored salt marshes occurred in the surface 10 cm of soil (from cores 30 cm deep). Belowground biomass soil cores were washed through a 2-mm sieve, dried at  $65^\circ\text{C}$  for 72 h, and weighed. We collected a second soil core from a second randomly selected subplot for bulk density analysis. Bulk density was calculated as the oven-dried ( $105^\circ\text{C}$  for 72 h) mass of the soil core divided by its volume. A third soil core was collected for soil chemistry and denitrification potential analyses, and was transported to the lab on ice, homogenized, and sieved through a 2-mm sieve, and stored at  $4^\circ\text{C}$  in a sealed container until analysis. Homogenized soils were mixed and brought to room temperature before analyses. We calculated soil moisture fraction (0 to 1; proportion of water in wet soil) by drying sieved soil at  $105^\circ\text{C}$  for 72 h.

## Denitrification potential

We used denitrification enzyme activity (DEA) assays with the acetylene inhibition method to quantify the denitrification potential of our soils (Bohen et al., 2001; Groffman et al., 1999). In 125-ml glass flasks with airtight seals, we mixed 5 g of homogenized soil with 10 ml of DEA solution containing excess nitrate, excess carbon, and chloramphenicol (3.6 mg  $\text{KNO}_3$ , 2.5 mg glucose, and 0.625 mg chloramphenicol per g wet soil). Prior to incubation, we flushed each flask with  $\text{N}_2$  gas to induce anoxic conditions, then replaced 10 ml of headspace gas with acetylene gas to inhibit the reduction of  $\text{N}_2\text{O}$  to  $\text{N}_2$ .

Discrete gas samples were drawn at four time points: approximately 0, 30, 60, and 90 min after incubations began. We measured the  $\text{N}_2\text{O}$  concentration of the gas samples using a Clarus 580 gas chromatograph with an electron capture detector, delivered with a TurboMatrix 40 Trap Headspace Autosampler (PerkinElmer, Shelton, CT).

We calculated rates of denitrification potential as the linear rate of accumulated headspace  $\text{N}_2\text{O}$  over time. From replicate determinations of gas standards, we calculated the minimum detectable concentration differences (MDCD) for  $\text{N}_2\text{O}$  following Yates et al. (2006). The accumulation rate of one flux estimate had concentration differences below MDCD and was set to half of the linear rate of accumulation assuming the concentration difference between the beginning and end (90 min) of the assay was MDCD. For fluxes above MDCD, when the  $r^2$  of the linear regression of  $\text{N}_2\text{O}$  accumulation over time was greater than 0.90, we used the slope over the full 90-min incubation. When  $\text{N}_2\text{O}$  accumulation saturated the headspace (i.e.,  $r^2 < 0.90$  of the linear regression), we calculated potential denitrification rates from the time of linear accumulation by excluding the 90- and/or 60-min time points ( $n = 5$  out of 69 DEA assays).

By removing carbon and nitrogen limitation on denitrification and adding chloramphenicol to inhibit protein synthesis, the DEA technique measures the capacity of the standing stock of enzymes to carry out denitrification, which we refer to as denitrification potential (Jordan et al., 2007; Webster et al., 2018). DEA is related to the size of the denitrifying enzyme pool and yields an index of the denitrifier population in soils that is generally reflective of long term in situ denitrification rates (Groffman & Tiedje, 1989). Denitrification potential assays do not directly account for the roles of coupled nitrification–denitrification or dissimilatory nitrate reduction to ammonia (DNRA),



microbial processes that can be important nitrogen transformations in salt marsh soils (Koop-Jakobsen & Giblin, 2010).

## Soil chemistry

To measure soil 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 15 min. After letting the sediment settle for 10 min, 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 soil ammonium ( $\text{NH}_4^+$ ) and nitrate ( $\text{NO}_3^-$ ), we mixed 2.5 g of soil with 25 ml of 2 mol/L KCl, shook the solution at 200 rpm for 30 min, centrifuged at 959 g for 5 min, and filtered the supernatant through Whatman 589/1 filters (adapted from Keeney & Nelson, 1982). We measured KCl-extractable  $\text{NH}_4^+$  using the phenate method (APHA, 1998) and KCl-extractable  $\text{NO}_3^-$  using cadmium reduction (APHA, 1998) on a SmartChem 200 discrete analyzer (Westco Scientific Instruments, Brookfield, CT). All but six  $\text{NO}_3^-$  concentrations were below our detection limit of  $0.01 \text{ mg N L}^{-1}$ , hence  $\text{NO}_3^-$  was excluded from all statistical analyses. Ten  $\text{NH}_4^+$  concentrations were below our detection limit of  $0.18 \text{ mg N L}^{-1}$  and were set to half the detection limit ( $0.092 \text{ mg N L}^{-1}$ ).

To extract sulfate ( $\text{SO}_4^{2-}$ ) from the soils, we mixed 2.5 g of field moist soils with 25 ml of deionized water, shook the solution at 200 rpm for 30 min, centrifuged at 884 g for 6 to 12 min, and filtered the supernatant through Whatman GF/F filters. We analyzed water-extractable  $\text{SO}_4^{2-}$  concentrations using a Dionex ICS-1100 ion chromatograph (Thermo Fisher Scientific, Waltham, MA). All analyses were conducted at the University of Connecticut.

