

## Nitrogen enrichment alters carbon fluxes in a New England salt marsh

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### ABSTRACT

**Introduction:** Nitrogen enrichment of coastal salt marshes can induce feedbacks that alter ecosystem-level processes including primary production and carbon sequestration. Despite the rising interest in coastal blue carbon, the effects of chronic nutrient enrichment on blue carbon processes have rarely been measured in the context of experimental fertilization. Here, we examined the ecosystem-level effects of nitrate ( $\text{NO}_3^-$ ) enrichment on the greenhouse gas dynamics of a *Spartina alterniflora*-dominated salt marsh. We measured  $\text{CO}_2$  and  $\text{CH}_4$  fluxes using static chambers through two growing seasons in a salt marsh that was nitrogen-enriched for 13 years and compared fluxes to those from a reference marsh.

**Outcomes:** We found that nitrogen enrichment increased gross primary productivity (GPP) by 7.7% and increased ecosystem respiration ( $R_{\text{eco}}$ ) by 20.8%. However, nitrogen enrichment had no discernible effect on net ecosystem exchange (NEE). Taken together, these results suggest that nitrogen-induced stimulation of  $R_{\text{eco}}$  could transform this salt marsh from a carbon sink into a source of carbon to the atmosphere.

**Conclusion:** Our results complement prior findings of nitrogen enrichment weakening soil structure and organic matter stability in tidal salt marshes, suggesting that increased nutrient inputs have the potential to alter the carbon storage function of these ecosystems through enhanced microbial respiration of previously sequestered carbon.

### ARTICLE HISTORY

Received 9 May 2017  
Revised 9 September 2018  
Accepted 9 September 2018

### KEYWORDS

*Spartina alterniflora*; blue carbon; eutrophication; gross primary productivity; net ecosystem exchange; nitrogen; ecosystem respiration; tidal salt marsh

### Introduction

Coastal salt marshes are among the most productive ecosystems on Earth and are responsible for numerous ecosystem services such as flood protection, water filtration, and carbon sequestration (De Groot, Wilson, and Boumans 2002). Despite only covering 4–6% of the Earth's surface (Mitra, Wassmann, and Vlek 2005), salt marshes contain a disproportionately large amount of the world's organic soil carbon (Chmura et al. 2003; Clarkson, Ausseil, and Gerbeaux 2014; Emery and Fulweiler 2014; Gorham 1991). High rates of annual carbon sequestration (Chmura et al. 2003), low organic matter decomposition rates (Kristensen et al. 2008), and negligible levels of  $\text{CH}_4$  emissions (Moseman-Valtierra et al. 2016; Poffenbarger, Needelman, and Megonigal 2011) enable these ecosystems to become large pools of coastal or “blue” carbon (McLeod et al. 2011; Pendleton et al. 2012). Due to their ability to sequester atmospheric carbon rapidly, salt marshes could represent valuable offsets in carbon markets; the conservation and restoration of coastal salt marshes are, therefore, of great interest to both scientists and policymakers (Emmett-Mattox, Crooks, and Findsen 2010). While climate change is expected to alter the carbon sequestration potential of salt marshes (Kirwan and Megonigal

2013), few studies have evaluated empirically how nutrient enrichment can influence blue carbon processes at the landscape scale (Hopkinson, Cai, and Hu 2012; Pendleton et al. 2012).

Anthropogenic activities are known to alter the structure and function of salt marshes. Urban and agricultural expansion (Asselen et al. 2013), infrastructure construction (Kirwan and Megonigal 2013), sea level rise (Church et al. 2013; Moorhead and Brinson 1995), and eutrophication (Hopkinson, Cai, and Hu 2012) have led to annual tidal wetland loss at rates of 0.7–7% (Hopkinson, Cai, and Hu 2012; Pendleton et al. 2012). Furthermore, sea levels are rising at accelerating rates and wetlands that cannot increase soil surface elevation (by trapping sediment and producing soil organic matter) at comparable rates are likely to lose vegetative cover and succumb to submergence (Church et al. 2013; Morris et al. 2002).

There is also evidence that nutrient enrichment of salt marshes through human activities may compromise ecosystem function. Agricultural intensification has resulted in a doubling of reactive nitrogen (N) entering the biosphere (Galloway et al. 2004), leading to increased concentrations of N (predominantly nitrate,  $\text{NO}_3^-$ ) in the waterways of industrialized

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nations (Fields 2004). Salt marshes have been particularly strongly affected, and are now among the most nutrient-enriched ecosystems in the world (Pardo et al. 2011). This has led to sharp declines in surface area (Hopkinson, Cai, and Hu 2012), as chronic nutrient enrichment can reduce belowground productivity (Darby and Turner 2008a, 2008b; Deegan et al. 2012), resulting in creek bank instability and ultimately converting salt marshes to mudflats through ecogeomorphic feedbacks (Deegan et al. 2012). Moreover, substantial N enrichment of coastal aquatic systems can cause algal blooms, hypoxia (Fields 2004), and shifts in wetland plant communities (Langley et al. 2013). Therefore, N enrichment could have unfavorable implications for carbon sequestration in salt marshes, especially in combination with elevated temperatures and CO<sub>2</sub> concentrations (Caplan et al. 2015; Wang et al. 2013).

