Denitrification Potential and Carbon Mineralization in Restored and Unrestored Coastal Wetland Soils Across an Urban Landscape

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Abstract

The recovery of wetland function after tidal flow restoration may be influenced by water pollution and sea level rise. Our objective was to examine the effects of tidal flow restoration on denitrification potential and carbon (C) mineralization across an urban coastal landscape. Soil cores were collected from 32 tidal wetlands in Connecticut, U.S.A., spanning a wide range of salinity (0.3–29 ppt) and watershed development (<1–79%). In brackish wetlands, denitrification potential increased with time since restoration, while C mineralization showed no significant relationship. Soil chemistry was also a strong predictor of process rates; best fit multiple linear regression models for denitrification included both soil chemistry variables and time since restoration. Although principal components analysis revealed soil chemistry overlapped by wetland type (freshwater, saline, or brackish), process rates in freshwater versus brackish wetlands had different relationships with soil chemistry. In freshwater wetlands, denitrification potential and C mineralization increased with soil metal content. In brackish wetlands, denitrification potential decreased with increasing salinity and C mineralization increased with increasing organic matter, soil moisture, and ammonium. Our results highlight the potential for biogeochemical processes to recover after wetland restoration, along with complex interactions between these processes and chemicals in developed coastal landscapes.

Introduction

Human alteration of coastal wetland hydrology through artificial drainage networks and installation of physical barriers that restrict tidal flow, such as berms or dikes, tidal gates, and culverts, is widespread (Gedan et al. 2009). Restricted tidal flow causes marshes to become fresher and receive less inorganic sediment inputs, which can alter vegetation communities and biogeochemical cycling. Tidal flow restoration techniques are increasingly implemented to restore wetland hydrology (Gedan et al. 2009), typically to improve fish passage, restore habitat, and reduce invasive plant species (Chambers et al. 2002; Elphick et al. 2015). Even though tidally restored wetlands tend to exhibit faster biogeochemical recovery than other types of restoration, recovery can take decades, the effect of restoration on carbon (C) and nitrogen (N) storage is highly variable, and there is typically less focus on improving and monitoring biogeochemical function post-restoration (Moreno-Mateos et al. 2012). Predicting and understanding biogeochemical recovery trajectories of coastal wetlands is difficult, likely in part because tidal flow restoration often occurs in densely populated coastal areas where wetlands experience multiple stressors simultaneously, including elevated nutrient and metals loading and sea level rise, which may confound changes in C and N cycling that occur as a result of restoration.

Land development in coastal zones contributes excess nutrients (Carpenter et al. 1998) and urban contaminants such as Cu and Pb (Bergback et al. 2001; Revitt et al. 2014) to wetlands. Coastal wetlands retain nutrients and metals in their soils and vegetation, and can act as long-term sinks for nutrients (Valiela and Teal 1979) and metals (Williams et al. 1994). Nutrient enrichment can alter microbial processes, such as

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denitrification (the microbial reduction of nitrate to N_2 gas) and soil C mineralization, directly by adding reactive N, as well as indirectly by increasing plant biomass and changing the composition of wetland plant communities (Deegan et al. 2007; Gedan et al. 2009). Carbon and N microbial processes are also linked with metals through enzymatic requirements, such as Cu for denitrification, (Glass and Orphan 2012), redox pairs for microbial metabolism (Mn and Fe reduction; Lovley and Phillips 1988; Lovley 1991; Nealson and Myers 1992; Thamdrup 2000), and toxicity effects on enzymes or microbial metabolism (Giller et al. 1998; Rajapaksha et al. 2004); however, the effects of elevated metals from developed landscapes on microbial C and N processes are not well understood in coastal wetland ecosystems.

Saltwater intrusion elevates concentrations of ions (i.e. Cl^-, Na^+, SO_4^{2-}, Mg^{2+}), which may have varying effects on microbial C and N cycling in wetlands. In a laboratory experiment, Magalhaes et al. (2005) found no effects of elevated salinity on denitrification, suggesting presence of salt tolerant denitrifying species. In other field and laboratory experiments, elevated salinity decreased denitrification (Rysgaard et al. 1999; Putnam Duhon et al. 2012) potentially due to osmotic stress of microbes (Panswad and Anan 1999). Denitrification may also be inhibited or enhanced by elevated sulfate (SO_4^{2-}) from seawater. Hydrogen sulfide produced by SO_4^{2-} reduction inhibits the last step of denitrification to N_2 gas (Senga et al. 2006; Pan et al. 2013). In contrast, other forms of sulfide may also serve as an alternate electron donor for denitrification (Burgin and Hamilton 2007), potentially increasing rates of denitrification.

Carbon cycling is influenced by saltwater intrusion through effects on microbial processing (Pathak and Rao 1998), plant communities (McKee and Mendelssohn 1989), and organic matter quality and quantity (Morrissey et al. 2014). The effects of salinity on C mineralization rates are still unclear (Herbert et al. 2015). After years of in-situ saltwater treatments, C mineralization rates were lowered in experimental plots with elevated salinity compared to freshwater plots (Neubauer et al. 2013). The reduction of methane (CH_4) production in soils with elevated sea salts suggests SO_4^{2-} reducers outcompete methanogens (Bartlett et al. 1987; Megonigal et al. 2004). In contrast, other researchers have found increased CH_4 emissions in wetland soil cores receiving saltwater treatments (Weston et al. 2011; Ardón et al. 2018; Helton et al. 2019). Effects of saltwater intrusion on C cycling are further complicated by interactions with plant nutrient cycling and community shifts (Krauss et al. 2012). Excess salinity caused plant mortality and led to a community shift dominated by salt tolerant species (Glenn et al. 1995). Factors such as the quality and quantity of autochthonous organic inputs of plants (Neubauer et al. 2013), the duration of saltwater intrusion (Weston et al. 2010; Marton et al. 2012; Neubauer et al. 2013), and the flooding regime of the wetland (Ardón et al.