## Statistical analyses

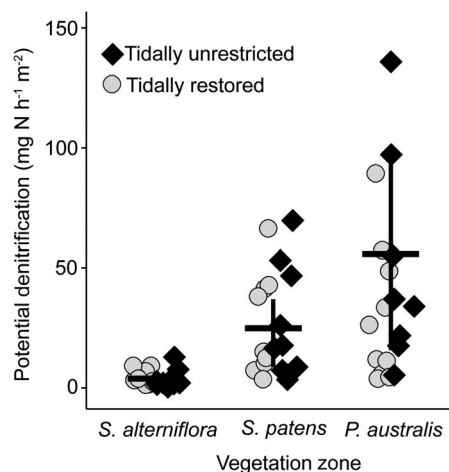
We conducted model selection on linear mixed effects models with the R function lme4 (R Core Team, 2020) to evaluate how denitrification varied among vegetation zones and restoration status. We fit models with vegetation zone (short-form *S. alterniflora*, *S. patens*, and *P. australis*), restoration status (unrestricted and tidally restored), and their interaction as fixed effects and salt marsh site as a random effect. We also included a null model with salt marsh site as a random effect. Finally, we fit a series of models that added pH, EC, and soil  $\text{NH}_4^+$  as fixed effects to evaluate if incorporating other soil characteristics would improve models. EC was strongly correlated to and thus used as a

proxy for soil moisture content ( $r = 0.79$ ,  $p < 0.0001$ ), belowground biomass ( $r = 0.71$ ,  $p < 0.0001$ ), soil  $\text{SO}_4^{2-}$  ( $r = 0.87$ ,  $p < 0.0001$ ), and bulk density ( $r = -0.79$ ,  $p < 0.0001$ ). We used Akaike's Information Criterion adjusted for small sample sizes ( $\text{AIC}_c$ ) to select the models that best predict denitrification potential. We also compared 95% confidence intervals (CIs) and considered non-overlapping CIs to indicate differences among vegetation zones and restoration status.

## Extrapolating high marsh denitrification under sea-level rise

The shift in *S. patens*-dominated high marsh to short-form *S. alterniflora* has been widely observed across the New England coast (Raposa et al., 2017; Smith, 2015; Warren & Niering, 1993). We coupled projections of changes to high marsh area due to SLR (Clough et al., 2015) with our estimates of denitrification potential in short-form *S. alterniflora* and *S. patens* zones to project possible outcomes for high marsh denitrification potential. We do not consider *P. australis* zones in our spatial extrapolation because of the high observed variation in denitrification potential (Figure 2) and the lack of available spatial predictions of *P. australis* zones under future landscape conditions. Our goal with this exercise is not to model specific patterns of future denitrification rates, but rather to illustrate the possible implications of projected shifts in salt marsh vegetation on denitrification potential at the landscape scale.

We obtained total area of high marsh from 2025 to 2070 under various SLR scenarios from the Sea Level



**FIGURE 2** Denitrification potential (per  $\text{m}^2$ ) by restoration status and vegetation zone (*Spartina alterniflora*, *S. patens*, *Phragmites australis*). Means represented by horizontal lines and 95% confidence intervals represented by vertical lines

Affecting Marsh Migration (SLAMM) model applied to the Connecticut coast (Clough et al., 2015). In SLAMM, high marsh is defined as irregularly flooded wetland (derived from the National Wetlands Inventory; Dahl et al., 2009), which entails tidal flooding less often than daily and typically occurs between 0.5 HTU (half-tide units) and the wetland boundary elevation. The SLAMM model implemented by Clough et al. (2015) used elevation, wetland cover, sediment accretion rates, tide ranges, marsh collapse, tidal muting resulting from tidal flow restrictions, and SLR scenarios derived from Rosenzweig et al. (2011) to project patterns of marsh conversion. The SLAMM model assumes that wetland occurrence is based on vertical elevations and tide ranges and predicts long-term changes in land cover classes based on equilibrium states with sea level. The model implementation for the Connecticut coast predicts relative SLR for  $5 \times 5$  m cells at each of six time steps (years 2025, 2040, 2055, 2070, 2085, and 2100) as the sum of the historic SLR eustatic trend, the cell specific rate of change of elevation due to subsidence and isostatic adjustment, and the accelerated SLR based on scenarios derived from Rosenzweig et al. (2011). The SLAMM model simulates the dominant processes involved in wetland conversion, including inundation, erosion, accretion, soil saturation, and barrier island overwash, and includes land cover classes derived from the National Wetlands Inventory (Dahl et al., 2009). The model predicts the conversion from one land cover class to another by comparing the cell elevation at a given time step to the class in that cell during the prior time step and its inundation frequency. When the cell elevation is below the minimum elevation of a land cover class, then the cell is converted to a new land cover class according to a decision tree incorporating geometric and qualitative relationships that represent conversions among land cover classes.

Land cover conversions include new marshes formed by upland expansion, yet inland marsh migration has been largely absent along the Connecticut coast (Field et al., 2017), even when accounting for topography and urban land use (cf. Doody, 2004; Valiela et al., 2018). The SLAMM model does not simulate water flow nor feedbacks between hydrodynamic and ecological systems. A detailed description of the model is available online (SLAMM 6.2 Technical Documentation, [warrenpinnacle.com/prof/SLAMM](http://warrenpinnacle.com/prof/SLAMM)).

To scale our empirical denitrification potential rates, we converted denitrification potential from mass- to area-based rates (i.e., rates per g dry soil to rates per  $\text{m}^2$  soil surface). First, we calculated the mass of the top 10 cm of soil per unit area ( $\text{g dry soil per m}^2$ ) by subtracting below-ground biomass from the dry mass of a 10 cm soil core and dividing by the surface area ( $0.00196 \text{ m}^2$ ) of the bulk

density cores. Then, we multiplied denitrification potential by soil mass per unit area ( $\text{ng N h}^{-1}$  per g dry soil by g dry soil per  $\text{m}^2$ ), with the final areal rates expressing the denitrification potential of the top 10 cm of soil per  $\text{m}^2$ . We do not evaluate the depth of plant–soil interactions in this study and only consider the top 10 cm of soil, which is where the highest root density occurs in salt marshes (Santini et al., 2019).