The effects of N enrichment on wetland ecosystems are largely context-dependent, varying, in part, as a function of the type of N addition. Although salt marsh plants use both inorganic and organic N (Mozdzer, Zieman, and McGlathery 2010; Mozdzer et al. 2011, 2014), recent evidence suggests that the form and method of N enrichment may influence responses at the ecosystem level (Johnson et al. 2016). Although NO<sub>3</sub><sup>-</sup> is the major form of N loading into most estuaries (Deegan et al. 2012; Lyons et al. 1995), most N enrichment studies add NH<sub>4</sub><sup>+</sup> (reviewed by Johnson et al. (2016)), which may explain inconsistencies in results reported in the literature. For example, N eutrophication, regardless of the N form added, typically leads to a decrease in belowground biomass (BGB) (Deegan et al. 2012; Langley et al. 2009; Valiela, Teal, and Persson 1976) or an increase in aboveground biomass (AGB) (Deegan et al. 2012; Langley et al. 2013; Sullivan and Daiber 1974; Valiela, Teal, and Persson 1976). However, N can also increase belowground biomass (Langley et al. 2013; Thormann and Bayley 1997) or have no impact on belowground biomass (Anisfeld and Hill 2012). Given the lack of consistency in responses to N enrichment of biomass, further research is needed to evaluate how N enrichment affects carbon processes in salt marsh ecosystems.

Given that N enrichment induces both direct and indirect effects on carbon cycle processes, the net effects of nutrient enrichment on carbon cycling and sequestration in tidal salt marshes are difficult to predict. For example, NH<sub>4</sub><sup>+</sup> enrichment typically enhances net ecosystem CO<sub>2</sub> exchange (NEE) and gross primary production (GPP) (Caplan et al. 2015; Wang et al. 2013). NO<sub>3</sub><sup>-</sup> can similarly stimulate primary production (Mallin, Paerl, and Rudek 1991; Mallin et al. 1993; Mendelssohn 1979), theoretically increasing NEE and GPP. However, NO<sub>3</sub><sup>-</sup> is also a powerful electron acceptor and can stimulate

anaerobic bacteria (Giblin et al. 2013; Peng et al. 2016), thereby also increasing ecosystem respiration (R<sub>eco</sub>) (Wigand et al. 2014). We are aware of no studies evaluating how ecosystem level NO<sub>3</sub><sup>-</sup> enrichment may stimulate R<sub>eco</sub> to influence ecosystem carbon processes. In tidal salt marshes, methane (CH<sub>4</sub>) emissions are typically low and do not alter the carbon sink function (Poffenbarger, Needelman, and Megoñigal 2011) and are, therefore, of lesser importance than CO<sub>2</sub> fluxes in salt marsh carbon cycling studies. Given the important role of coastal wetlands as blue carbon stores (McLeod et al. 2011), there is a pressing need to understand how landscape-level nutrient pollution alters carbon sequestration (GPP and NEE) and efflux (R<sub>eco</sub>) to influence ecosystem carbon dynamics.

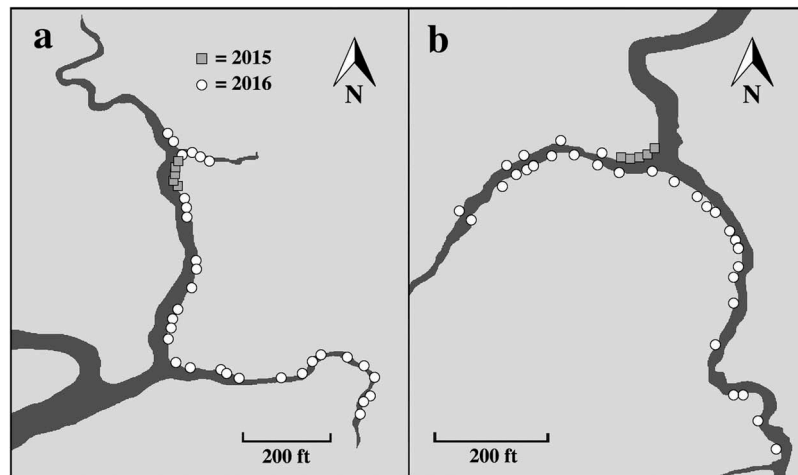
Low-marsh and creek bank communities, frequently dominated by the foundation species *Spartina alterniflora*, are typically more productive than high-marsh communities (Morris et al. 2002) and are also more exposed to increased N loading and sea level rise (Deegan et al. 2012; Hartig et al. 2002; Kirwan et al. 2016; Moseman-Valtierra et al. 2016). While the effects of global change factors on high-marsh vegetation are well studied (Chmura et al. 2016; Morris et al. 2002; Moseman-Valtierra et al. 2016; Olsson et al. 2015), few have investigated how creek bank carbon fluxes could be affected by these factors. Measurements of ecosystem responses in the portions of marshes at lower elevations could allow for more accurate predictions of wetland ecogeomorphic processes under global change alterations such as N enrichment (Kirwan et al. 2016).

We compared the rates of CO<sub>2</sub> and methane fluxes within a chronically enriched tidal salt marsh (13 years of N fertilization) to those in an unfertilized reference marsh in Massachusetts, USA. We specifically quantified the effects of N enrichment on *S. alterniflora* carbon flux dynamics along the low-marsh creek banks. We hypothesized that perturbations in coastal N loading in the form of NO<sub>3</sub><sup>-</sup> would increase GPP, NEE, and R<sub>eco</sub> in a *S. alterniflora*-dominated marsh by stimulating rates of both photosynthesis and ecosystem respiration.