2018; Helton et al. 2019) may influence the magnitude and response of C cycling. Thus, tidal flow restoration occurs within the context of many possible, and sometimes contrasting, drivers of C and N processing.

Our overall goal was to quantify patterns of denitrification potential and C mineralization in coastal wetland soils across an urban landscape with a wide range of salinity and watershed development. Specifically, the objectives of this study were to 1) measure how soil chemistry, denitrification, and C mineralization vary between tidal flow restored versus unrestored wetlands and with age of tidal flow restoration, and 2) identify potential controls on denitrification and C mineralization across this heterogeneous landscape. The patterns of ecosystem function across diverse chemical conditions offer insight into how wetlands may respond to future changes in saltwater intrusion and land development.

Methods

Study Sites

We collected soil cores from 32 tidal wetlands along the Long Island Sound in Connecticut (CT), U.S.A, including 17 restored tidal wetlands and 15 unrestored tidal wetlands (Fig. 1). Restored and unrestored sites were identified with help from CT Department of Energy and Environmental Protection (CT DEEP; P. Capotosto and R. Wolfe, *personal communication*, March 2, 2015). Completion of tidal flow restoration at sampling sites ranged from 1 to 23 years prior to sampling. For our purposes, tidal flow restoration included any combination of restoration practices that restored tidal hydrology to a tidally restricted wetland, for example culvert replacement, tidal gate removal, and installation of self-regulating tide gates. Unrestored wetland sites were chosen as tidal wetlands from the 1990s tidal wetlands shapefile (CT DEEP 1999) with no known tidal flow restoration. Because virtually all salt marshes were ditched or altered for mosquito control practices (Rozsa 1995), unrestored sites represent current conditions of a range of wetlands in the coastal landscape of CT, rather than reference sites. Wetland sampling sites ranged in surface water salinity from 0.03 to 29.04 ppt (556 MPS, YSI Inc., Yellow Springs, OH) at time of sampling, and included six saline, 19 brackish, and seven freshwater wetlands as defined by polyhaline (>18 ppt), oligohaline to mesohaline (0.5–18 ppt) and freshwater (< 0.5 ppt) salinity classes (Cowardin et al. 1979). Wetland sampling sites also encompassed a range of watershed land development, from less than 1% to 79% (mean ± SEM, 20 ± 2.6%) of watershed area with mean watershed size of 3867 ± 1204 km^2 (NHDPlus 2011).
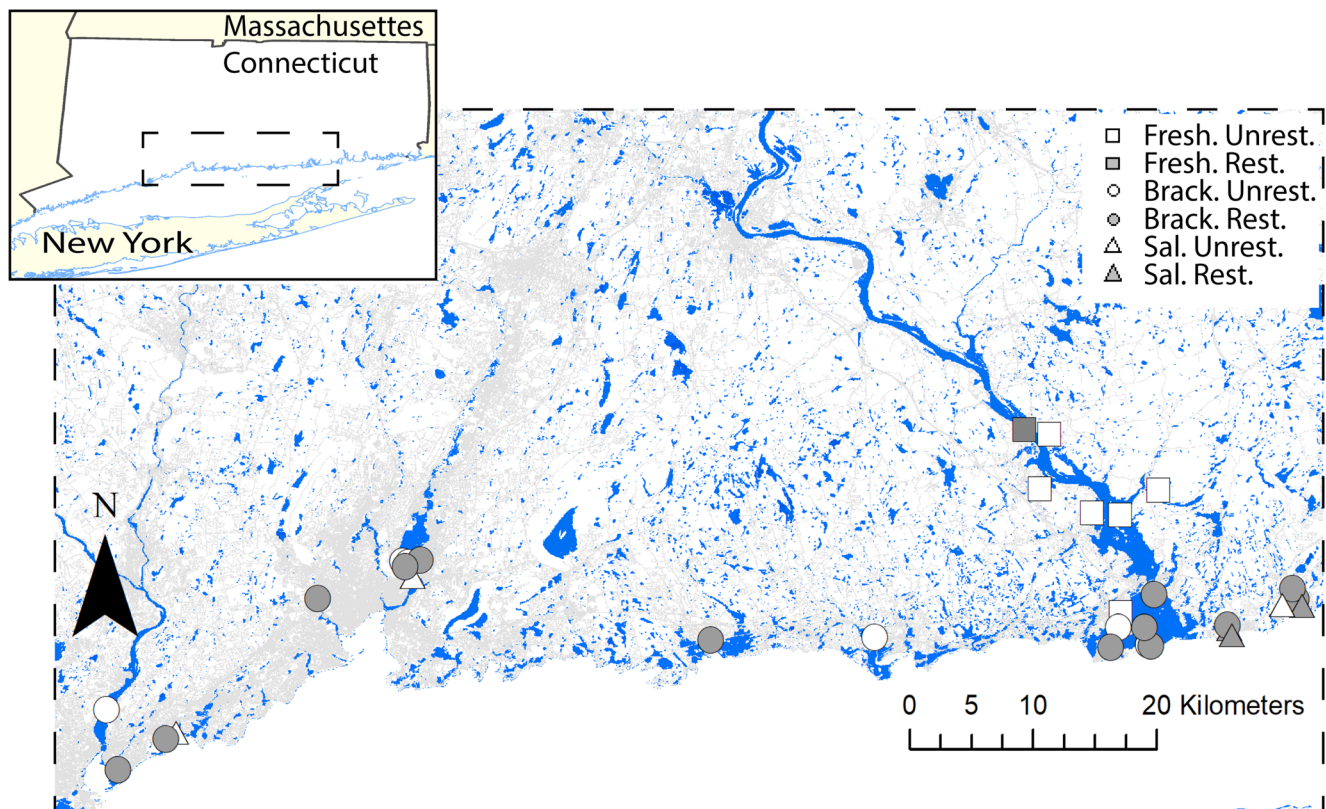
Fig. 1 Wetland sampling site locations in Connecticut with developed land cover (grey) and water (black) from 2010 land cover data (CLEAR 2015)

Field Sampling and Soil Processing

At each site, three to four soil cores were collected with a slide hammer (5 cm dia., 15 cm length) within three hours of high tide during July of 2015. Samples were collected within ~500 m of the terrestrial wetland edge. We analyzed the top five centimeters of soil. Large roots were removed and soil cores were composited, sieved (2 mm), and homogenized before analysis.