We extrapolated the denitrification potential of Connecticut-wide high marshes for low, medium, and high SLR scenarios and different vegetation cover scenarios: *S. patens* dominated, short-form *S. alterniflora* dominated, and equal coverage of both species using the mean and 95% CI of measured denitrification potential for each species. While the replacement of *S. patens* by *S. alterniflora* is widespread, the rate of replacement varies widely across salt marshes. While historical losses in high marsh area (*S. patens*, *Distichlis spicata*, *Juncus gerardii*) reach up to 89% in some marshes, corresponding increases in *S. alterniflora* area can be both relatively high and low (Cameron Engineering and Associates, 2015; Smith, 2015). Hence, our vegetation scenarios are designed to span the range of possible replacement scenarios. Low, medium, and high SLR scenarios correspond to 381, 914, and 1905 mm sea level rise by 2100, respectively, relative to a 2000 to 2004 baseline, and are based on multiple climate projection data sets (Clough et al., 2015). We multiplied the mean and upper and lower bounds of the 95% CI of denitrification potential by the total area of high marsh for each model scenario. We report scaled denitrification potential for years that SLAMM model output was available and for which there was >5% of high marsh area remaining (2025, 2045, 2055, and 2070).

These scenarios only consider the potential change associated with shifting vegetation zones in high marsh and are intended to be illustrative of possible future scenarios. They do not account for the many land use and other climate-associated changes that will likely occur in tandem with SLR-induced shifts in high marsh vegetation. They should be viewed as a spatial extrapolation of our empirical results that provide a starting point for understanding the landscape-scale changes that are likely to occur.

## RESULTS

Among vegetation zones, the short-form *S. alterniflora* zone had the lowest denitrification potential (mean  $\pm$  SE:  $4.1 \pm 0.7 \text{ mg N h}^{-1} \text{ m}^{-2}$ ), averaging 16% of that in the *S. patens* zone ( $26 \pm 5 \text{ mg N h}^{-1} \text{ m}^{-2}$ ) and 7% of the *P. australis* zone value ( $56 \pm 19 \text{ mg N h}^{-1} \text{ m}^{-2}$ ; Figure 2). Despite differences in soil bulk density across zones (Table 1), denitrification potential based on soil

mass (i.e., per g dry soil) showed a similar pattern; denitrification potential was lower in the short-form *S. alterniflora* zone (mean, 95% CI: 98, 66–130 ng N h<sup>-1</sup> g dry soil<sup>-1</sup>) than both *S. patens* (387, 248–527 ng N h<sup>-1</sup> g dry soil<sup>-1</sup>) and *P. australis* zones (835, 223–1448 ng N h<sup>-1</sup> g dry soil<sup>-1</sup>). Our model containing only vegetation zone was the best descriptor of denitrification potential in our model set with an Akaike weight of 0.78 (Table 2) and explained 52% of variation in denitrification potential. Incorporating restoration status and soil characteristics (EC, pH, and NH<sub>4</sub><sup>+</sup>) did not improve AIC<sub>c</sub>, and both the model containing restoration status alone and the null model were considerably worse. Sampling site included as a random effect did not result in better models.

The 95% confidence intervals (CIs) overlapped substantially for restored and unrestricted sites for each

vegetation zone. The 95% CIs of denitrification potential at restored sites had almost complete overlap with those in unrestricted sites for both *S. alterniflora* (3–7 vs. 1–6 mg N h<sup>-1</sup> m<sup>-2</sup>, respectively) and *S. patens* (10–43 vs. 9–42 mg N h<sup>-1</sup> m<sup>-2</sup>). Although 95% CIs for *P. australis* zones largely overlapped for restored and unrestricted sites as well (9–49 vs. -1 to 172 mg N h<sup>-1</sup> m<sup>-2</sup>), unrestricted sites had a greater range of potential denitrification rates with the two highest rates occurring in unrestricted sites (Figure 2). Sites that were restored ranged from 5 to 39 years in time since restoration, but we found no significant relationship between denitrification potential and time since restoration for any vegetation zone (all zones  $F_{1,24} = 1.25, p = 0.28$ ; *S. alterniflora*  $F_{1,7} = 3.1, p = 0.12$ ; *S. patens*  $F_{1,6} = 0.17, p = 0.69$ ; *P. australis*  $F_{1,7} = 0.87, p = 0.38$ ).

**TABLE 1** Soil characteristics reported as mean (95% confidence intervals) by vegetation zone (total  $n = 60$  for all variables)

Variable	Vegetation zone		
	Short-form <i>S. alterniflora</i>	<i>S. patens</i>	<i>P. australis</i>
EC (mS cm <sup>-1</sup> )	7.90 (7.31–8.50) <sup>a</sup>	7.00 (6.45–7.53) <sup>a</sup>	4.80 (3.89–5.70) <sup>b</sup>
Soil moisture (water: wet soil)	0.83 (0.78–0.89) <sup>a</sup>	0.81 (0.75–0.86) <sup>a</sup>	0.62 (0.51–0.72) <sup>b</sup>
Soil SO <sub>4</sub> <sup>2-</sup> (mg g wet soil <sup>-1</sup> )	1.5 (1.34–1.74) <sup>a</sup>	1.4 (1.2–1.5) <sup>a</sup>	0.81 (0.65–0.97) <sup>b</sup>
Belowground biomass (kg m <sup>-2</sup> )	13.35 (12.07–14.63) <sup>a</sup>	10.40 (9.24–11.56) <sup>b</sup>	5.18 (4.37–5.99) <sup>c</sup>
Bulk density (g cm <sup>-3</sup> )	0.2 (0.13–0.27) <sup>a</sup>	0.27 (0.18–0.35) <sup>a</sup>	0.49 (0.32–0.66) <sup>b</sup>
pH	6.55 (6.24–6.86)	6.71 (6.54–6.89)	6.66 (6.44–6.88)
Soil NH <sub>4</sub> <sup>+</sup> (μg N g wet soil <sup>-1</sup> )	5.05 (3.52–7.06) <sup>a</sup>	10.24 (6.72–13.76) <sup>ab</sup>	10.91 (8.05–13.77) <sup>b</sup>

