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Wetland Soil Co₂ Efflux Along a Latitudinal Gradient of Spatial and Temporal Complexity

L.T. Simpson[1,2,3] · T. Z. Osborne[3] · I. C. Feller[1]

Abstract

Foundation plant species play an important functional role in modifying microenvironment through vegetation structure and by influencing soil properties. Mangroves and salt marsh differ in vegetation structure, yet offer similar ecosystem services. This work aimed to understand how different vegetation classes and abiotic factors along a latitudinal gradient of spatial and temporal complexity affect soil CO_2 efflux. Soil CO_2 efflux, biomass, soil properties, and soil and air temperature were measured in July 2015 and January 2016 in situ at 10 sites along a 342-km latitudinal gradient on the Atlantic coast of Florida. Mean CO_2 flux values ranged from 0.41 ± 0.19 to 2.03 ± 0.19 µmol m^{-2} s^{-1} across vegetation classes, and efflux values in mangrove plots were not significantly different between sampling dates, whereas ecotone and salt marsh efflux values were. On average, CO_2 flux was 1.11 ± 0.18 µmol m^{-2} s^{-1} greater in July than in January across plots. There was no significant trend between efflux and aboveground biomass and a positive trend between belowground biomass and CO_2 efflux. Edaphic parameters (organic matter content (%), soil N, organic C, and pH) were comparable across all vegetation class soils and there was a positive trend between soil temperature and flux. Soil efflux had an inverse relationship with latitude; in January, there is an increase in efflux with a decrease in latitude, while in July, efflux increases with an increase in latitude. Consequently, we assert that differences in CO_2 efflux were due to soil temperature and species productivity along the latitudinal gradient studied.

Keywords Soil respiration · Blue carbon · Mangrove expansion · Salt marsh · Soil temperature · Productivity

Introduction

Carbon (C) cycling and storage are important ecosystem services provided by mangrove forests (Alongi 2014; Kristensen et al. 2008; Twilley et al. 1992), and carbon dioxide (CO_2) efflux from mangrove soils is a significant component of the global C budget (e.g., Alongi 2014; Donato et al. 2011). Net soil C sequestration is a key source of uncertainty in coastal wetland C budgets (Bauer et al. 2013) due to variability associated with both physical and biological factors (e.g., Reddy and DeLaune 2008) that vary along spatial and temporal gradients. The Atlantic coast of Florida moves from a subtropical habitat dominated by mangroves in the south to a temperate habitat dominated by salt marsh in the north, with a gradient of change evident in both habitat structure (e.g., Simpson et al. 2017) and Köppen climatic classification (Climate-Data.org 2017). Mild winter temperatures are currently facilitating the expansion of woody mangroves into herbaceous and gramonoid salt marshes along the Atlantic coast of Florida (Cavanaugh et al. 2014), thus providing an excellent opportunity to quantify variability in soil CO_2 efflux along a latitudinal gradient of change.

Vegetation type plays an important role in regulating soil efflux through controlling a variety of environmental factors. Communities may modify microenvironment and resource availability by altering the dynamics of biomass, organic matter, and nutrient cycling (Dias et al. 2010; Han et al. 2014; Howes et al. 1986; Maestre and Cortina 2003;

✉ L.T. Simpson
lsimpson@ufl.edu

[1] Smithsonian Environmental Research Center, Edgewater, MD 21037, USA

[2] Smithsonian Marine Station, Fort Pierce, FL 34949, USA

[3] Whitney Laboratory for Marine Bioscience, University of Florida, St. Augustine, FL 32080, USA

Raich et al. 1997; Wang et al. 2009), which are intricately tied with CO_2 efflux. Mangrove and salt marsh belowground biomass pools and soil biogeochemistries differ suggesting that replacement of salt marsh with mangroves might alter ecosystem C dynamics (Comeaux et al. 2012; Doughty et al. 2016; Leopold et al. 2013; Lewis et al. 2014; Osland et al. 2013; Patterson and Mendelssohn 1991). Temperature is one of the key regulators influencing biogeochemical processes in wetlands and air temperature varies spatially and temporally along the latitudinal gradient. Air temperature drives soil temperature (Zheng et al. 1993), and there have been many studies showing a positive correlation between temperature and soil efflux (Raich and Schlesinger 1992). Sediment temperatures have been shown to influence CO_2 efflux in mangrove ecosystems (Chen et al. 2012; Leopold et al. 2015; Liang et al. 2013) and when coupled with vegetation type will likely alter soil CO_2 efflux across latitudes (Inglett et al. 2011).