## Materials and methods

### Site description

This study was conducted at the Great Marsh in Rowley, Massachusetts, USA (42°47'55"N, 70°48'40"W), which is part of the Plum Island Ecosystems Long-Term Ecological Research (LTER) site. It specifically focused on two branches of the Rowley River and took place in 2015 and 2016 (Figure 1). The field site is a typical intertidal New England salt marsh with a 3 m tidal range and a mean tidewater salinity range of 8–28 ppt (Pascal and Fleeger 2013). Tall-form *S. alterniflora* (smooth cordgrass) dominates the marsh creek banks,



**Figure 1.** Study sites at the Plum Island Ecosystem LTER site in Rowley, Massachusetts, USA (42°47'55"N, 70°48'40"W). Locations of carbon flux sampling collars at (a) West Creek (reference) and (b) Sweeney Creek (enriched) are overlain.

while *Spartina patens* (salt marsh hay) dominates the high-marsh platform. Soils at these sites are organic, containing approximately 35% organic matter (T. Mozdzer, unpublished data). Our study focused on the creek bank habitat of the low-marsh, given that previous studies have suggested that changes in low-marsh productivity can substantially alter ecosystem carbon processes (Deegan et al. 2012; Langley et al. 2013).

To determine how chronic N eutrophication influences greenhouse gas (GHG) fluxes, we leveraged a long-term nutrient enrichment experiment known as the TIDE Project, in which two pairs of first-order creeks were fertilized from 2004 to 2016 (Deegan et al. 2007, 2012; Johnson et al. 2016). The concentration of  $\text{NO}_3^- \text{N}$  in floodwater was fertilized to approximately 70–100  $\mu\text{M}$   $\text{NO}_3^-$  in the two N-enriched creeks (two branches of Sweeney creek), which is approximately 15 $\times$  that of the reference creeks (two branches of West Creek). Fertilization took place each growing season from May through October, but ceased in September 2016. Creeks were fertilized with N + phosphorus (P) until 2010, when it was determined that P was naturally in excess of the Redfield ratio even at the higher levels of N and thus discontinued (Johnson et al. 2016). Nutrient enrichment was consistently applied over the first 10 years (Johnson et al. 2016), but was half of typical values from May through July 2014 ( $\sim 35$   $\mu\text{M}$   $\text{NO}_3^-$ ); full enrichment resumed in August ( $\sim 70$   $\mu\text{M}$   $\text{NO}_3^-$ ). In 2014, an earthquake in Chile resulted in a global disruption of  $\text{NO}_3^-$  fertilizers, preventing N enrichment in May and June; nutrient enrichment resumed during second week of July 2014.

### Carbon flux measurements

To evaluate how ecosystem carbon fluxes were altered by N enrichment, we measured fluxes of  $\text{CO}_2$  and

$\text{CH}_4$  using the static chamber approach during the 2015 and 2016 growing seasons. In 2015, we identified a 20 m creek bank zone dominated by *S. alterniflora* at both sites that were at similar elevations. Six aluminum collars (30  $\times$  30  $\times$  2015 cm, L  $\times$  W  $\times$  H) were inserted into the sediment within each zone at each site in May 2015 ( $n = 12$  collars) two weeks prior to the first flux measurement to allow plants and soils to acclimate to the installation disturbance. The chambers used in 2015 were similar to those described by Mueller et al. (2016); they were constructed by sealing Lexan polycarbonate sheets to aluminum frames (30  $\times$  30  $\times$  150 cm) and lining chamber bases and lids with closed-cell neoprene foam.

During two sampling periods (July and August 2015), measurements of  $\text{CO}_2$  and  $\text{CH}_4$  fluxes were made using a portable Greenhouse Gas Analyzer (model 915-0011, Los Gatos Research, San Jose, USA). Flux measurements took place between 900 and 1500 h during low tide on sunny or partly cloudy days. Gas concentrations were recorded at 1 s intervals for 2–3 min with the chambers fully exposed to saturating sunlight (photosynthetically active radiation (PAR)  $>1200$   $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and then for 2–3 min with the chambers covered by a reflective, opaque material. Chambers remained in place between coupled measurement phases, with approximately 30 s between light and dark measurements. Fluxes began with headspace  $\text{CO}_2$  concentrations near ambient atmospheric concentrations ( $\sim 390$  ppm), with  $\leq 160$  ppm drawdown of  $\text{CO}_2$  from NEE. Chambers were not flushed between the coupled light and dark flux measurements, and although  $\text{CO}_2$  concentrations reached 810 ppm during  $R_{\text{eco}}$  measurements, elevated  $\text{CO}_2$  concentrations have not been found to significantly affect *S. alterniflora* given that it uses the  $\text{C}_4$  photosynthetic pathway (Jones et al. 2018). Ambient air temperature, soil temperature,

and PAR were recorded every five seconds using a HOBO Micro Station Data Logger (Onset H21-002; Onset Corporation, Melrose, USA) while a battery-powered fan circulated air inside the chamber. Fluxes were calculated from the linear (i.e., steady state) portion of the CO<sub>2</sub> or CH<sub>4</sub> time series; changes in concentrations were converted to fluxes using the ideal gas law. All CO<sub>2</sub> fluxes were determined from regressions with R<sup>2</sup> > 0.98. CH<sub>4</sub> fluxes were determined from regressions with R<sup>2</sup> ≥ 0.80. Efflux of CH<sub>4</sub> was measured during the sunlit phase of measurement. Ecosystem respiration (R<sub>eco</sub>) was measured during the dark phase; GPP was subsequently calculated as the sum of NEE and R<sub>eco</sub>.