Note: Variables are soil electrical conductivity (EC, 1:5 soil-to-water ratio; mS cm<sup>-1</sup>), soil sulfate (SO<sub>4</sub><sup>2-</sup>, mg g wet soil<sup>-1</sup>), soil moisture fraction (water: wet soil), belowground biomass down to 10 cm (kg m<sup>-2</sup>), bulk density (g cm<sup>-3</sup>), pH, and soil ammonium (μg NH<sub>4</sub><sup>+</sup> μg N g wet soil<sup>-1</sup>). Different letters indicate non-overlap of CIs among vegetation zones. Genera are *Spartina* and *Phragmites*.

**TABLE 2** Linear mixed effect models of denitrification potential in Connecticut salt marshes

Variables	K	AIC <sub>c</sub>	Δ AIC <sub>c</sub>	w <sub>i</sub>
Vegetation	3	70.15	0.00	0.78
Vegetation + pH	4	74.61	4.46	0.08
Vegetation + restoration	4	74.83	4.68	0.08
Vegetation + EC	4	76.43	6.28	0.03
Vegetation + restoration + vegetation × restoration	5	78.36	8.21	0.01
Vegetation + pH + vegetation × pH	5	79.65	9.50	0.01
Vegetation + NH <sub>4</sub> <sup>+</sup>	4	79.90	9.75	0.01
Vegetation + EC + vegetation × EC	5	82.47	12.32	0.00
Site (null model)	2	93.05	22.90	0.00
Vegetation + NH <sub>4</sub> <sup>+</sup> + vegetation × NH <sub>4</sub> <sup>+</sup>	5	96.22	26.07	0.00
Restoration	3	96.86	26.71	0.00

Note: Akaike Information Criterion values adjusted for small sample size (AIC<sub>c</sub>) are included with number of variables, including error and site as a random effect (K), difference in AIC<sub>c</sub> compared to the top model (ΔAIC<sub>c</sub>), and model weight (w<sub>i</sub>).

Abbreviations: EC, soil electrical conductivity; NH<sub>4</sub><sup>+</sup>, soil ammonium; Restoration, tidally restored or unrestricted marsh; Vegetation, vegetation zone dominated by short-form *S. alterniflora*, *S. patens*, or *P. australis*.

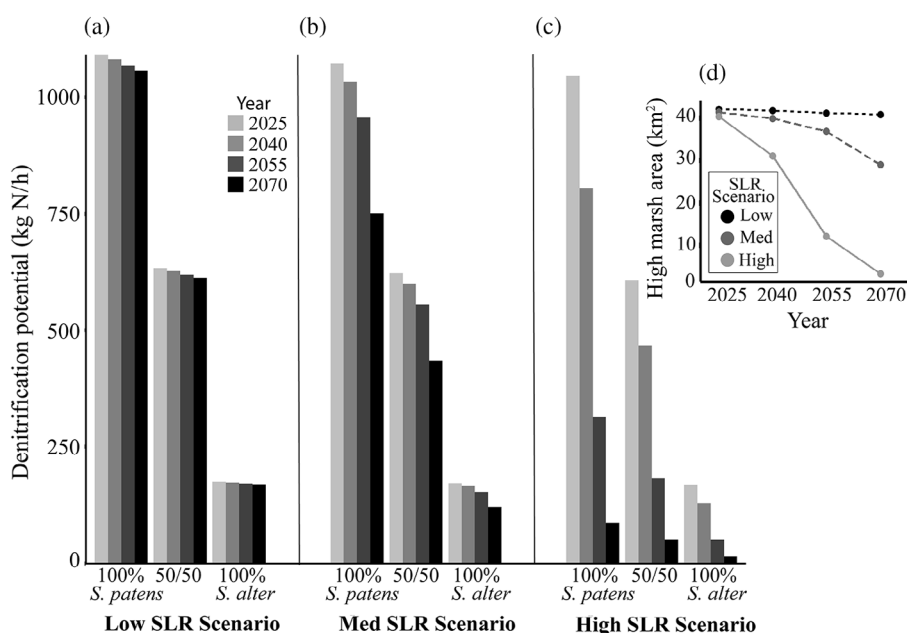
Although adding soil parameters did not improve model fit, there were differences in soil parameters by vegetation zone. As expected, the *P. australis* zone, the zone farthest from tidal channels, was associated with lower EC, lower soil moisture, and lower soil  $\text{SO}_4^{2-}$  (Table 1). Ammonium in the short-form *S. alterniflora* zone (mean, 95% CI; 5.05, 3.03–7.07  $\mu\text{g N h}^{-1} \text{g wet soil}^{-1}$ ) was less than half that in the *P. australis* zone (10.91, 8.05–13.77  $\mu\text{g N h}^{-1} \text{g wet soil}^{-1}$ ). Soil pH was similar across vegetation zones (all 95% CIs within pH of 6 and 7).