Understanding the factors that influence soil CO_2 efflux is of critical importance to global C cycles. Soil CO_2 flux represents the second largest source of terrestrial C release to the atmosphere on a global scale (Harden et al. 2017; Jobbagy and Jackson 2000; Raich and Schlesinger 1992; Schlesinger and Andrews 2000) and mangroves are among the world's most productive ecosystems, with their net primary production (NPP) estimated at 218 ± 72 Tg C year^{-1} (Bouillon et al. 2008). Soil efflux is directly correlated with NPP, which is also intricately tied with C storage, suggesting that understanding the spatial and temporal drivers of soil CO_2 efflux will be highly valuable for predicting future C storage potential. While soil CO_2 efflux is included in budgets of total C storage (e.g., Alongi 2014), the rate of CO_2 loss through efflux and the high degree of variability across latitudes is often overlooked. Quantifying CO_2 flux in wetland systems and understanding the factors influencing C storage and exchange has become increasingly important because there is still a limited understanding of the factors controlling the temporal and across-ecosystem variability of soil efflux (Reichstein et al. 2003). However, this knowledge is necessary to develop process-based models and to produce reliable regional estimates of soil CO_2 efflux.

In this study, we investigated soil CO_2 efflux over a latitudinal gradient of spatial and temporal complexity. We hypothesized that alterations in biotic (community structure) and abiotic (temperature) drivers, which are expected to change in response to global climate change (IPCC 2014), will likely modify soil CO_2 efflux rates and C dynamics of coastal ecosystems. We sought to answer the following questions: (1) do differences in mangrove and salt marsh productivity lead to differences in soil CO_2 efflux and, (2) how does soil temperature affect soil CO_2 efflux along a gradient of spatial and temporal complexity? Quantifying soil efflux along a latitudinal gradient

enables inferences on how changes in habitat structure will alter C dynamics of these important coastal ecosystems.

Methods

Study Sites

Ten sites, spanning 342 km (26°–29° N) along the east coast of Florida, were sampled to observe soil CO_2 efflux rates in structurally different habitats along a latitudinal gradient (Fig. 1). The spatial expanse of sampling sites allowed for quantification and comparison of ecosystem processes in four types of contrasting vegetation structures (class): (a) ecotonal mangroves, (b) pure salt marsh, (c) pure fringing mangroves, and (d) pure interior mangroves. In total, 54 plots were sampled across the ten sites. At each plot, soil CO_2 efflux, above- and belowground biomass, and environmental variables were measured, and soil cores were collected.

Within each of the ten sites, 10×10-m permanent plots were established in the fringe and interior. Pure salt marsh and ecotonal (salt marsh and mangrove) plots were sampled in the north (28°–29° N), while pure mangrove stands were sampled in the south (26°–27° N) (Fig. 1). The five northern sites had six plots per site, three plots in the fringe (ecotone), and three in the interior (salt marsh). Pure salt marsh stands contained monocultures or polycultures of herbaceous or graminoid salt marsh species and ecotonal stands were composed of a mixture of short-statured (dwarf) *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle* mangroves and salt marsh species. Salt marsh species included *Batis maritima*, *Distichlis spicata*, *Salicornia bigelovii*, *Salicornia virginica*, *Spartina alterniflora*, and *Sueda linearis*. Northern sites had an average winter temperature of 21.91 ± 0.20 °C (ranging from -0.77 to 28.63 °C) and average summer temperature of 30.04 ± 0.14 °C (ranging from 12.02 to 38.34 °C). The sites also had an average precipitation of 3.73 ± 1.27 mm day^{-1} in January 2016 and 5.00 ± 1.27 mm day^{-1} in July 2015.

