



Carbon and nitrogen pools and mobile fractions in surface soils across a mangrove saltmarsh ecotone

David Bruce Lewis^{a,*}, Kristine L. Jimenez^a, Amr Abd-Elrahman^b, Michael G. Andreu^c, Shawn M. Landry^d, Robert J. Northrop^e, Cassandra Campbell^a, Hilary Flower^f, Mark C. Rains^d, Christina L. Richards^a

^a University of South Florida, Department of Integrative Biology, 4202 E. Fowler Ave., SCA 110, Tampa, FL 33620, USA

^b University of Florida, School of Forest, Fisheries, and Geomatic Sciences, Gulf Coast Research and Education Center, 1200 North Park Road, Plant City, FL 33563, USA

^c University of Florida, School of Forest, Fisheries, and Geomatic Sciences, 351 Newins-Ziegler Hall, PO Box 110410, Gainesville, FL 32611, USA

^d University of South Florida, School of Geosciences, 4202 E. Fowler Ave, NES 107, Tampa, FL 33620, USA

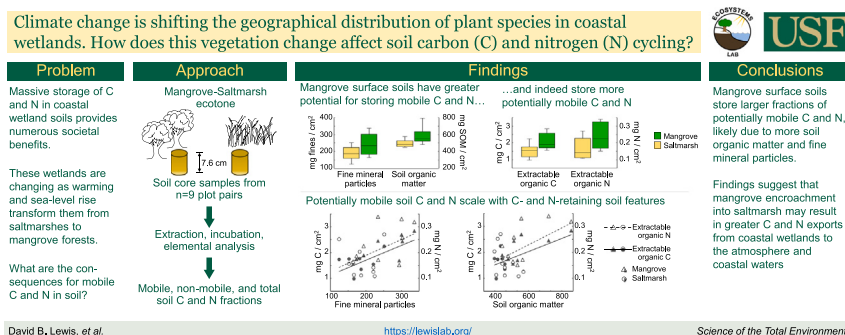
^e University of Florida, Institute of Food and Agricultural Sciences Extension—Hillsborough County, 5339 South County Road 579, Seffner, FL 33584, USA

^f Eckerd College, Department of Environmental Studies, 4200 54th Avenue South, Saint Petersburg, FL 33711, USA

HIGHLIGHTS

- Mobile carbon and nitrogen accumulate in mangrove surface soil.
- Fine sediment accumulation in mangroves may account for mobile C and N accumulation.
- Fine sediment and mobile C and N stocks are smaller in more landward saltmarsh.
- Total C and N pools are similar between mangrove and saltmarsh surface soils.
- Mangrove replacement of saltmarsh may accelerate coastal wetland exports of C and N.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 27 November 2020

Received in revised form 23 July 2021

Accepted 24 July 2021

Available online 29 July 2021

Editor: Paulo Pereira

Keywords:

Biogeochemistry
Climate change
Sea-level rise
Soil texture
Subtropics
Tidal wetland

ABSTRACT

In the subtropics, climate change is pushing woody mangrove forests into herbaceous saltmarshes, altering soil carbon (C) and nitrogen (N) pools, with implications for coastal wetland productivity and C and N exports. We quantified total C and N pools, and mobile fractions including extractable mineral N, extractable organic C and N, and active (aerobically mineralizable) C and N, in surface soils (top 7.6 cm) of adjacent mangrove (primarily *Avicennia germinans*) and saltmarsh (*Juncus roemerianus*) vegetation zones in tidal wetlands of west-central Florida (USA). We tested whether surface-soil accumulations of C, N, and their potentially mobile fractions are greater in mangrove than in saltmarsh owing to greater accumulations in the mangrove zone of soil organic matter (SOM) and fine mineral particles (C- and N-retaining soil constituents). Extractable organic fractions were 39–45% more concentrated in mangrove than in saltmarsh surface soil, and they scaled steeply and positively with SOM and fine mineral particle (silt + clay) concentrations, which themselves were likewise greater in mangrove soil. Elevation may drive this linkage. Mangrove locations were generally at lower elevations, which tended to have greater fine particle content in the surface soil. Active C and extractable mineral N were marginally ($p < 0.1$) greater in mangrove soil, while active N, total N, and total C showed no statistical differences between zones. Extractable organic C and N fractions composed greater shares of total C and N pools in mangrove than in saltmarsh surface soils, which is meaningful for ecosystem function, as persistent leaching of this fraction can

* Corresponding author.

E-mail addresses: davidlewis@usf.edu (D.B. Lewis), aamr@ufl.edu (A. Abd-Elrahman), mandreu@ufl.edu (M.G. Andreu), landry@usf.edu (S.M. Landry), northrop@ufl.edu (R.J. Northrop), campbell29@usf.edu (C. Campbell), flowerhd@eckerd.edu (H. Flower), mrains@usf.edu (M.C. Rains), clr@usf.edu (C.L. Richards).

perpetuate nutrient limitation. The active (mineralizable) C and N fractions we observed constituted a relatively small component of total C and N pools, suggesting that mangrove surface soils may export less C and N than would be expected from their large total C and N pools.