Extrapolating denitrification potential across all Connecticut high marsh suggests that the denitrification potential of high marsh could be substantially reduced with SLR, but the magnitude of the reduction depends on the rate and extent to which *S. patens* converts to short-form *S. alterniflora* (Appendix S1: Table S2; Figure 3). Under the low SLR scenario, high marsh area is predicted to decrease by 3% from 2025 to 2070, resulting in similarly small losses of denitrification potential. However, should *S. patens* dominance be completely replaced with that of short-form *S. alterniflora*, losses of denitrification potential could be approximately 25 $\times$  greater than that due to high marsh area loss alone. Under the medium SLR scenario, the predicted loss of high marsh area results in a 30% loss of denitrification potential among vegetation scenarios; yet potential denitrification loss due to shifts in high marsh vegetation is still greater, with denitrification 6 $\times$  higher in 100% *S. patens* than 100% *S. alterniflora* scenarios by 2070. Under the high SLR

scenario, only 8% of high marsh area remains, and the effect of marsh area loss outweighs the effect of vegetation zone change; replacement of *S. patens* by short-form *S. alterniflora* only accounts for 7% of the total loss of denitrification potential in high marshes by 2070. New marsh area formed by transgression at the upland edge is limited by topography and infrastructure in New England, and high marsh migration has been minimal along the Connecticut coast (Field et al., 2017). Potential gains in low marsh area with SLR may offset denitrification losses in high marsh area, but additional data would be required to quantify these gains.

## DISCUSSION

Vegetation zones in salt marshes are good indicators of soil conditions such as flooding frequency and salinity since they reflect the competitive capacity of dominant plant species within narrow ranges of environmental conditions (Bertness, 1991; Mitsch & Gosselink, 2015). We found that (1) vegetation zone was the strongest predictor of denitrification potential and was more important for predicting denitrification potential than pH, EC, soil  $\text{NH}_4^+$ , and tidal restoration status. We also found (2) no significant difference in potential denitrification rates between tidally restored and unrestricted salt marshes, highlighting the utility of vegetation as a scaling factor even across management conditions. Finally, (3) extrapolating denitrification potential with vegetation



**FIGURE 3** Change to denitrification potential of the high marsh zones in salt marshes across the Connecticut coast under low (a), medium (b), and high (c) sea-level rise (SLR) scenarios, and for three vegetation patterns (100% *Spartina patens*, 100% short-form *Spartina alterniflora*, and 50% of each); change to total high marsh area (km<sup>2</sup>) for each SLR scenario (d)



zone shifts suggested that SLR-driven replacement of *S. patens* with short-form *S. alterniflora* could result in substantial losses to high marsh denitrification potential even under low SLR scenarios.

## Vegetation zones as indicators of denitrification

Salt marsh vegetation zone explained 52% of variation in potential denitrification rates measured during the summer across 20 coastal salt marshes. A recent meta-analysis of denitrification in wetlands across the globe (North America, South America, Europe, Asia, and Australia) found that across 36 dominant wetland plant species in eight wetland types (including salt marsh) and 11 denitrification measurement methods, dominant plant species explained 28% of the variation in denitrification rates (Allred & Baines, 2016). Within the meta-analysis, short-form *S. alterniflora*, *S. patens*, and *P. australis* (the focal species of our study) had overlapping confidence intervals (Allred & Baines, 2016); yet, with the experimental control of our single study (uniform method across a single wetland type and region), we found significant differences among these vegetation zones across southern New England. This suggests the need for more replication in studies over larger geographic areas to quantify how denitrification varies with vegetation zones among wetland types and geophysical regions.

While soil characteristics impart well-understood constraints on denitrification and have been shown to correlate with denitrification rates in salt marshes (Santoro, 2010; Simek & Cooper, 2002), our results suggest that vegetation zones in southern New England salt marshes supersede commonly measured soil characteristics in predicting denitrification potential. Short-form *S. alterniflora* zones had lower potential denitrification rates than in the *S. patens* zones despite having similar mean EC, soil  $\text{SO}_4^{2-}$ , soil moisture, bulk density, soil  $\text{NH}_4^+$ , and pH. This may be because short-form *S. alterniflora* outcompetes *S. patens* in areas of prolonged flooding partially due to its ability to efficiently oxidize the rooting zone (Mendelssohn et al., 1981), which can increase oxic conditions in the soil that decrease denitrification. Another mechanism for higher potential denitrification in *S. alterniflora* zones is that prolonged flooding (and lower redox) may also be associated with higher sulfide, which can inhibit heterotrophic denitrification (Yin et al., 2015). Although we did not measure dissolved oxygen concentrations or soil redox as part of our study, high seasonal and diurnal variation in dissolved oxygen concentrations driven by tidal inundation dynamics (Baumann et al., 2015) suggests that vegetation zone may

better represent average soil redox conditions than point measurements of dissolved oxygen or other soil water chemistry metrics.

Our results in short-form *S. alterniflora* and *S. patens* zones were consistent with other research from our study region. Our areal-based measured rates of denitrification potential in the short-form *S. alterniflora* zone (mean  $4.1 \text{ mg N h}^{-1} \text{ m}^{-2}$ ) were higher than the average rates reported for salt marshes across regions and measurement methods in the meta-analysis by Allred and Baines (2016;  $0.69 \text{ mg N h}^{-1} \text{ m}^{-2}$ ,  $n = 17$ ), but similar to those reported in New England salt marshes by Hill et al. (2018; mean  $2.7 \text{ mg N h}^{-1} \text{ m}^{-2}$ ) using similar methods. Denitrification potential in our *S. patens* zones (mean  $25 \text{ mg-N h}^{-1} \text{ m}^{-2}$ ) were similar to those reported for salt marshes by Allred and Baines (2016; mean  $24 \text{ mg N h}^{-1} \text{ m}^{-2}$ ,  $n = 18$ ), which included only salt marshes in New England using similar methods.