In the five southern sites, there were three sites with six plots (three plots in the fringe (mangrove) and three plots in the interior (mangrove)) (see Fig. 2 in Simpson et al. 2017), while two of the sites only had three plots in the fringe. Southern sites were dominated by all three species of mangrove and were devoid of salt marsh species. Trees found fringing the seaward edge were typically tall (~ 5 m), while those in the landward interior were shorter (~ 3 m) and denser in stature. Southern sites had an average winter temperature of 21.97 ± 0.21 °C (ranging from 5.04 to 36.96 °C) and an average summer temperature of 27.73 ± 1.06 °C (ranging from 17.68 to 42.25 °C). Southern sites had an average precipitation of 6.60 ± 1.02 mm day^{-1} in January 2016 and 5.08 ± 1.27 mm day^{-1} in July 2015.
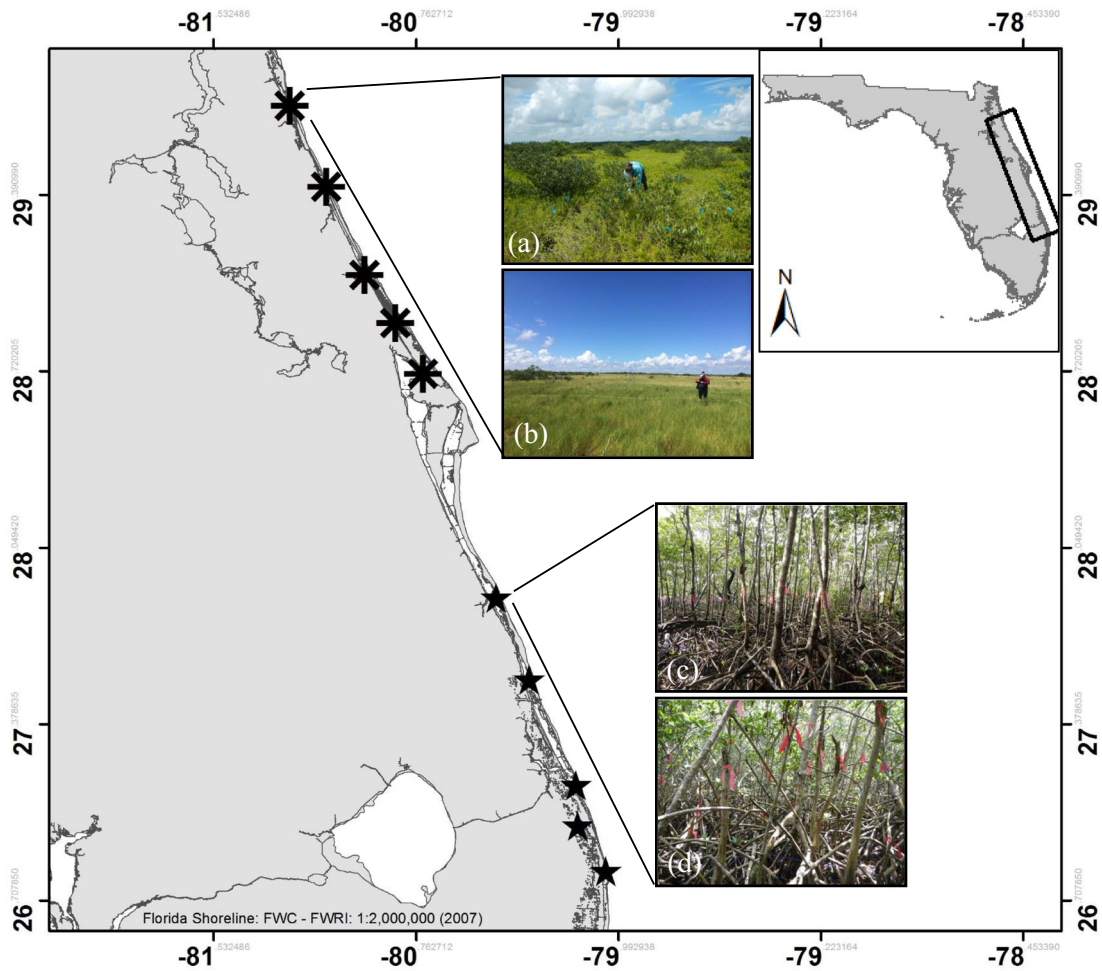
Fig. 1 Ten sites were studied along a 342-km latitudinal gradient. Each symbol represents a site. Asterisks represent sites composed of **(a)** mangrove–salt marsh ecotone and **(b)** pure salt marsh; stars represent sites that were **(c)** fringing and **(d)** interior mangroves

Fig. 2 Soil CO_2 efflux (μmol m^{-2} s^{-1}) and soil temperature (°C) across vegetation classes in January 2016 and July 2015. A two-way ANOVA revealed an interaction between vegetation class and time on CO_2 efflux ($F_{7,103} = 4.37$, $p = 0.0049$). Soil temperature was significantly different across vegetation class and sampling date (January and July) ($F_{7,95} = 5.78$, $p = 0.0011$). Values ± SE are presented. SE was left off of soil temperatures for visual clarity. Different letters denote significantly different groups
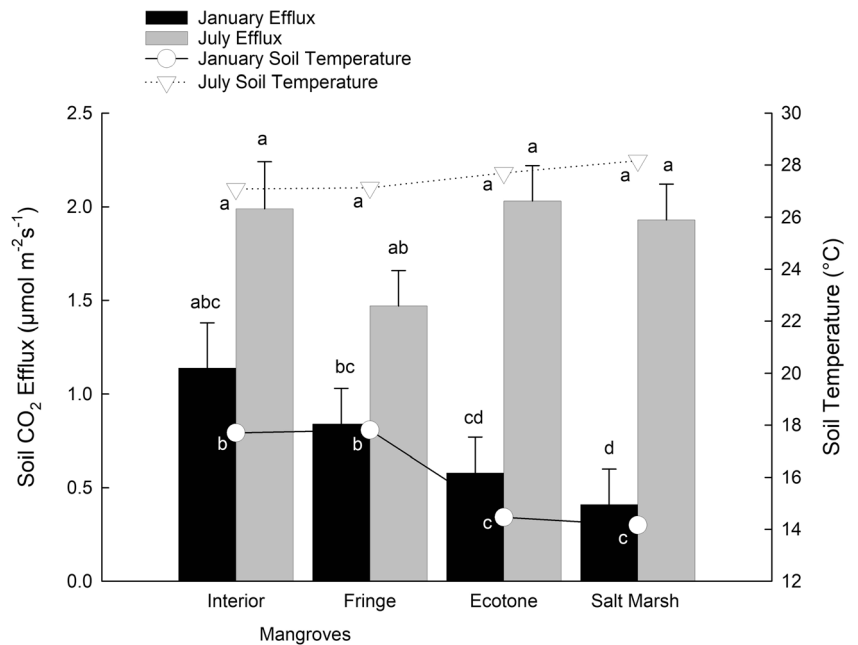
Field Sampling