Soil Chemistry

Soil organic matter was determined by loss on ignition. Samples were dried at 105 °C for 72 h to determine moisture content and combusted at 550 °C for four hours to determine percent organic matter (adapted from USDA-NRCS 1996).

We extracted soil ammonium (NH_4^+) and nitrate (NO_3^-) with 2 N KCl by adding 25 ml of KCl solution to 2.5 g of field moist soils, shaking for 30 min at 200 rpm, centrifuging for 5 min at 2400 rpm, and filtering supernatant through Whatman 589/1 filters (adapted from Keeney and Nelson 1982). Extracts were analyzed on a SmartChem®200 discrete analyzer (Westco Scientific Instruments, Brookfield, CT) by the phenate method (APHA, WEF, AWWA 1999) for NH_4^+ and by colorimetric determination with enzymatic

reduction (Campbell et al. 1997; Patton and Kryskalla 2011) for NO_3^-. Ninety-seven percent of samples analyzed for soil extractable NO_3^- were below the detection limit (0.11 mg N L^{-1}). Therefore, NO_3^- was not included in further analysis. All NH_4^+ concentrations were above the detection limit (0.12 mg N L^{-1}).

Soil electrical conductivity (EC) was determined using the soil:water ratio, by volume, of 1:5 ($EC_{1:5vol}$) (USDA-NRCS 2011). Soil EC measurements were made with an Oakton Con5 Acorn Series Conductivity/°C Meter (Oakton Instruments, Vernon Hills, IL). Additionally, we extracted soil chloride (Cl^-) and sulfate (SO_4^{2-}) by adding 25 ml of distilled, deionized water to 2.5 g of field moist soil, shaking for 30 min at 200 rpm, centrifuging for 5 min at 2400 rpm, and filtering supernatant through Whatman GF/F filters. Water extractable Cl^- and SO_4^{2-} concentrations were analyzed by ion chromatography (ICS-1100; Thermo Fisher Scientific, Waltham, MA). As expected, Cl^- and SO_4^{2-} concentrations were positively correlated with each other ($r^2 = 0.85$, $p < 0.001$) and with soil EC (Cl^-, $r^2 = 0.89$; SO_4^{2-}, $r^2 = 0.78$; $p < 0.001$). Thus, soil EC was included in analysis as a surrogate of combined effects of both salt anions (i.e. Cl^- and SO_4^{2-}).

Total soil metal concentrations of redox active metals, Fe and Mn, and common urban metals, Cu, Pb, and Zn were determined by acid digestions with 70% HNO_3 (trace metal grade) and 30% H_2O_2 according to Method 3050B (US EPA

1996). Metals were analyzed with an Inductively Coupled Plasma Mass Spectrometer (ICP-MS, Agilent 7700x with He collision cell, Agilent, Delaware, USA).

Soil Process Rates

We measured denitrification enzyme activity (DEA) on homogenized soils (Groffman et al. 1999). Denitrification enzyme activity is a measure of denitrification potential since the assays remove limiting factors; they are conducted under anoxic conditions with excess C and NO_3^-. Following the procedure in Groffman et al. (1999), we added 5 g of field moist soil to 10 ml of DEA media (0.72 g KNO3, 0.5 g glucose, 0.125 g Chloramphenicol per liter of distilled, deionized water) in 125 ml glass flasks with gas-tight seals and flushed the headspace with N_2 gas to create anoxic conditions. We added 10 ml of acetylene gas to block the reduction of N_2O to N_2 gas. Headspace gas was sampled for four time-points (i.e. approximately 0, 30, 60, and 90 min after start of incubation) and analyzed for N_2O on a Clarus 580 gas chromatograph (GC) equipped with an electron capture detector (PerkinElmer, Shelton, CT). Samples were delivered to the GC with a TurboMatrix 40 Trap Headspace Autosampler (PerkinElmer, Shelton, CT). Denitrification rates were calculated as the linear rate of evolved N_2O-N over time per gram of dry soil.

We calculated the minimum detectable concentration difference (MDCD) for N_2O following Yates et al. (2006). For fluxes above MDCD, when the $r^2 > 0.85$ we used the slope based on the full 90 min incubation. When gas accumulation was non-linear (i.e., $r^2 < 0.85$) over the full incubation, we calculated flux excluding time 90 and/or time 60. Nitrous oxide fluxes in four assays were below MDCD, and we set these fluxes to zero for analysis.

Soil C mineralization rates were measured as CO_2 accumulation from 5 g of field moist soils in a 100-mL sealed serum bottle over a three-day incubation. Headspace CO_2 was sampled immediately after bottles were sealed and after one and three days. We used the substrate-induced respiration (SIR) method (Anderson and Domsch 1978; West and Sparling 1986) as an index for soil microbial activity. SIR is positively correlated with total microbial biomass (Beare et al. 1990) and is commonly used as an indirect measurement of total microbial biomass (Bååth and Anderson 2003). SIR was measured as CO_2 accumulation after adding 10 mL of yeast solution to 5 g of field moist soil in 40 mL sealed amber vials. Headspace CO_2 was sampled immediately after vials were sealed and after 2 and 4 h. Headspace CO_2 samples for C mineralization and SIR were immediately injected into a LI-840A CO_2/ H_2O Gas Analyzer (LI-COR, Lincoln, NE) to measure CO_2 concentration. Carbon mineralization and SIR were

calculated as the linear rate of accumulated CO_2-C over time per gram of dry soil.