In the summer of 2016, we measured ecosystem carbon fluxes using static flux chambers at five time points, approximately two weeks apart, spanning June through August. Instead of installing static chamber bases for repeated measurements at the same locations, we increased spatial coverage by changing collar locations for each of the five campaigns. At each time point, 6 flux collars per site were installed along the creek bank within *S. alterniflora* patches of similar elevation. Spatial coordinates of the flux collars were recorded at each sampling location to ensure that fluxes were never measured within 2 m of previously measured locations (Figure 1). PVC collar bases (10 cm long × 20 cm diameter) were inserted approximately 3 cm into the soil at least 36 h before flux measurements.

The static chambers used in 2016 were similar to those described by Emery and Fulweiler (2014); chambers were made from polycarbonate tubes (128 cm length × 22 cm diameter) capped with polycarbonate lids. Closed-cell neoprene foam was used to create a gas-tight seal between the chamber, base, and lid. This chamber design allowed for greater portability than that used the prior year. As in 2015, NEE, R<sub>eco</sub>, and CH<sub>4</sub> fluxes were calculated from changes in CO<sub>2</sub> or CH<sub>4</sub> concentrations over 2–3 min intervals, with R<sub>eco</sub> measured while the chamber was dark and GPP calculated as the sum of NEE and R<sub>eco</sub>. Ambient air temperature was measured with a digital thermometer and PAR was measured with a photovoltaic light meter (LI-250A, LICOR Biosciences, Lincoln, USA), both at 15 s intervals. A battery-powered fan circulated air within the chamber during all flux measurements.

### Biomass determination

Aboveground biomass (AGB) within each flux collar was destructively sampled in August 2015 and at each time point in 2016. In July 2015, we measured the height and basal diameter of each plant within the flux plots to non-destructively estimate biomass using an allometric equation derived from plant

morphometrics collected in July and August 2015 (Morris and Haskin 1990). After final flux measurements, all aboveground biomass was clipped at the sediment surface, dried at 60°C to constant mass, and weighed.

In August 2015, we measured belowground biomass (BGB) by taking two soil cores (5 cm diameter × 30 cm deep) within each collar. In 2016, we collected one soil core (also 5 × 30 cm) within each flux collar after AGB was destructively harvested. Cores were washed over a 2 mm sieve; live roots and rhizomes were removed, separated, and then dried at 6°C to constant mass and weighed.

We compared ABG values with estimates of end-of-season live (EOSL) biomass that were measured at the landscape level approximately two weeks after the last flux measurement in 2015 and 2016 (described in Johnson et al. (2016)). Briefly, 25 individual shoots were collected along permanent transects, dried to constant mass, and weighed to determine an average shoot biomass (n = 3 per primary creek). We also measured shoot density in 0.25 m<sup>2</sup> quadrats on each transect; EOSL biomass was calculated as the product of density and mean shoot mass.

### Statistical analysis

We used mixed-effects linear models to determine how strongly N enrichment influenced carbon fluxes and *S. alterniflora* biomass. Fixed effects used in the models were creek (reference or enriched), day of year (DOY), temperature (ambient for all response variables except R<sub>eco</sub>, Methane, and BGB, which used soil temperature), year (either 2015 or 2016), and PAR level. All possible two-way interaction effects between these variables were also included. A random effect for sampling group was included in all models; this accounted for repeated measurements within locations in 2015 or within creek branches in 2016. We used multi-model inference to quantify the influence of fixed effects on response variables. This approach accounts for model selection uncertainty and produces coefficients (denoted β) that are proportional to effect sizes in place of binary signifiers of significance (P values) (Anderson and Burnham 2002; Grueber et al. 2011). We used model averaging to calculate the means and standard error (SE) of coefficients (across all models with ΔAICc < 4) and determined effect sizes and directions from the magnitudes and signs of β coefficients. Statistical analyses were conducted using R 3.4.0 (R Development Core Team 2014) with functions from the packages *lme4* and *MuMIn* used for mixed-effects modeling and multi-model inference, respectively. Finally, the stimulation effect of N enrichment on response variables

was calculated as the difference between enriched and reference values, relativized to reference values.

## Results

Mean  $R_{eco}$  was greater in the N enriched creek than in the reference creek ( $\beta_{Creek} = -0.29$ , Table 1). N enrichment stimulated mean  $R_{eco}$  by an average of  $20.8 \pm 7.9\%$  SE (2.7 to 66.2% increases, except in June 2016, when stimulation was  $-42.5\%$ ; Figure 2(a)). In addition, there was evidence that  $R_{eco}$  increased as the growing season progressed (DOY;  $\beta_{DOY} = 0.21$ ), though 95% CIs for the effects did not exclude zero (Table 1). The data presented no evidence that  $R_{eco}$  differed between 2015 and 2016.