Soil CO$_2$ Efflux

Soil CO$_2$ efflux was measured using a LI-COR 6400 portable photosynthesis system configured with the LI-COR soil CO$_2$ flux chamber (LI-COR Corp, Lincoln, NE, USA). The chamber was set to penetrate only 0.5 mm into the soil to avoid damaging surface roots. Settings for soil flux measurements were determined at each site following standard procedure (LI-COR Inc. 2003). At each plot, three CO$_2$ efflux measurements were taken and averaged together. Conspicuous microbial mats or biofilms were removed before taking measurements as suggested by Lovelock (2008). Crab burrows and pneumatophores were excluded from the chamber, which have been shown to alter biogeochemical processes and facilitate flux from soils (Bouillon et al. 2008; Kristensen et al. 2008; Pülmanns et al. 2014; Troxler et al. 2015). Sampling was done over 10 days (one site per day) and all measurements were taken at low tide. Interior plots were measured first, then fringe plots as a means to keep tidal range and exposure duration constant between plots and across sites. Sampling was conducted once in July 2015 and once in January 2016 to capture any temporal variability across the seasonal endmembers.

Biomass Measurements

To measure the aboveground biomass pool in mangroves, diameter at breast height (DBH) measurements was taken on all trees to calculate biomass through species-specific allometric equations (Supplementary Table 1). Mangrove root biomass was calculated using the general formula by Komiyama et al. (2008). Aboveground biomass estimates for salt marsh plant species were determined via destructive harvesting of one 1-m^2 subplot in each plot. Soil cores (20 cm in length and 5 cm in diameter) were taken to estimate salt marsh belowground biomass. Biomass measurements were then scaled up to Mg ha^{-1}.

Soil and Environmental Characteristics

At each plot, 50-cm soil cores were collected using a 10-cm inner diameter stainless steel corer. Soil cores were taken from each plot in April 2015 and subsamples of a known volume were oven-dried at 70 °C to a constant mass to determine bulk density (BD). Bulk density (g cm^{-3}) of each sample was calculated by dividing the oven-dried mass by the volume of the sample. Samples were ball milled with a Mixer/Mill 8000D (SPEX, Metuchen, New Jersey, USA) to ensure homogeneity prior to analysis for total organic C (TC), total N (TN), and loss on ignition (LOI). Subsamples of the homogenized soils were combusted using a CE–440 elemental analyzer (Exeter

Analytical, Inc. Chelmsford, Massachusetts, USA) for TC and TN. Remaining subsamples were combusted at 500 °C for 4 h in a Lindberg/Blue MTM Moldatherm box furnace (Thermo Fischer Scientific, Waltham, Massachusetts, USA) for LOI measurements. OC (%) pools were obtained as the product of total organic soil C (TC) and bulk density to 50 cm. Total organic soil C per sampled depth interval was calculated for each core then summed and scaled up to determine total soil C (Mg C ha^{-1}) at each sampling location.

Porewater salinity, pH, and soil temperature were measured during each sampling trip. Porewater was extracted from the ground at 15 cm using a sipper (McKee et al. 1988) and measured with a refractometer for salinity. pH and soil temperature were measured in situ at 5 cm depth in each sampling location with an IQ 150 (Spectrum Technologies, Inc., Aurora, IL, USA). Air temperature was recorded from January 2015 to January 2016 in every plot, with HOBO pendant temperature loggers (Onset Computer Corporation, Bourne, Massachusetts, USA). Additionally, regional air temperatures for January 2015–2016 and regional daily precipitation for July 2015 and January 2016 were obtained online from Weather Underground.

Soil strength, a proxy of belowground decomposition, was measured in each plot, in July 2015, at a depth of 15 cm with a shear vane tester (Geotech Society, Inc. N.Z.). Soil shear stress (hereafter referred to as soil strength) measurements give a relative value of plant decomposition based on the presumption that the integrity of root matrix is directly related to shear vane values (Turner et al. 2009). The handheld instrument measures maximum resistance (torque) when a rod fitted with vanes is rotated at a standard soil depth. Soil strength was calculated as: τ (kPa) = M/K, where M is the torque to shear the soil and K is a constant, calculated by the manufacturer, depending on dimensions and shape of the vane.

Statistical Analysis

A two-way ANOVA was used to test for interactions between sampling time (January or July) and vegetation class (fringe, interior, ecotonal, salt marsh) on soil CO$_2$ efflux. In addition, a two-way ANOVA was used to test for interactions between sampling time (January or July) and latitude (26°–29° N) on soil CO$_2$ efflux, soil temperature, and monthly precipitation. Soil variables (LOI, BD, OC, soil N, soil C, C/N, soil strength) were analyzed across latitude using one-way ANOVAs. Normality was assessed using the Shapiro–Wilks test and homogeneity of samples was assessed using Levene's test. When required, variables were log or square root transformed to comply with normality and homogeneity of variances when testing linear models. When significant differences were found, pairwise comparisons were explored with Tukey's honestly significant differences test. Alpha (α) was set at ≤ 0.05.