Statistical Analyses

We determined statistically significant differences among wetland (fresh, brackish, saline) and management (restored, unrestored) categories for soil chemistry and biogeochemical processes (denitrification potential, C mineralization, and SIR) using the method of analysis of multiple means described by Herberich et al. (2010), which does not require normality, equal variances, or equal sample sizes. Because we were only able to sample one restored freshwater wetland, that category was not included in this analysis.

We used principal component analysis (Mardia et al. 1979; prcomp function in R Core Team 2015) of soil chemical variables 1) to understand patterns in soil chemistry among wetland and management categories and 2) as composite variables in regression analysis to avoid violating the multi-collinearity assumptions of regression. For the whole dataset we used simple linear regression ((R function 'lm()') to determine relationships between principal components and soil process rates. Because the number of restored wetlands sampled was low in freshwater ($n = 1$) and saline ($n = 3$), we used restored brackish wetlands ($n = 13$) to determine relationships between 1) time since restoration and soil processes using simple linear regression, and 2) time since restoration, principal components, and soil processes using multiple linear regression. We performed multiple linear regression model selection by exhaustive search (R function 'regsubsets()'). The best fit models were selected by the lowest Akaike Information Criterion (AIC) (R function 'extractAIC()') given all combinations of parameters (Burnham et al. 2011). Statistical analyses were performed using R version 3.1.3 (R Core Team 2015).

Results

Soil Chemistry

Across all sites ($n = 32$), soil EC reflected a wide range in wetland salinity with soil EC significantly highest in saline and lowest in freshwater wetlands, as expected (Fig. 2a). Percent organic matter was also highest in saline and lowest in freshwater wetlands (Fig. 2b). Ammonium was not significantly different among wetland and management types but tended to be higher in restored versus unrestored wetlands (Fig. 2c). Metal concentrations tended to be lower in restored saline wetlands than in other wetland types; however, because of high variability in metal concentrations, the difference was only significant between restored saline wetlands and unrestored brackish wetlands for Mn and restored brackish wetlands for Cu, Pb, and Fe (Table 1).
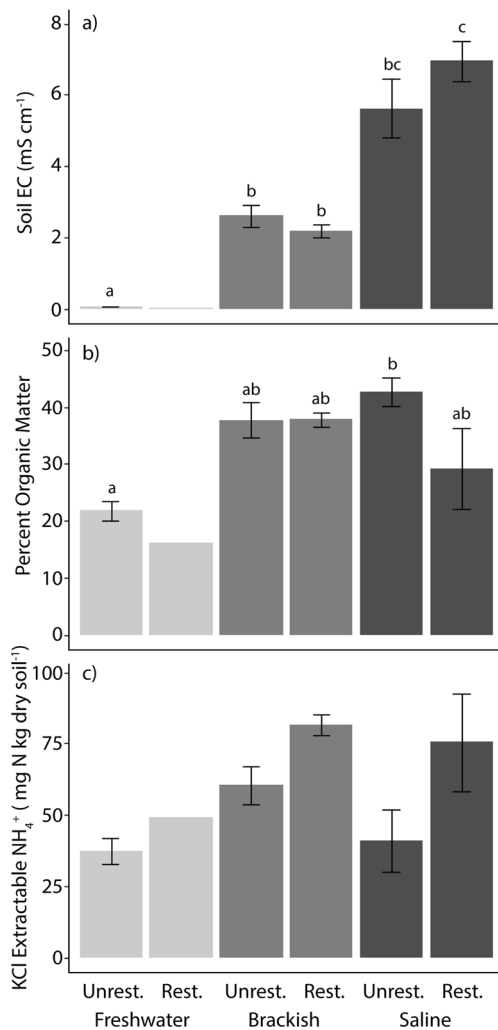
Fig. 2 Mean (± standard error) for **a)** soil electrical conductivity (EC), **b)** percent organic matter, and **c)** KCl extractable NH$_4^+$ by management and wetland type. Letters denote significant differences at p < 0.05

related to percent organic matter, soil moisture, cation exchange capacity, and soil NH$_4^+$. Component 2 (PC2) represents a continuum of metal concentration; it is negatively related to soil Fe, Pb, Zn, and Cu. Component 3 (PC3) represents a salinity continuum; it is positively related to salinity and negatively related to soil Mn.

High variation in soil chemistry among wetland types led to indistinct groupings along principal component axes. Wetland types largely overlapped along the PC1 axis (Fig. 3). Similarly, wetland types largely overlapped along the PC2 axis, except restored saline wetlands (grey triangles in Fig. 3a) tended to have higher values for PC2, representing lower metal content in these wetlands (Table 2). Component 2 was also negatively related to the percent of developed land cover in the draining watershed ($r^2 = 0.25$, $p = 0.003$), suggesting metal loading increases with increasing developed watershed land cover. Freshwater and saline wetlands had distinct separation along the PC3 axis (triangles versus squares in Fig. 3b), with higher PC3 values for saline wetlands, which have lower Mn and higher salinity. Except for PC2 for saline wetlands, we did not observe distinct separation in soil chemistry between restored and unrestored wetlands for any wetland type.

Within the restored brackish wetland group (n = 13), neither PC1 ($p = 0.90$) nor PC2 ($p = 0.51$) was significantly related to time since restoration. Component 3 was negatively related to time since restoration ($r^2 = 0.24$, $p = 0.09$). Manganese (which had a high loading for PC3) was the only soil chemistry variable with a significant relationship with time since restoration, increasing with time since restoration ($r^2 = 0.29$, $p = 0.05$). This pattern was driven by one wetland sampled 22 years post restoration that had Mn concentration greater than four times the next highest value.