Mean GPP was, on average,  $7.7 \pm 2.9\%$  SE greater in the N enriched creek than in the reference creek (Figure 2(b)). GPP increased with enrichment consistently in 2015 (3.50 to 34.76%), but the effect was inconsistent in 2016 ( $-41.5$  to  $40.2\%$ ,  $\beta_{Creek} = 0.24$ ,  $\beta_{Creek \times Year} = -0.45$ , Table 1). In addition, GPP exhibited a clear increase in magnitude through the growing season in 2016 but remained nearly constant through the sampled portion of 2015 ( $\beta_{DOY} = -0.42$ ,  $\beta_{DOY \times Year} = -0.79$ ).

N enrichment had no overall effect on NEE, only stimulating NEE in 2015 ( $\beta_{Creek \times Year} = -0.69$ ; Table 1). In 2015, N enrichment stimulated mean NEE by 4.3 to 10.2%, and in 2016 by 13.4 to 44.1% (Figure 2(c)). As with GPP, NEE increased in magnitude through the 2016 growing season but remained nearly constant through the sampled portion of 2015 ( $\beta_{DOY} = -0.38$ ,  $\beta_{DOY \times Year} = -1.08$ ). There was also evidence that NEE increased in magnitude with

warmer temperatures but that the effect was stronger in 2015 than in 2016 ( $\beta_{Temp \times Year} = 0.80$ ).

Methane emissions did not differ between the reference and enriched creeks. The mean rate of methane emission was  $4.02 \pm 0.81 \text{ nmol m}^{-2} \text{ s}^{-1}$ , i.e., three to four orders of magnitude lower than carbon fluxes (Figure 2(d)). The statistical model indicated that methane efflux increased through the growing season ( $\beta_{DOY} = 0.52$ , Table 1), but this appeared to be entirely due to atypically high rates in late 2015 ( $\beta_{DOY \times Year} = -0.72$ ).

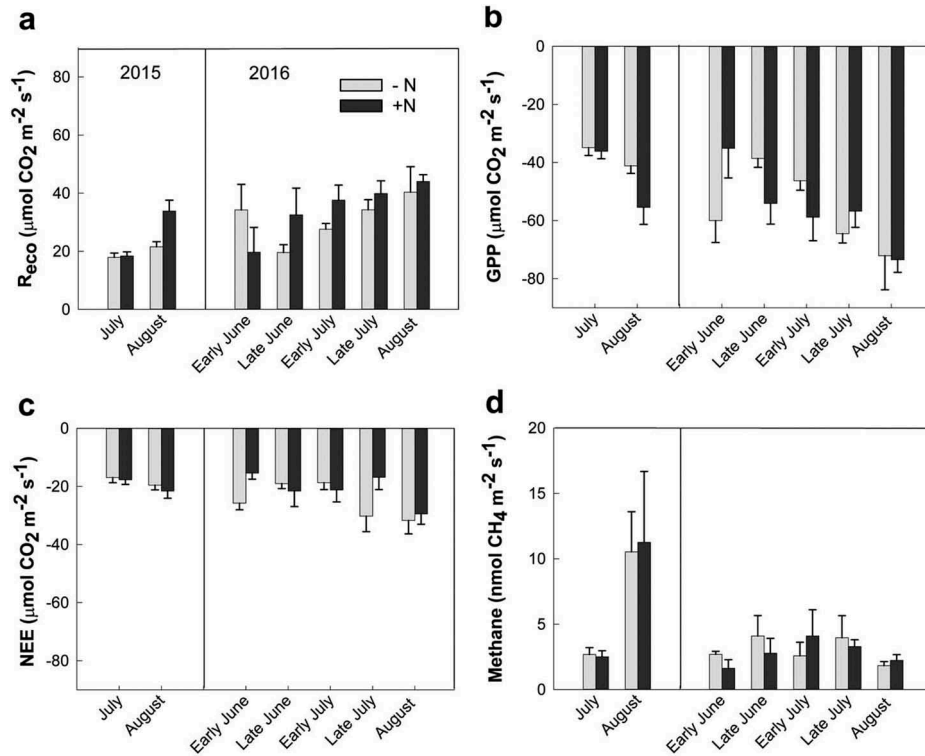
*S. alterniflora* aboveground biomass (AGB) increased throughout the growing season in both creeks ( $\beta_{DOY} = 0.54$ , Table 1), but did so more rapidly under N enrichment ( $\beta_{Creek \times DOY} = -0.40$ , Table 1). However, the net effect of N enrichment on AGB was ambiguous ( $\beta_{Creek} = -0.30$ ). EOSL biomass was approximately twice as large in 2016 as it was in 2015 (Figure 3(a)). Variation in belowground biomass (BGB) could not be attributed to the factors that we tested, as the fit of the models was too poor to interpret (model  $R^2 = 0.04$ , Table 1, Figure 3(b)).