Linear regression correlations were used to explore interactions between soil efflux and environmental characteristics (soil temperature, pH, salinity, soil C, soil N, C/N) across all sites. Interactions between biomass components and soil efflux were also explored with simple linear regressions. Stepwise regression modeling was used to test the effects of multiple environmental parameters (soil temperature, pH, salinity, soil C, soil N, soil strength, biomass) on soil efflux. Analyses were performed using JMP 5.0. (S.A.S Inc., Cary, North Carolina, USA). Throughout the manuscript, data are reported as mean ± standard error.

Results

Vegetation Class

CO_2 efflux values in mangrove plots (fringe and interior) were not significantly different between sampling dates, whereas northern plot (ecotone and salt marsh) efflux values were $F_{7, 103} = 4.57$, $p = 0.0049$ (Fig. 2). On average, CO_2 efflux was 1.11 ± 0.18 μmol m^{-2} s^{-1} greater in July than in January across plots. Additionally, mangrove efflux was significantly different from salt marsh efflux in January ($p = 0.0226$). There was a significant difference in aboveground biomass (AGB) across vegetation classes ($p = < 0.0001$) (Table 1); however, there was no significant trend between efflux and AGB. Efflux values ranged from 0.41 ± 0.19 to 2.03 ± 0.19 μmol CO_2 m^{-2} s^{-1}, which is in line with other reported values in the literature (e.g., Chen et al. 2010, 2014; Lovelock 2008; Poungparn et al. 2009; Liang et al. 2013; Troxler et al. 2015). Belowground biomass (BGB) was significantly different across vegetation classes (Table 1), and as

BGB increases, there was an increase in soil CO_2 efflux ($R^2 = 0.22$, $p = < 0.001$).

LOI, salinity, pH, soil N, and OC (%) were not significantly different across vegetation classes, whereas soil strength, BD, and C/N were (Table 1). Salinity and pH were not significant across vegetation classes and explained minimal variability within CO_2 efflux ($R^2 = 0.18$, $p = < 0.0001$; $R^2 = 0.11$, $p = 0.002$, respectively). Soil strength values were highest in interior plots and lowest in salt marsh plots ($F_{3,103} = 26.6$, $p = < 0.0001$), and BD was significantly different between fringe and ecotonal plots ($F_{3,103} = 3.69$, $p = 0.0143$). Soil C/N values were low (< 15) in ecotonal and salt marsh and greater in mangrove plots ($F_{3,103} = 24.1$, $p = < 0.0001$). Soil C was significantly different across vegetation classes, ecotonal and salt marsh sites having significantly less soil C than mangrove sites (fringe and interior) ($F_{3,103} = 4.086$, $p = 0.0087$). All plots averaged 27.3 ± 0.36 °C in July. In January, fringe and interior plot soil temperatures averaged 17.8 ± 0.97 °C, whereas ecotone and salt marsh averaged 4.5 ± 0.87 °C ($F_{7,95} = 5.78$, $p = 0.0011$) (Fig. 2).

Latitude

Differences in efflux across the latitudinal gradient were investigated because vegetation class translates to vegetation variation across latitude. Fringe and interior mangrove plots equate to southern plot locations (26–27° N) and ecotone and salt marsh plots were those found in 28–29° N (Fig. 1). Soil efflux has an inverse relationship with latitude; in January, there is an increase in efflux with a decrease in latitude, while in July, efflux increases with an increase in latitude ($F_{3,98} = 11.03$, $p = < 0.0001$) (Fig. 3a). Soil CO_2 efflux does not vary between sampling dates at 26° N, whereas efflux was greater

Table 1 Variables across vegetation class

	Mangroves		Ecotone	Salt marsh
	Interior	Fringe		
AGB (Mg ha^{-1})	85.1 ± 7.19[a]	62.3 ± 5.56[ab]	44.2 ± 5.56[b]	2.06 ± 5.57[c]
BGB (Mg ha^{-1})	114 ± 10.7[a]	84.9 ± 8.31[a]	49.6 ± 8.30[b]	$.001 \pm 8.33$[c]
Soil C (Mg ha^{-1})	182 ± 14.5[a]	141 ± 11.2[ab]	125 ± 11.2[b]	124 ± 11.3[b]
Soil N (Mg ha^{-1})	8.37 ± 0.97[a]	$7.65 \pm .751$[a]	$9.22 \pm .751$[a]	$8.86 \pm .771$[a]
Soil C/N	27.8 ± 1.38[a]	18.5 ± 1.07[b]	13.9 ± 1.07[c]	14.7 ± 1.07[bc]
Bulk density (g cm^{-3})	0.52 ± 0.06[ab]	$.472 \pm .051$[b]	$.671 \pm .050$[a]	$.491 \pm .053$[ab]
Organic matter (LOI)	30.5 ± 4.68[a]	19.2 ± 3.63[a]	18.7 ± 3.62[a]	25.9 ± 3.68[a]
Organic C (%)	15.5 ± 1.90[a]	10.8 ± 1.50[a]	10.7 ± 1.50[a]	13.7 ± 1.53[a]
Shear vane (kpa)	159 ± 9.32[a]	99.3 ± 7.22[b]	86.7 ± 7.22[b]	54.4 ± 7.35[c]
pH	7.00 ± 0.15[a]	$6.86 \pm .120$[a]	$6.71 \pm .123$[a]	$6.61 \pm .112$[a]
Salinity (ppt)	36.1 ± 2.68[a]	36.7 ± 1.90[a]	39.6 ± 1.72[a]	38.1 ± 1.73[a]