Our measurements of denitrification potential in *P. australis* zones were substantially different than values reported in the literature, likely because of the wide range of soil conditions within which *P. australis* grows. Denitrification potential in *P. australis* zones in our study (mean  $56 \text{ mg N h}^{-1} \text{ m}^{-2}$ ) were higher than those reported across wetland types, regions, and measurement methods (mean  $13 \text{ mg N h}^{-1} \text{ m}^{-2}$ ,  $n = 57$ ; Allred & Baines, 2016). In contrast, our measured rates of denitrification in *P. australis* zones (per soil mass, mean  $835 \text{ mg N h}^{-1} \text{ m}^{-2}$ ) were less than half the rates measured at 12 *P. australis*-dominated plots across a single New England salt marsh complex (mean  $1749 \text{ ng N h}^{-1} \text{ g}^{-2}$ ; Windham & Meyerson, 2003). Within our data set, *P. australis* denitrification rates were highly variable (coefficient of variation,  $\text{CV} = 149$ ) relative to *S. alterniflora* ( $\text{CV} = 84$ ) or *S. patens* ( $\text{CV} = 79$ ) and occurred across a wider range of soil conditions (EC, soil moisture, soil  $\text{SO}_4^{2-}$ , and bulk density, Table 2).

Although average denitrification rates were similar for *P. australis* and *S. patens* across our 20 salt marsh sites, local soil characteristics may drive different patterns among these two vegetation zones for individual salt marshes. Invasive *P. australis* is able to exploit a wide range of soil conditions; thus, strong spatial gradients driven by soil characteristics or external inputs (e.g., nitrogen; White & Reddy, 1999) could account for this variability. Barry et al. (2022) found that the two *P. australis* plots with the highest denitrification rates also had higher relative abundances of nitrogen-fixing bacteria, suggesting rapid utilization of nitrogen by the microbial community that would not be reflected in our soil chemical measurements. *P. australis* also have a deeper rooting system than native marsh grasses and are able to exploit deeper porewater nutrients than native

grasses (Mozdzer et al., 2016), which could also account for the lack of relationship between *P. australis* zone denitrification potential and soil properties in the upper 10 cm of soil. Important plant–soil interactions may occur deeper in the soil profile that are not captured by our study.

## Tidal restoration

Restoration status was not a good predictor of denitrification potential across the 20 salt marshes in our study, and we did not find a significant relationship between denitrification potential and time since restoration for any of the three vegetation zones. Although a positive correlation between time since restoration and denitrification potential has been found in brackish wetlands in Connecticut (Doroski et al., 2019), the lack of a relationship in our study aligns with observations from Elphick et al. (2015) who found that upper high marsh vegetation like *S. patens* did not fully return to tidally restored salt marshes even decades after restoration. Our findings suggest that shifts in vegetation zones may be better indicators of landscape-scale changes in salt marsh denitrification than restoration status or age alone.

Tidal flow restoration in New England salt marshes is typically conducted with the goal of replacing invasive *P. australis* zones with native salt marsh species like *S. alterniflora* and *S. patens* (Roman & Burdick, 2012). Given that *S. patens* and *P. australis* zones had comparable 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 *P. australis* be replaced by short-form *S. alterniflora* rather than *S. patens*, as is common in New England salt marshes (Burdick et al., 1996; Elphick et al., 2015; Roman et al., 2002), then the landscape-scale denitrification potential may decrease after tidal flow restoration. The direction of change may also depend on local soil characteristics and site-specific restoration of marsh elevation and hydrology since denitrification potential in *P. australis* zones is highly variable. Understanding variability in denitrification rates across *P. australis* zones is an important challenge for being able to predict denitrification outcomes of tidal restoration in salt marshes.

There are some potentially important effects of restoration on denitrification not captured by our study design that should be considered when interpreting our results. First, we did not weight our sampling efforts by the spatial extent of different vegetation zones in the restored versus reference wetlands, so our design compares

denitrification potential among vegetation zones but does not account for changes in the spatial distribution of vegetation zones that occurs with restoration. Second, our research focused on potential denitrification in the homogenized upper 10 cm of soil and we may have missed longer-term effects of tidal restoration on the soil denitrifier community that can increase with soil depth (Bernhard et al., 2015). Third, the management history and types of restoration activities (Appendix S1: Table S1) varied among our sites, likely driving unaccounted differences in recovery trajectories across restored wetlands. Finally, though we measured some marsh-specific soil properties, other parameters with strong responses to salt marsh tidal restoration may have varied among sites (e.g., sulfide, iron; Portnoy & Giblin, 1997; Portnoy, 1999) depending on site specific soil characteristics, management history, and hydrology. In a meta-analysis of 621 wetland sites, recovery of C and N storage after restoration was highly variable and denitrification was not documented well enough in the literature to be included (Moreno-Mateos et al., 2012). Our work suggests that how restoration alters the plant community could potentially be a good indicator of its effects on salt marsh denitrification, yet continued measurement of the recovery trajectories of denitrification after tidal flow restoration may better inform variation of recovery within dominant vegetation zones.