Denitrification Potential and Carbon Mineralization

Denitrification potential tended to decrease from fresh to saline wetlands and tended to be lower for restored wetlands across wetland types; however, because of high variation for some wetland types the difference was not significant between groups (Fig. 4a). Across the whole dataset,

Principal components analysis of the soil chemistry variables resulted in 10 components. Component 1 (35%), component 2 (27%), and component 3 (14%) each explained greater than 10% of the variation and the majority of cumulative variance (76%), so we focus our results on these three components (Table 2). Component 1 (PC1) is positively

Table 1 Mean (standard error) soil metal concentrations

Wetland Type	Management	Number of sites	Cu (mg kg^{-1} soil)	Pb (mg kg^{-1} soil)	Zn (mg kg^{-1} soil)	Mn (mg kg^{-1} soil)	Fe (kg kg^{-1} soil)
Fresh	Unrestored	6	[ab]29.0 (2.88)	[ab]39.4 (3.56)	[a]77.3 (19.1)	[ab]422.6 (47.3)	[ab]15.4 (1.28)
	Restored	1*	48.5	16.7	75.7	467.1	34.2
Brackish	Unrestored	6	[ab]113.5 (16.5)	[ab]87.1 (11.0)	[a]125.6 (31.1)	[a]229.1 (12.4)	[ab]20.3 (1.26)
	Restored	13	[a]53.3 (2.68)	[a]89.9 (6.10)	[a]78.7 (11.5)	[ab]284.0 (29.1)	[a]23.2 (1.08)
Saline	Unrestored	3	[ab]98.9 (22.9)	[ab]104.2 (22.1)	[a]62.4 (17.0)	[ab]158.5 (13.3)	[ab]26.4 (7.47)
	Restored	3	[b]19.7 (2.34)	[b]18.9 (2.34)	[a]42.2 (6.8)	[b]96.3 (8.80)	[b]9.79 (1.20)

Letters denote significant differences at $p < 0.05$. *Not included in statistical analysis

Table 2 Loadings to each component from principal component analysis with loadings > 0.40 bolded
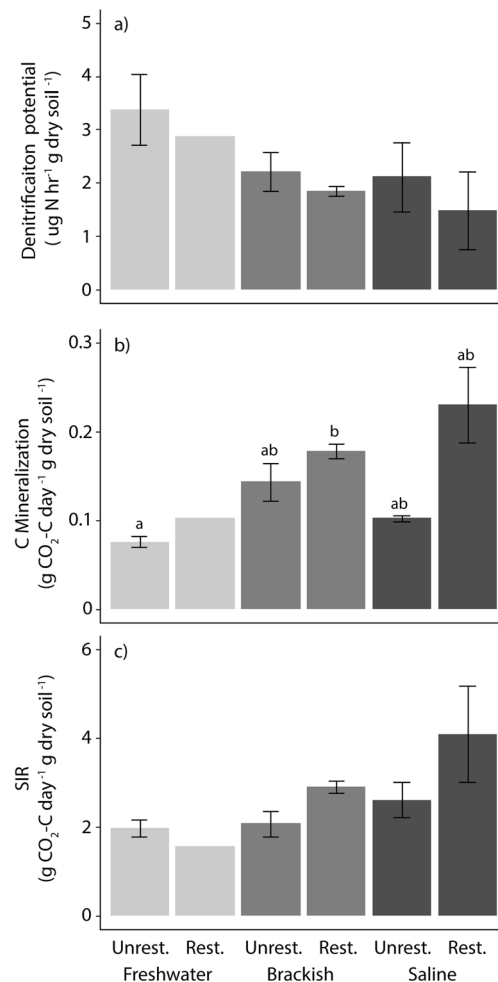
	PC1	PC2	PC3
Percent OM	**0.49**	−0.12	0.05
Soil Moisture	**0.49**	0.02	0.19
NH_4^+	**0.42**	0.02	0.28
CEC	**0.42**	−0.15	0.05
Soil EC	0.21	0.12	**0.62**
Mn	−0.19	−0.28	**−0.58**
Fe	−0.23	**−0.40**	0.02
Cu	0.14	**−0.48**	−0.14
Zn	0.001	**−0.51**	−0.02
Pb	0.001	**−0.46**	−0.37
Cum. Variance	0.35	0.62	0.76

denitrification potential was not significantly related to PC1 ($p = 0.20$) or PC2 ($p = 0.11$) but declined with PC3 ($r^2 = 0.23$, $p = 0.007$) (Fig. 5a–c). Carbon mineralization was significantly higher in brackish restored wetlands than freshwater wetlands (Fig. 4b), and SIR was not significantly different among wetland types (Fig. 4c). Across the whole dataset, PC1 was a strong predictor of both C mineralization ($r^2 = 0.56$, $p < 0.001$) and SIR ($r^2 = 0.43$, $p < 0.001$) (Fig. 5d, g). Carbon mineralization and SIR were not significantly related to PC2 or PC3 ($p > 0.10$) (Fig. 5). Carbon mineralization and SIR were also strongly correlated with each other ($r^2 = 0.62$, p < 0.001). Denitrification potential increased with SIR ($r^2 = 0.25$, $p = 0.004$), but was not significantly related to C mineralization ($p = 0.15$).