## Discussion

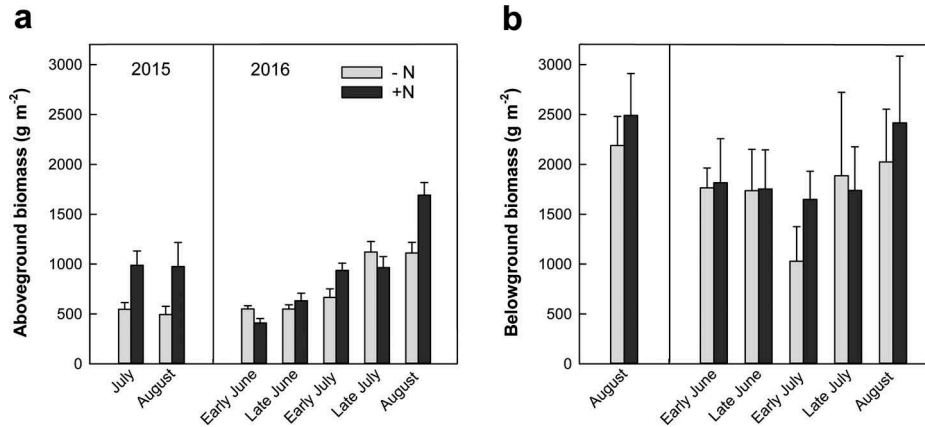
Our results demonstrate that chronic nutrient fertilization can fundamentally alter carbon fluxes in tidal salt marsh creek banks via increases in  $R_{eco}$ . We found that N enrichment increased both  $R_{eco}$  and GPP, both of which have been observed in other systems (Anisfeld and Hill 2012; Caplan et al. 2015; Morris and Bradley 1999; Wang et al. 2013). Our data suggest that N enrichment can increase carbon losses from the ecosystem through increases in

**Table 1.** Summary of statistical models for relationships between response variables.  $N_{obs}$ , number of observations after data cleaning;  $N_{mod}$ , number of models included in model averaging; DOY, day of year; Temp, temperature (soil or ambient); Year, year of data collection, either 2015 (+0.5) or 2016 (−0.5); Creek, reference (+0.5) or enriched (−0.5). Bolded coefficients are those whose confidence intervals (95% CI) do not include zero.

Response	$R^2$	$N_{obs}$	$N_{mod}$	Term	Coefficient	SE	95% CI
$R_{eco}$	0.33	87	225	Creek	−0.29	0.10	(−0.138, 0.091)
				DOY	0.21	0.19	(−0.158, 0.587)
GPP	0.48	87	166	<b>Creek</b>	<b>0.24</b>	<b>0.11</b>	<b>(0.034, 0.446)</b>
				<b>DOY</b>	<b>−0.42</b>	<b>0.18</b>	<b>(−0.774, −0.071)</b>
				Year	−0.18	0.14	(−0.462, 0.097)
				DOY x Year	−0.79	0.45	(−1.668, 0.092)
				Creek x Year	−0.45	0.25	(−0.930, 0.034)
				Creek	0.12	0.10	(−0.079, 0.327)
NEE	0.37	87	54	<b>DOY</b>	<b>−0.38</b>	<b>0.17</b>	<b>(−0.712, −0.054)</b>
				<b>Creek x Year</b>	<b>−0.69</b>	<b>0.22</b>	<b>(−1.120, −0.252)</b>
				<b>DOY x Year</b>	<b>−1.08</b>	<b>0.45</b>	<b>(−1.953, −0.202)</b>
				Temp x Year	0.80	0.47	(−0.128, 1.719)
				<b>DOY</b>	<b>0.52</b>	<b>0.13</b>	<b>(0.261, 0.788)</b>
Methane	0.42	87	53	DOY x Year	−0.72	0.42	(−1.531, 0.099)
				Creek	−0.30	0.20	(−0.696, 0.091)
AGB	0.70	87	90	<b>DOY</b>	<b>0.54</b>	<b>0.11</b>	<b>(0.333, 0.755)</b>
				<b>Creek x DOY</b>	<b>−0.40</b>	<b>0.15</b>	<b>(−0.690, −0.115)</b>
				<b>DOY x Year</b>	<b>0.61</b>	<b>0.31</b>	<b>(0.014, 1.209)</b>
				Creek	−0.03	0.08	(−0.197, 0.134)
BGB	0.04	68	31	<b>DOY</b>	<b>0.20</b>	<b>0.83</b>	<b>(−1.422, −1.819)</b>
				Year	−0.05	0.70	(−1.414, 1.322)
				Year	−0.05	0.70	(−1.414, 1.322)



**Figure 2.** Mean ( $\pm$ SE) carbon flux rates at reference and nitrogen-enriched creeks in 2015 and 2016, divided by a vertical border. (a)  $R_{\text{eco}}$ , ecosystem respiration; (b) GPP, gross primary productivity; (c) NEE, net ecosystem exchange; and (d)  $\text{CH}_4$ , methane emissions. Values from the control (WE) creek are indicated in light gray, and those from the nitrogen-enriched creek (SW) are indicated in black.



**Figure 3.** Mean ( $\pm$ SE) standing crop aboveground (a) and belowground (b) biomass at the reference and nitrogen-enriched creeks. July 2015 AGB values were estimated via allometry. No data were available for belowground biomass in July 2015. Values from the control (WE) creek are indicated in light gray, and those from the nitrogen-enriched creek (SW) are indicated in black.

heterotrophic respiration of organic matter. Our study is among the first to measure carbon fluxes along the creek bank, and  $R_{\text{eco}}$  rates were similar to those of the  $C_4$  plant *Spartina patens* measured in a Chesapeake Bay tidal marsh (DeJong, Drake, and Pearcy 1982). N enrichment had no effect on  $\text{CH}_4$  emissions, as seen in previous studies (Chmura et al. 2016; Moseman-Valtierra et al. 2016).

Our results suggest that  $\text{NO}_3^-$  enrichment has the potential to transform salt marsh ecosystems from well-established carbon sinks to carbon sources.