Values are means ± SE

ABG aboveground biomass, *BGB* belowground biomass, *LOI* loss on ignition (%)

Fig. 3 **(a)** Soil CO_2 efflux (μmol m^{-2} s^{-1}) and **(b)** soil temperature (°C) across latitudes (26°–29°) in January 2016 and July 2015. Values ± SE are presented. Different letters denote significantly different groups
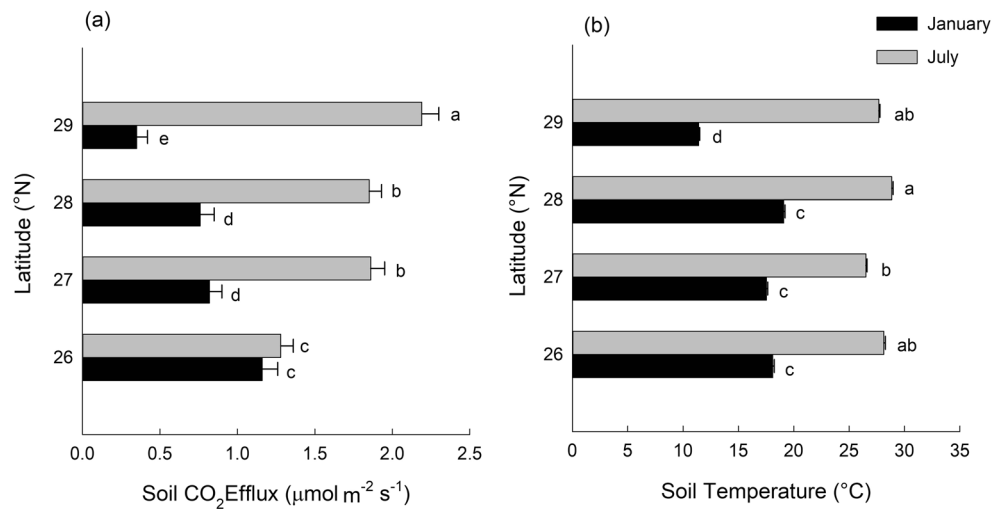
in July than in January across the latitudes of 29°–27° N (Fig. 3a). The plots at 29° N had the greatest difference in soil efflux between January and July (0.35 ± 0.14 to 1.84 ± 0.15 μmol CO_2 m^{-2} s^{-1}).

Soil temperatures were significantly different between January and July sampling dates; however, within the sampling dates, soil temperature was variable across latitude ($F_{7,96} = 51.58$, $p = < 0.0001$) (Fig. 3b). Soil temperature was greater in July than in January across all latitudes ($F_{1,99} = 463.81$, $p = < 0.0001$) and accounts for 46% of the variability seen in soil CO_2 efflux. As soil temperature increases, soil efflux and variability

within increase ($R^2 = 0.46$, $p = < 0.0001$; y = 0.08x–0.62) (Fig. 4). Air temperatures were cooler in January than in July and decreased with increase in latitude ($F_{7,12,331} = 526$, $p = < 0.0001$). Additionally, soil strength is significantly different across latitude, with higher stress measurements in southern latitudes ($F_{3,102} = 11.8$, $p = < 0.0001$) (Table 2). Soil C (Mg C ha^{-1}) also decreases with an increase in latitude ($F_{3,102} = 4.74$, $p = 0.004$), which may be foreshadowed by the similar trend seen in soil C/N ($F_{3,102} = 19.3$, $p = < 0.0001$) (Table 2). Precipitation was not significantly different across latitude ($p = 0.1610$) or time ($p = 0.9105$).