Within wetland groups with more than three wetlands sampled (restored brackish, unrestored brackish, and unrestored freshwater), relationships between principal components suggest contrasting predictors of soil processes for fresh versus brackish wetlands. For unrestored freshwater wetlands, PC2 was a strong predictor of denitrification potential ($r^2 = 0.86$), C mineralization ($r^2 = 0.94$), and SIR ($r^2 = 0.68$) (Table 3). The negative relationship between process rates and PC2 suggests

Fig. 3 Principal component values for **a**) component 2 (PC2) and **b**) component 3 (PC3) versus component 1 (PC1). Lines are convex hulls by management and wetland type

Fig. 4 Mean (± standard error) for **a**) denitrification potential, **b**) carbon mineralization, and c) substrate induced respiration (SIR) by management and wetland type. Letters denote significant differences at p < 0.05
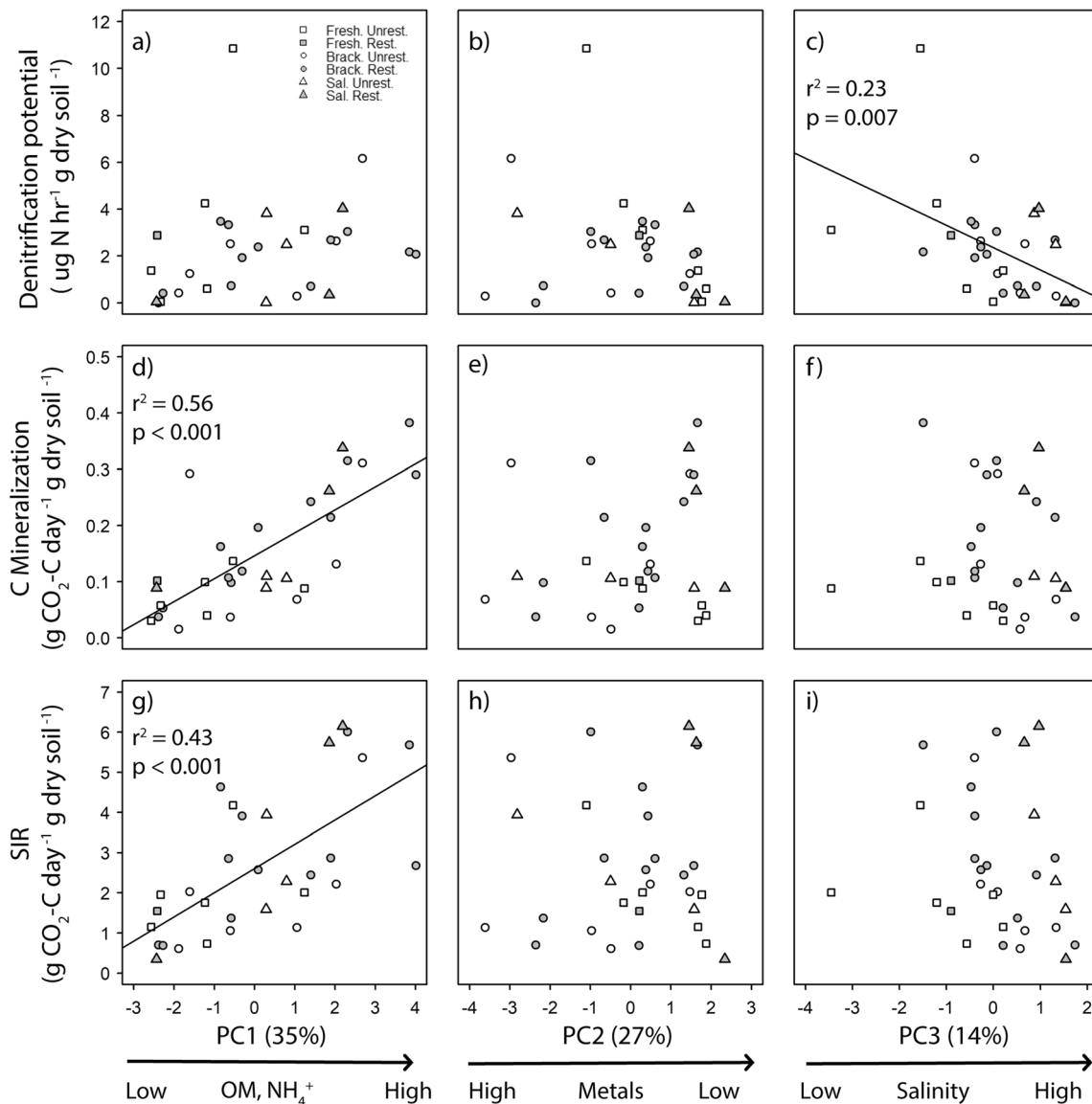
Fig. 5 **a-c)** Denitrification potential, **d-f)** carbon mineralization, and **g-i)** substrate induced respiration (SIR) versus principal component values. Lines are significant simple linear regressions

that in freshwater wetlands, denitrification potential and C mineralization increase with increasing soil metal content. In

contrast, PC2 was not related to soil processes for brackish wetlands. Instead, for brackish wetlands denitrification

Table 3 Simple linear regression results as intercept, slope (r^2, p value) for unrestored freshwater wetlands ($n = 6$), restored brackish wetlands ($n = 13$), and unrestored brackish wetlands ($n = 6$)

Wetland Type	Denitrification potential			C Mineralization			SIR		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Fresh Unrest.	ns	5.5, −3.0 (0.86, 0.007)	ns	ns	0.10, −0.03 (0.94, 0.001)	ns	ns	2.5, −0.79 (0.68, 0.04)	ns
Brackish Rest.	ns	ns	3.0, −2.4 (0.53, 0.10)	ns	ns	ns	2.7, 0.5 (0.36, 0.04)	ns	3.2, −1.3 (0.40, 0.03)
Brackish Unrest.	ns	ns	2.0, −0.71 (0.28, 0.07)	0.15, 0.05 (0.89, <0.001)	ns	ns	ns	ns	2.7, −1.9 (0.53, 0.10)

Principal components (PC) are defined in Table 2

potential and SIR decreased with PC3, and SIR and C mineralization increased with PC1 (Table 3).