## Sea-level rise and high marsh change

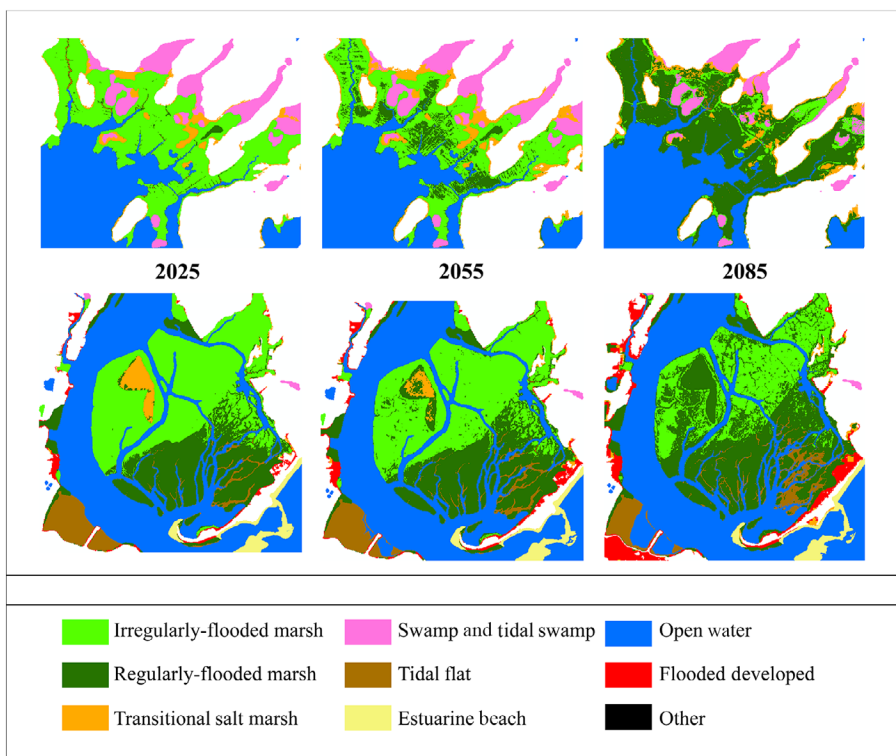
While prior research has shown that loss of salt marsh area will lead to losses in denitrification potential (Craft et al., 2009), our results indicate that the loss of denitrification due to shifts in dominant vegetation zones have the potential to be substantially greater than the loss of denitrification due directly to loss of high marsh land area under low and medium SLR scenarios (Appendix S1: Table S2). As SLR alters the hydrology of salt marshes, *S. patens* zones are disappearing due to increased flooding frequency and being replaced by the more inundation- and salinity-resistant short-form *S. alterniflora* (Donnelly & Bertness, 2001; Pezeshki & Delaune, 1993; Smith, 2015). Despite their proximity in the high marsh, short-form *S. alterniflora* vegetation zones were associated with lower average denitrification potential than *S. patens* zones, which could be reflective of the difference in their adaptation to different soil conditions (Bertness, 1991). Consequently, the denitrification potential in the high marsh is threatened not only by loss of area but also from shifting vegetation zones that may reflect fundamental changes in underlying soil characteristics and plant–soil feedbacks. Under the high SLR scenario, 92% of high marsh would be replaced by regularly flooded marsh,

rendering the effect of dominant vegetation less important for high marsh denitrification than high marsh area loss.

Given the current and historical trend of both high marsh vegetation shifts and areal loss representing substantial losses to denitrification potential, we suggest that management efforts consider not only conserving high marsh area but also maintaining *S. patens* coverage and soil conditions that are conducive to *S. patens* success. This approach would align with ongoing management agency plans to protect salt marsh specialist species that are threatened with extinction, such as the Saltmarsh Sparrow *Ammospiza caudacuta* (Atlantic Coast Joint Venture, 2020; Field et al., 2017). Yet, the extent of high marsh loss is highly variable across individual salt marshes (Figure 4), which is consistent with historical trends in the region (Cameron Engineering and Associates, 2015; Smith, 2015). In southern New England, marsh migration and new marsh formation is limited by topography and infrastructure, and even in zones where high marsh migration is predicted along the Connecticut coast, there is little evidence for widespread inland shifts (Field et al., 2017). Though we show a potential decrease in denitrification potential for high marsh, the same loss of denitrification potential we estimate in our scaling exercise due to

vegetation shifts would likely not occur in areas where substantial marsh migration is expected (Kirwan et al., 2016). Important management decisions will have to focus on how conservation efforts are distributed among preserving the most resilient or restoring more susceptible marshes, and whether substantial marsh migration is expected to occur in a given area.

While our results showed that the replacement of *S. patens* by short-form *S. alterniflora* could have substantial consequences for denitrification potential, this pattern of change is ultimately limited to the low-to-high marsh transition zone. Extending our understanding of the effects of SLR-driven vegetation change on denitrification beyond high marsh will require characterization of other major vegetation zones, especially tall-form *S. alterniflora*. At our 20 study marshes, the primary habitat of tall-form *S. alterniflora* was creek banks, although it is more extensive in some Connecticut marshes. Tall-form *S. alterniflora* zones have been associated with higher nitrogen retention by sediments and plant biomass than the marsh interior, an effect attributed to better soil aeration, more frequent tidal flushing, higher nutrient inputs, and lower sulfide (Anderson et al., 1997; Gribsholt et al., 2005; Howes & Goehring, 1994).



**FIGURE 4** Land cover change to Barn Island Wildlife Management Area, Stonington, Connecticut (top panels) and Charles E. Wheeler Wildlife Management Area (bottom panels) as predicted by SLAMM (Clough et al., 2015) 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 and Wheeler representative of the most resilient wetlands

Furthermore, studies have shown that tall-form *S. alterniflora* is associated with higher denitrification rates than both short-form *S. alterniflora* (Dollhopf et al., 2005; Kaplan et al., 1979) and *S. patens* zones (Wigand et al., 2004). The SLAMM model predicts a 20%, 144%, and 282% increase in low marsh area across the low, medium, and high SLR scenarios, respectively, by 2070, although the area will begin to decrease after 2070 in the high SLR scenario. With SLR-driven expansion of low marsh habitat, 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*. How denitrification potential in newly formed tall-form *S. alterniflora* zones will compare to current high marsh denitrification potential, and the extent to which low marsh will survive SLR without drowning, remain important uncertainties for scaling denitrification in coastal salt marshes. Marsh drowning (or the conversion of low marsh to open water) may be locally important but according to SLAMM model predictions, net loss of low marsh area is only expected to occur substantially across the Connecticut coast under the most extreme SLR scenarios (High-Med and High) and at earliest between 2070 and 2085.