Fig. 4 As soil temperature increases, soil CO_2 efflux increases ($R^2 = 0.46$, $p = < 0.0001$). Equation for the line is y = 0.08x–0.62
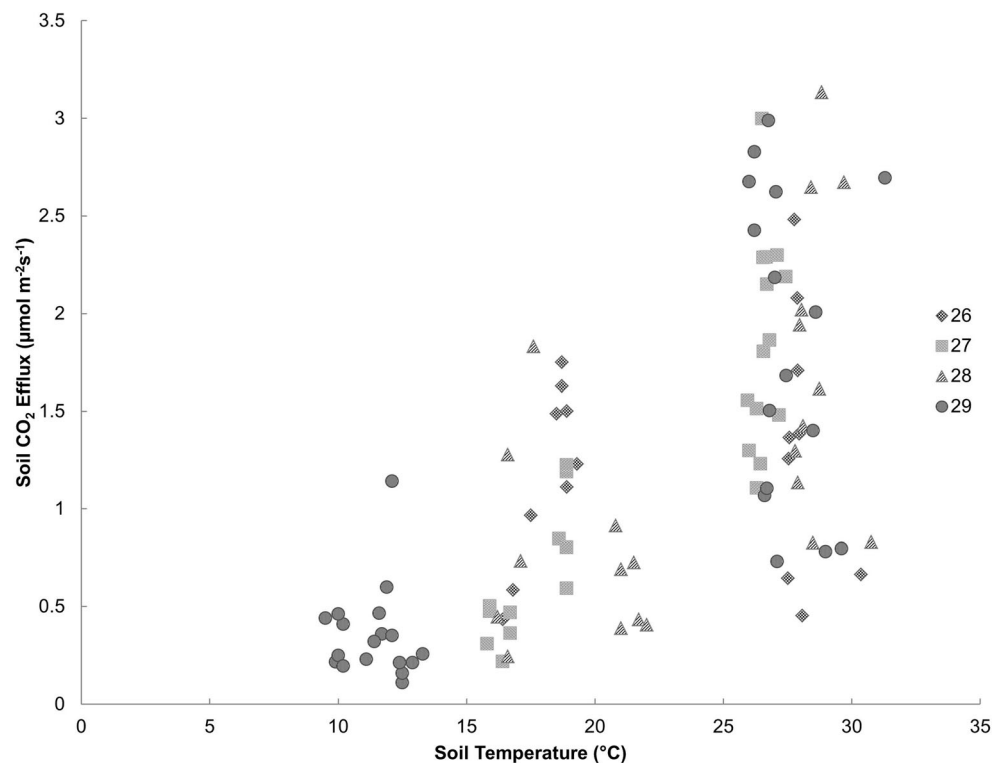
Table 2 Soil variables across latitude

	29° N	28° N	27° N	26° N
Soil strength (kpa)	70.6 ± 7.63[b]	68.2 ± 9.34[b]	129 ± 8.35[a]	108 ± 10.7[a]
Soil C/N	14.8 ± 1.02[b]	13.6 ± 1.25[b]	24.8 ± 1.11[a]	17.2 ± 1.44[b]
Soil C (Mg C ha^{-1})	116 ± 14.8[b]	131 ± 18.2[b]	140 ± 16.2[ab]	184 ± 20.9[a]

Values are means ± SE

Discussion

Woody encroachment in coastal ecosystems is likely to alter the soil microenvironment through dynamic interactions of biomass structure and resource availability (Dias et al. 2010; Han et al. 2014; Howes et al. 1985; Maestre and Cortina 2003; Raich et al. 1997; Wang et al. 2009). Biomass pools were variable across vegetation classes, and correlation with soil efflux was highly variable as seen in other studies (e.g., Comas and Eissenstat 2004; Jackson et al. 2009; Lovelock et al. 2006; Lovelock 2008; Shi et al. 2006). Both AGB and BGB were significantly greater in mangrove plots than in ecotonal and salt marsh (Table 1) and there was a strong positive relationship between BGB and efflux. Experiments in a range of ecosystems have echoed this finding; increases in BGB equate to increases in soil efflux (e.g., Geng et al. 2012; Hanson et al. 2000; Jackson et al. 2009). Differences in root biomass may lead to a higher rate of efflux by living fine roots due to high metabolic activity and high rates of nutrient uptake (Pregitzer et al. 2002). Additionally, the soil microenvironment which regulates soil CO_2 efflux was similar across all vegetation class soils (Table 1). Edaphic variables, which are linked to productivity and organic matter inputs of an ecosystem (Reddy and DeLaune 2008), are expected to change with encroachment of woody species into herbaceous and succulent dominated systems. While vegetation class structure and biomass ratios differ, organic matter content (%), soil N, organic C, and pH were comparable across all vegetation class soils (Table 1). Lack of differences suggests that the soil microenvironment is slow to change with mangrove encroachment (e.g., Henry and Twilley 2013; Perry and Mendelssohn 2009), thus highlighting the importance of other spatial and temporal drivers on soil efflux along the Atlantic coast of Florida.

Soil temperature has a well-documented influence on CO_2 efflux in mangrove soils (Chen et al. 2012; Leopold et al. 2015; Liang et al. 2013) and fluxes exhibit a striking seasonal pattern with higher rates during summer months (Alongi et al. 2005; Chen et al. 2016; Howarth and Teal 1979; Kirwan and Blum 2011). Soil efflux trends with soil temperature across vegetation zones (Fig. 2) and vegetation zone reflects differences in latitude along the gradient studied. Many global- and regional-scale analyses on the influence of air temperature on mangrove productivity have used latitude as a surrogate variable (Alongi 2009). Soil temperature is relatively constant along the latitudinal gradient during prospective sampling dates; yet, soil efflux has an inverse relationship with latitude. In January, there is an increase in efflux with a decrease in latitude, while in July, efflux increases with an increase in latitude. This inverse relationship may be driven in part by biomass productivity of the system.