Within the restored brackish wetland group, denitrification potential significantly increased with time since restoration (Fig. 6a). The best fit regression model explained 65% of the variation and included a positive coefficient for time since restoration and a negative coefficient for PC3 (Tables 4, 5). Similarly, SIR increased with time since restoration (Fig. 6c). The best fit regression model explained 61% of the variation and included positive coefficients for time since restoration and PC1 and a negative coefficient for PC 3 (Tables 4, 5). Conversely, C mineralization was not related to time since restoration (Fig. 6b). The best fit regression model for C mineralization explained 88% of variation and included only a positive coefficient for PC1 (Tables 4, 5).

Discussion

Tidal flow restoration occurs within the potentially complex chemical context of developed coastal landscapes, where the intersection of saltwater intrusion and urban contaminants can
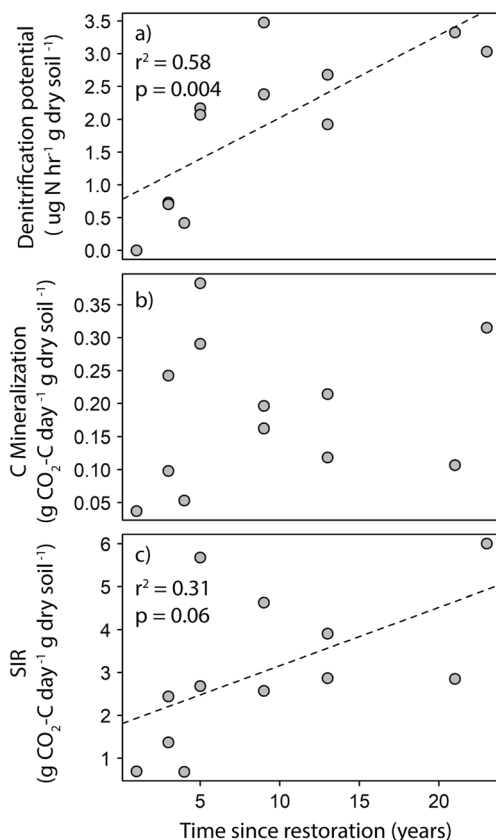

Fig. 6 **a**) Denitrification potential, **b**) carbon mineralization, and **c**) substrate induced respiration (SIR) versus time since restoration for brackish restored wetlands. Lines are significant simple linear regressions

Table 4 Candidate multiple regression models for restored brackish wetlands for denitirficaiton potential (DEA), C mineralization, and SIR for each possible number of model coefficients (K), including the intercept

Model:	K	r_{adj}^2	AIC	Δ_i
DEA				
Yr. Rest.	2	0.54	162.2	2.3
Yr. Rest., PC3	**3**	**0.65**	**159.9**	**0**
Yr. Rest., PC3, PC1	4	0.64	160.8	0.9
Yr. Rest., PC3, PC1, PC2	5	0.59	162.7	2.8
C Mineralization				
PC1	**2**	**0.88**	**−77.0**	**0**
PC1, PC3	3	0.89	−76.8	0.2
PC1, PC3, PC2	4	0.87	−74.9	2.1
PC1, PC3, PC2, Yr. Rest.	5	0.85	−72.9	4.1
SIR				
PC3	2	0.34	10.2	5.0
Yr. Rest., PC1	3	0.50	7.7	2.5
Yr. Rest., PC1, PC3	**4**	**0.61**	**5.2**	**0**
Yr. Rest., PC1, PC3, PC2	5	0.59	6.2	1

Reported statistics include adjusted r^2 (r_{adj}^2), Akaike's Information Criterion (AIC), and the difference between the candidate and best model's AIC (Δi). Candidate models with lowest AIC are in bold and coefficients for those models are reported in Table 5. Principal components (PC) are defined in Table 2

affect wetland ecosystem function (Helton et al. 2014; Doroski et al. 2019). Our field study reveals two patterns that are particularly important for understanding how soil C and N cycling may change in the context of sea level rise, urban pollution, and wetland management. First, even though the restored wetlands in our study experienced a wide range of salinity, nutrient and metal concentrations, we found a strong increase in denitrification potential with time since tidal flow

Table 5 Best fit multiple linear regression models for restored brackish wetlands for denitrification potential (DEA), C Mineralization, and SIR with regression intercept and coefficient estimates for each parameter included in the model

	DEA	C Min.	SIR
Intercept	0.968*	0.159*	2.066*
Yr. Rest.	0.111*		0.098*
PC1		0.048*	0.330*
PC2			
PC3	−0.490*		−0.776*
p value	0.004	<0.001	0.01

Best fit models were selected based on lowest Akaike's Information Criterion (AIC; Table 4). * indicates significance at p < 0.05. Principal components (PC) are defined in Table 2

restoration for brackish wetlands. Denitrification potential increased more than five-fold across sites that represent one to over 20 years post restoration. Second, soil chemistry gradients were also strong predictors of wetland C and N process rates; however, fresh and brackish wetlands had different predictors. Freshwater wetlands were strongly related to metal content of soils whereas brackish wetlands were related to organic matter and salinity gradients. Thus, understanding how C and N processes change over time and after restoration may vary among these wetland types. Below we discuss potential drivers and implications of each of these patterns.

Denitrification potential increases with time since restoration

Our results show that denitrification potential increases with time since restoration, suggesting a potential recovery of denitrification over time after wetland restoration. In a 55 year chronosequence of palustrine depressional wetlands, soil properties likely linked with denitrification (organic matter and cation exchange capacity) also increased over time but did not recover to reference conditions (Ballantine and Schneider 2009). Recovery of C and N storage after restoration was highly variable in a recent meta-analysis (Zhou et al. 2017); however, denitrification was not documented well enough in the literature to be included in this meta-analysis. We also did not find clear trends in soil organic matter or chemistry with time since restoration; however, we did find a significant increase in SIR with time since restoration, suggesting an increase in microbial biomass or change in the microbial community. Research shows differences in microbial community structure in restored versus reference wetlands (e.g., Peralta et al. 2010). Less understood is how microbial biomass or community structure changes with time since restoration. Continuing to add to our measurements of denitrification and its drivers over time after restoration and across chronosequences of restoration ages is critical for understanding how N cycling in degraded wetlands responds to hydrologic restoration.