This would be the case if the cumulative effects of N enrichment on  $R_{\text{eco}}$  were greater than those of GPP when summed through the full growing season. Given that microbial respiration continues at night, i.e., when GPP ceases entirely, the net growing season effect of N enrichment would be a loss of soil carbon. While our data only represent maximum potential rates, this possibility is supported by a study of a *S. alterniflora*-dominated salt marsh in South Carolina that found elevated N to induce greater net decreases in soil carbon storage (Morris and Bradley 1999).

Although the microbial substrate differs, priming of microbial communities (provided by carbon subsidies in Morris and Bradley (1999) and  $\text{NO}_3^-$  in our study) would have both decreased the accumulation of soil carbon. Also, while our NEE values are higher than those previously measured in the Plum Island LTER system on the high-marsh platform (using the eddy covariance method described by Forbrich and Giblin (2015)), this can be expected from the differences in biomass between the more productive low-marsh zone and the high-marsh platform.

This study and previous research suggest that  $\text{NO}_3^-$  enrichment can alter carbon cycling in wetland soils by increasing microbial respiration of organic matter (Min, Kang, and Lee 2011; Wigand et al. 2009). While our study did not partition  $R_{\text{eco}}$  between microbial and autotrophic respiration, the most parsimonious explanation for our results is that changes in  $R_{\text{eco}}$  were due to changes in soil microbial activity, given the similar levels of above and belowground biomass in our study (Figure 2). In addition, previous research at our site has demonstrated that fertilization with  $\text{NO}_3^-$ , which is a strong electron acceptor, has stimulated denitrification (Koop-Jakobsen and Giblin 2010), increased litter respiration (Deegan et al. 2012), and decreased soil organic matter stabilization (Mueller et al. 2017). Work in another temperate tidal salt marsh, the Great Sippewisset Marsh, has demonstrated that N enrichment can alter the active soil microbial community to favor denitrifying bacteria (Peng et al. 2016) and increase  $R_{\text{eco}}$  (Martin et al. 2018). Nonetheless, temporal changes in AGB (Figure 2) and higher foliar N content (Deegan et al. 2012) suggest that some fraction of increased  $R_{\text{eco}}$  may be attributable to higher maintenance respiration of N enriched *S. alterniflora* (Hymus et al. 2003). However, these increases in autotrophic respiration are likely small, and thus unlikely to account for the large differences in measured  $R_{\text{eco}}$  we observed under N enrichment.

Higher GHG fluxes in the second year of study may have been due to external environmental drivers that influenced ecosystem level productivity. Ecosystem wide, EOSL biomass from the annual census was approximately 30% lower at both sites (T. Mozdzer, unpublished data). On average, air temperatures during flux measurements were higher in 2016 than they were in 2015; for example, during July flux measurements, average air temperatures were 26°C in 2015 and 32°C in 2016. Similarly, air temperatures during August flux measurements were 29.5°C and 36°C in 2015 and 2016, respectively. Increased air temperatures are known to be associated with increased GPP and  $R_{\text{eco}}$  in the Plum Island LTER study system (Forbrich and Giblin 2015). Therefore, higher flux values in 2016 than in 2015 may be

attributable, in part, to higher air temperatures during sampling. Precipitation also differed considerably between 2015 and 2016. In 2016, rainfall for May–August was less than half of that in 2015 (113.5 vs. 241.0 mm). Through 2016, our site also experienced either moderate or severe drought according to the Palmer Drought Severity Index (Diamond et al. 2013). Changes in fresh water availability may have increased plant respiration through increased osmotic stress (Flexas et al. 2005; Mu et al. 2007), resulting in higher rates of  $R_{\text{eco}}$  in the second year of study. The 20.8% mean annual increase in  $R_{\text{eco}}$  correlates well with the ~30% reduction in EOSL biomass observed in 2016, suggesting that 2016 stimulation in  $R_{\text{eco}}$  can be attributed in part to increased autotrophic respiration at both sites.

Methodological differences between years may have contributed to greater variation in flux rates in 2016 vs. 2015. Using stationary sampling locations (2015) produced lower within-time point variation than using multiple, single-sample locations (2016). However, by spreading the sampling over a greater area, we decreased the probability of plot-specific results and increased the applicability of the results to the entire ecosystem. Even with greater variability in 2016, we still found that  $R_{\text{eco}}$  was consistently greater in the enriched vs. the reference treatment. The only exception to this pattern was observed in early June 2016, at the start of the growing season. While inserting new flux collars may have increased  $R_{\text{eco}}$  to a greater extent in 2016 than in 2015, this approach is commonly applied in this ecosystem (Emery and Fulweiler 2014; Moseman-Valtierra et al. 2016). Future studies are planned to determine if methodological differences may have contributed to these results. Regardless, these disturbances would have been similar between treatments, and therefore did not influence our finding of increased  $R_{\text{eco}}$  with N enrichment.