Mangrove and salt marsh species habitat varies spatially and productivity differs temporally. Herbaceous and succulent salt marsh make up 50–60% of northern plots (28–29° N), whereas mangroves make up 100% of the southern plots (26–27° N). Salt marsh species have seasonal pulsed turnover rates (Hopkinson et al. 1978), which contrast to mangroves long lived aboveground biomass pools (Tomlinson 1986). Seasonal differences in productivity will lead to differences in the amount of organic matter available for mineralization. High turnover rates in northern latitudes may contribute more organic matter available for microbial breakdown and mineralization, leading to higher rates of CO_2 efflux. Peak soil efflux is expected in the summer months, due to high soil temperatures and the availability of labile substrates (Howes et al. 1985; Teal and Howes 1996). Additionally, litter quality significantly affects organic matter decomposition (Couteaux et al. 1995; Mooshammer et al. 2012; Strickland et al. 2009) and the dominant species in northern plots were *S. alterniflora*, *B. martima*, *S. virginica*, and *A. germinans*, all with low litter C/N (35.4 ± 1.74, 18.37 ± 0.20, 27.05 ± 0.40, and 26.4 ± 0.86, respectively) as compared to *R. mangle* (42.5 ± 0.52), the dominant species in southern plots. Low litter C/N supports increases in decomposition, and increased CO_2 efflux rates and subsequent decomposition in northern latitudes were supported by low soil strength values and soil C/N (Table 1). Northern plots have the greatest occurrence of salt marsh species and *A. germinans* pneumatophores. Pneumatophores oxidate the rhizosphere through oxygen leakage from roots (McKee et al. 1988), thus allowing for greater exchange of oxygen in surface and anoxic sediments. Large inputs of labile organic matter and a greater exchange of oxygen suggest that surface soils of northern plots have greater C turnover than southern plots which are composed mainly of *R. mangle*. Physical and chemical changes in these surface soils may be contributing to the loss of C via leaching/remineralization. High organic matter turnover and CO_2 flux in July is met by a large decrease in plant productivity (Hopkinson et al. 1978)

and efflux in January, as soil temperatures decrease significantly. Soil efflux involves fluctuating populations of numerous organisms, each undergoing a complex series of reactions, some of which may have different temperature sensitives (Rees et al. 1988). Decreasing soil temperatures can halt microbial breakdown and decrease microbial species richness (Lynch et al. 2004) and when accompanied by decreases in plant productivity, can lead to decreases in soil efflux.

Reductions in mineralization rates may lead to decreases in soil efflux and may increase C accumulation in the system. Hence, the dynamic nature of soil temperature and efflux in northern latitudes has likely diminished C accumulation potential. Increases in latitude are echoed with decreases in average soil C (Mg C ha^{-1}) pools (Table 2). Mangrove plots in the south, which are not subject to such large temporal changes in soil temperature as seen in the northern plots, and the resulting flux of CO_2 to the atmosphere, have 23.7% higher soil C pools (Mg C ha^{-1}) (Fig. 3; Table 2). This may be influenced in part by plant productivity, extended growing season, and highly recalcitrant litter. Higher soil strength in southern mangrove plots suggests increased live rooting volume, which helps bind sediments and promotes C accumulation (Baustian et al. 2012). The high rates of mangrove productivity seen in southern plots, coupled with anoxic soils, have contributed to peat development and the high soil C observed. However, increased CO_2 efflux in northern latitudes due to increases in soil temperature and species turnover would likely lead to a slower C accumulation in these systems.

Understanding the impacts of spatial and temporal variables on soil efflux, and ultimately soil respiration, is important for an accurate prediction of the future terrestrial C balance in the context of changing climate. Soil CO_2 respiration is the sum of heterotrophic and autotrophic respiration in the soil (e.g., of roots, microbes, and soil fauna). In the long term, all CO_2 produced in the soil must be emitted by the surface and soil CO_2 efflux must correspond to soil respiration. However, in the short term, soil CO_2 efflux deviates from total soil respiration due to many spatial and temporal reasons (Maier et al. 2011; Roland et al. 2015). Our study provides values of soil CO_2 flux over a range of environmental conditions and illustrates the importance of both spatial and temporal drivers in mangrove ecosystem C balance by identifying important sources of variability in C flux. Fifty-six percent of the variability in soil efflux could be explained by a combination of soil temperature, pH, soil C, and belowground biomass, with soil temperature explaining 46% of the model. Sources of variability may be regulated by the microenvironment and are hard to elucidate over such a large spatial expanse, and the differences across the latitudinal gradient are highly variable and location-dependent. The factors that drive variation in CO_2 efflux, and ultimately soil respiration, will influence sources and sinks of C along the Atlantic coast of Florida. Our results provide a foundation for better understanding of the effects of vegetation class and soil temperature on soil

efflux and C cycling in a changing landscape. Within the context of climate change, studies on the spatial and temporal drivers of soil efflux are especially important because they can help scientists and environmental managers better anticipate and prepare for the ecological consequences of changing climatic conditions (Glick et al. 2011; Stein et al. 2014).

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