Although differences were not significant, NH_4^+ and C mineralization tended to be higher in restored than unrestored wetlands across wetland types (Figs. 2 and 4), although neither was related to time since restoration. Greater NH_4^+ and C mineralization in restored wetlands suggest enhanced nutrient deposition or transformation (Megonigal and Neubauer 2009). Our results are similar to previous studies in which restored wetland sites exhibited greater C mineralization compared to reference sites (Craft et al. 2003; Glatzel et al. 2004; Lawrence et al. 2013). Greater nutrient bioavailability after restoration may be driven by shifts in plant productivity and hydrologic regime post restoration, although we did not directly measure these drivers during our study.

Patterns of C and N process rates differ in fresh versus brackish wetlands

Although there was large overlap of soil chemistry among wetland types (i.e., Fig. 3), we found C and N process rates were most strongly associated with different aspects of soil chemistry depending on wetland type. In freshwater wetlands, denitrification potential and C mineralization increased with increasing metal content of soils (i.e., negative relationship with PC2, Table 3). Metal concentrations were comparable to those found in another Connecticut coastal wetland (Benoit et al. 1999), and were generally low. Average Cu and Zn were lower than the Effects Range-Low (ERL) and average Pb was lower than the Effects Range-Median (ERM) toxicity guidelines; maximum Cu, Zn, and Pb were all lower than the ERM guidelines. This suggests metal concentrations were less than concentrations in which biological effects in higher organisms frequently occur, but within levels at which effects would occasionally occur (Long et al. 1995).

Additions of lower concentrations of Cu or Zn to wetland sediments has been shown to increase denitrification rates, but decreases in rates were observed at higher metal concentrations that might cause toxicity effects (Sakadevan et al. 1999; Holtan-Hartwig et al. 2002). A positive association between denitrification potential and lower metal content of soils may be due to several potential mechanisms: 1) Lower metal content may be associated with more reduced conditions (Gambrell 1994), which may indicate environmental conditions conducive to a larger or more active denitrifier community. 2) Copper is a cofactor for many enzymes essential for cell growth (Samanovic et al. 2012), and metalloenzymes involved in denitrification primarily contain Fe or Cu (Glass and Orphan 2012), thus higher concentrations may reduce potential metal limitations. 3) Metals, particularly Fe, are also important redox pairs for microbial metabolism in anoxic wetland soils (Lovley and Phillips 1988; Lovley 1991; Nealson and Myers 1992; Thamdrup 2000; Zhu et al. 2013). Iron can act as an alternate electron donor for nitrate reduction, potentially increasing rates of denitrification (Burgin and Hamilton 2007). Thus, at the relatively low concentrations of metals across our study sites, elevated metal content likely led to an increase of C mineralization and denitrification potential.

For brackish wetlands, even though soil metal content spanned a similar range, we did not find a significant relationship with soil metal content. Rather, we found that denitrification potential decreased with increasing salinity and that C mineralization increased with organic matter, soil moisture, and ammonium content (see relationships with principal components, Table 3). Decreased denitrification potential with salinity may be driven by multiple mechanisms including direct microbial and enzyme effects, formation of toxic compounds (i.e., sulfide), and mobilization of nutrients. In a meta-analysis Zhou et al. 2017 found

salinity as a key regulating factor decreasing denitrification in coastal ecosystems primarily as a result of sulfide toxicity and changes in microbial composition. Sulfide can have inhibitory effects on biota and certain steps of the nitrogen cycle (Joye and Hollibaugh 1995; Camargo and Alonso 2006; Pan et al. 2013). Previous research has shown inhibition of N_2O reduction to N_2 due to sulfide (Senga et al. 2006), which is supported by greater N_2O emissions with increasing SO_4^{2-} or sulfide (Brunet and Garcia-Gil 1996; Helton et al. 2014). Increased salinity enhances the flux of NH_4^+ to the water column which can then be exported with tides (Giblin et al. 2010; Ardón et al. 2013). Export of soil NH_4^+ effectively decreases the N supply for coupled nitrification-denitrification in coastal wetlands.

A recent review shows relatively consistent decreases in C mineralization from fresh to saline wetlands along natural gradients; however, the relationship with C mineralization and salinity in brackish wetlands along natural gradients is less clear (Luo et al. 2017). In our study, in situ salinity was not significantly related to C mineralization for brackish marshes. Our results suggest other factors such as C and N availability and soil moisture potentially play a stronger role in regulating C mineralization across these brackish wetlands, similar to findings in some previous studies (Blagodatskaya and Kuzyakov 2008; Setia et al. 2011).

Conclusions

Our results highlight the potential for biogeochemical recovery in restored wetlands over time, along with the complex interactions between microbial processes and urban chemicals in developed coastal landscapes. Although soil chemistry was not significantly related to time since restoration, spatial patterns of denitrification potential across brackish coastal wetlands were best explained by time since restoration and soil chemistry properties combined. The strongest predictors of denitrification potential and C mineralization also varied by wetland salinity class; process rates in freshwater wetlands were more strongly associated with soil metal content whereas process rates in brackish wetlands were associated with salinity and organic matter gradients. As tidal flow restoration techniques are increasingly used in highly developed coastal landscapes, understanding how restoration practices change biogeochemical function in the context of multiple chemical stressors will be important for predicting the future role of coastal wetlands in C and N cycling.

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