Rates of methane emissions at our sites are comparable to those measured in other salt marsh studies (Chmura et al. 2016; Olsson et al. 2015; Poffenbarger, Needelman, and Megonigal 2011), which we attribute to high sulfate availability limiting methanogen activity (Poffenbarger, Needelman, and Megonigal 2011). The lack of an N enrichment effect on  $\text{CH}_4$  emissions has a precedent in other tidal marshes; several studies have found  $\text{CH}_4$  emissions to remain constant despite changes in N availability or aboveground plant productivity (Chmura et al. 2016; Moseman-Valtierra et al. 2016). This is likely because the N only has indirect influences on methane emissions, namely through changes in the rhizosphere (Olsson et al. 2015; Torres-Alvarado et al. 2005) such as root exudates altering methanogenesis or methane oxidation (Mozdzer and Megonigal 2013).

Given that biomass typically controls carbon fluxes, the fact that our biomass results align well

with landscape level patterns suggests that our carbon flux data should approximately scale to the landscape level. For example, the lack of an N effect on ABG is consistent with our previous findings (Johnson et al. 2016). Our estimates of ABG within flux collars are within the range of landscape level observations in EOSL biomass, except for our measurement in August 2016 at the N enriched creek, which was slightly higher. However, we did not observe significant differences in BGB with N enrichment, in contrast to prior results (Deegan et al. 2012); this is likely attributable to differences in methodology and sample size. The cores we used (5 cm diameter) were four times smaller than those collected by Deegan et al. (2012) (10 cm diameter), such that they yielded increased sample variability and possibly lacked enough rhizome material to identify differences in BGB. Additionally, given the high degree of variation inherent in BGB measurements, our sample size was relatively small ( $n = 6$  per time point, compared to 20 by Deegan et al. 2012) and may not have detected differences between treatments.

### Conclusions

Our results suggest that N enrichment could potentially reverse the carbon sink function of tidal wetlands through long-term stimulation of  $R_{\text{eco}}$ . As highly productive ecosystems with negligible  $\text{CH}_4$  emissions, tidal wetlands generally act as efficient carbon sinks (Whiting and Chanton 2001; Mcleod et al. 2011; Stefanik and Mitsch 2014). However, a >20% stimulation of  $R_{\text{eco}}$  due to  $\text{NO}_3^-$  enrichment could potentially transform tidal wetlands into sources of atmospheric carbon if long-term increases in  $R_{\text{eco}}$  exceed stimulations to GPP. Given the established role of soil organic matter in maintaining surface elevation, losses of soil carbon could also therefore potentially cause soil surface elevation to decrease (Langley et al. 2009). In this scenario, respired soil carbon would reduce the surface elevation of enriched marshes and make these ecosystems more susceptible to sea level rise (Kirwan et al. 2013; Kirwan and Megonigal 2013). Moreover, losses of soil carbon may accelerate ecogeomorphic feedbacks such as marsh bank collapse (Deegan et al. 2012), accelerating further marsh loss and ultimately exporting centuries' worth of sequestered soil carbon into the oceans.

### Acknowledgments

We thank David Behringer, Amanda Davis, Ian Craick, and Linda Deegan for field, logistical, and technical assistance. We also thank Anne Giblin, Inke Forbrich, Linda Deegan, and two anonymous reviewers for numerous insightful comments.

### Disclosure statement

No potential conflict of interest was reported by the authors.

### Funding

Funding for this project was provided by the National Science Foundation [award DEB-1354124 to TJM, award DEB-1719621 to the TIDE Project, and awards DEB-1637630 & DEB-1238212 to the PIE-LTER]. The study was further supported by startup funds from Bryn Mawr College to TJM.

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# Ecosystem Health and Sustainability

A SCIENCE PARTNER JOURNAL

## Nitrogen enrichment alters carbon fluxes in a New England salt marsh

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**Citation:** Geoghegan E, Caplan J, Leech F, Weber P, Bauer C, Mozdzer T. Nitrogen enrichment alters carbon fluxes in a New England salt marsh. *Ecosyst Health Sustain.* 2018;4 (11):1532772. DOI: 10.1080/20964129.2018.1532772

### ABSTRACT

**Introduction:** Nitrogen enrichment of coastal salt marshes can induce feedbacks that alter ecosystem-level processes including primary production and carbon sequestration. Despite the rising interest in coastal blue carbon, the effects of chronic nutrient enrichment on blue carbon processes have rarely been measured in the context of experimental fertilization. Here, we examined the ecosystem-level effects of nitrate ( $\text{NO}_3^-$ ) enrichment on the greenhouse gas dynamics of a *Spartina alterniflora*-dominated salt marsh. We measured  $\text{CO}_2$  and  $\text{CH}_4$  fluxes using static chambers through two growing seasons in a salt marsh that was nitrogen-enriched for 13 years and compared fluxes to those from a reference marsh.

**Outcomes:** We found that nitrogen enrichment increased gross primary productivity (GPP) by 7.7% and increased ecosystem respiration ( $R_{\text{ECO}}$ ) by 20.8%. However, nitrogen enrichment had no discernible effect on net ecosystem exchange (NEE). Taken together, these results suggest that nitrogen-induced stimulation of  $R_{\text{ECO}}$  could transform this salt marsh from a carbon sink into a source of carbon to the atmosphere.

**Conclusion:** Our results complement prior findings of nitrogen enrichment weakening soil structure and organic matter stability in tidal salt marshes, suggesting that increased nutrient inputs have the potential to alter the carbon storage function of these ecosystems through enhanced microbial respiration of previously sequestered carbon.

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*Ecosystem Health and Sustainability* (ISSN 2332-8878) is published by the American Association for the Advancement of Science. 1200 New York Avenue NW, Washington, DC 20005.

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