Our spatial extrapolations of future denitrification potential, given plausible SLR-induced changes across the landscape, illustrate the importance of vegetation change, marsh loss, and migration, to changes in marsh function. Given the considerable challenges associated with spatial extrapolation, we caution against overinterpreting the specific landscape-scale denitrification potential values we report here. Our results simply illustrate the potential importance of vegetation shifts on changes in denitrification at the landscape-scale. Nonetheless, we see our estimates as an important first step, and the magnitude of our initial projected changes as a sign that refining these estimates will be key to understanding how salt marsh denitrification services will change under future climatic conditions.

## Denitrification across dynamic salt marsh landscapes

Our measurement of denitrification potential using denitrification enzyme assays (DEAs) represents the maximum capacity of the standing stock of enzymes to denitrify given unlimited electron donor and acceptor supply. Denitrification potential rates are often thought to represent average long-term denitrification rates, since the denitrifier population responds over time to environmental drivers. Thus, denitrification potential does not capture the dynamics of active, in situ plant–soil interactions (e.g., rhizosphere oxidation and fresh root exudates)

or environmental drivers (e.g., floods, changing oxygen, nitrogen, and carbon availability), but rather the indirect effects of those mechanisms over time on the denitrifier population. In our salt marshes with low in situ nitrate availability, we expect denitrification rates measured using DEAs to be generally higher than in situ denitrification rates. Yet, Alldred and Baines (2016), did not find a significant effect of denitrification method in their meta-analysis across wetland types, with laboratory rates similar in magnitude and patterns among vegetation zones as in situ rates. Although laboratory-based assays lack some representation of environmental drivers, they are efficient for analyzing numerous samples and can inform where and when to use more resource-intensive in situ techniques that are difficult to apply across many field sites.

Our study focused on denitrification potential during the late summer. Denitrification rates can vary seasonally in salt marshes, though there is considerable uncertainty around dominant seasonal patterns. Most research on salt marsh denitrification has been conducted during the summer (Alldred & Baines, 2016), and research focused on seasonal differences has reported varying patterns, with denitrification peaking in the winter (Sousa et al., 2012), during warmer months and the growing season (Kleinhuizen & Mortazavi, 2018; Velinsky et al., 2017), or in the spring and fall outside of the peak growing season (Eriksson et al., 2003; Granville et al., 2021; Hamersley & Howes, 2005). In one of our study wetlands, Granville et al. (2021) found denitrification potential peaked early (May) and late (October) in the growing season. During the growing season, plants may inhibit denitrification rates by directly competing with denitrifiers for soil  $\text{NO}_3^-$  or by transporting oxygen into the soil, creating conditions unfavorable for denitrification (Colmer, 2003; Hamersley & Howes, 2005; Nelson & Zavaleta, 2012). In another New England salt marsh, Kaplan et al. (1979) found that in situ denitrification rates peaked during summer months and were directly related to air temperature, presumably driven by higher microbial processing rates at warmer temperatures. Disentangling drivers of seasonal patterns of denitrification and how vegetation zonation is interrelated with those patterns is an important next step for understanding whether vegetation is a strong predictor of denitrification rates across seasons.

We expect that vegetation zones could also be helpful indicators for other important nitrogen transformation pathways not explicitly considered in this study. Nitrification, the oxidation of ammonium to nitrate, can be a substantial source of nitrate for denitrification, particularly in salt marshes with low nitrate availability (Koop-Jakobsen & Giblin, 2010). We expect that coupled



nitrification–denitrification could differ among the vegetation zones we considered since short-form *S. alterniflora* more efficiently oxidizes its rhizosphere than *S. patens* or *P. australis* (Mendelsohn et al., 1981). Soil  $\text{NH}_4^+$  was higher in *P. australis* than the other two vegetation zones, suggesting either more  $\text{NH}_4^+$  available for nitrifiers or a lack of nitrification leading to the accumulation of soil  $\text{NH}_4^+$ . The dissimilatory reduction of nitrate to ammonium (DNRA) can also be an important nitrate transformation in salt marshes (Koop-Jakobsen & Giblin, 2010) and elevated sulfide concentrations are correlated with a shift from denitrification to DNRA (Murphy et al., 2020). Elevated sulfide in salt marshes may also favor sulfide-oxidizing-bacteria, which can use sulfide as an alternate electron donor for denitrification (Lu et al., 2018). Because *S. alterniflora* zones are associated with more prolonged flooding, they are likely also associated with higher sulfide and associated alternate nitrate reduction pathways (sulfur-driven denitrification and DNRA), though the DEA method we used does not directly account for these nitrogen transformations. Ultimately, denitrification is an emergent soil process driven by environmental factors linked to nitrogen and other elemental transformation pathways.

## CONCLUSIONS

Our results show that salt marsh vegetation zones are strong indicators of denitrification potential and that the influence of tidal restoration on denitrification should be tracked through vegetation response rather than restoration status alone. Furthermore, we found that 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 transition zone. 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.

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## CONFLICT OF INTEREST


The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Lawrence et al., 2021) are available in Dryad at <https://doi.org/10.5061/dryad.vmcvdcns7>.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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