© 2021 Elsevier B.V. All rights reserved.

1. Introduction

Under a changing climate, temperature warming and water redistribution are causing globally pervasive shifts in plant species ranges and associated changes in biogeochemical cycles. This intersection of climate, vegetation, and biogeochemical change is particularly important in marine coastal wetlands owing to their dynamic plant communities and large carbon (C) and nitrogen (N) stores. Coastal wetlands are highly productive ecosystems that trap tidal inputs of organic matter and accumulate disproportionately large masses of C (McLeod et al., 2011; Saintilan et al., 2014; Van de Broek et al., 2018; Sanderman et al., 2018). This wetland C inventory is an essential piece of the marine blue C reservoir, itself critical to the global C balance (Nellemann et al., 2009), and is particularly concentrated in soil organic matter (SOM) (Donato et al., 2011; Doughty et al., 2016; Johnson et al., 2000). Nitrogen is likewise stored in SOM, so coastal soils serve as massive blue N sinks, as well. Indeed, soils may hold 90% or more of total ecosystem N stocks in coastal wetlands such as saltmarshes and mangrove forests (Haines et al., 1977; Alongi et al., 2003; Ramos e Silva et al., 2007). Given their massive size, mobilizing even small fractions of coastal soil C and N pools can produce large fluxes of these elements to the atmosphere and adjacent coastal waters (Boto and Wellington, 1988; Twilley et al., 1992; Childers et al., 2002; Dittmar et al., 2006; Bouillon et al., 2008), where they take forms that adversely impact air and water quality. Yet, the mobilization of soil C and N through depolymerization, dissolution, and mineralization also liberates the organic energy and mineral nutrients that drive soil microbial activity and plant growth within coastal wetlands, thereby giving rise to the many ecosystem services for which these habitats are valued (Teal, 1962; Robertson et al., 1992; Nedwell et al., 1994; Anderson et al., 1997; Alongi et al., 2002; Barbier et al., 2011). An examination of the potential mobility of soil C and N will thus contribute to understanding ecological function in coastal wetlands as well as their material exports to air and adjacent surface waters.

One source of variation in soil nutritional pools is vegetation assemblage. Plant productivity and functional traits regulate flows of energy and matter, thereby shaping soil conditions that feed back to define site suitability for plant species (McKee, 1993; Chapman et al., 2006; Kulmatiski et al., 2008; van der Putten et al., 2013). This coupling between soil conditions and vegetation form is conspicuous in coastal environments, where plant communities are arrayed in distinct zones across edaphic gradients (Pennings and Callaway, 1992; McKee, 1993; Matthijs et al., 1999; Cui et al., 2011; Osland et al., 2018). Plant zonation is not simply an outcome of edaphic gradients, but also helps create them through numerous plant influences on soil. Coastal plants accrete soil by depositing autochthonous organic material and by trapping particulate matter delivered in tides and other currents (Morris et al., 2002; McKee et al., 2007; Fagherazzi et al., 2012; Kirwan and Guntenspergen, 2012; Kelleway et al., 2017; Van de Broek et al., 2018). They also regulate soil loss by forming barriers that slow erosive currents, binding soil with roots, and mediating soil respiration (Augustinus, 1995; Reed, 1995; Simpson et al., 2019a). Plants further imprint coastal soils by hosting distinct microbial and animal communities with varying metabolic functions and engineering behaviors (Barreto et al., 2018; Scheffel et al., 2018). Differences in soil biogeochemistry are accordingly observed between the various plant formations that occupy different coastal zones (Adams, 1963; Sherman et al., 1998; Lewis et al., 2014a; Kelleway et al., 2017) and successional states (Craft et al., 2003; Osland et al., 2012; Dontis et al., 2020).

Associations between plants and soils assume heightened importance as plant geographical distributions move in response to global environmental change. As plant species advance on new areas, they may encounter limiting soil conditions that inhibit further encroachment (Huenneke et al., 1990), or may cause biogeochemical change as they replace previously dominant species (Blank, 2008), both of which characterize woody plant encroachment into herbaceous communities (Archer et al., 2017). These possibilities compel efforts to understand how soils vary across ecotones that are moving in response to climate change, such as ecotones on subtropical coastlines where woody mangrove forests are expanding into herbaceous saltmarshes (Krauss et al., 2011; Saintilan et al., 2014). Mangrove expansion increases C storage both above and below ground (Bianchi et al., 2013; Kelleway et al., 2016; Krauss et al., 2017; Lamont et al., 2020; Alongi, 2020). The magnitude of this effect is variable (Perry and Mendelsohn, 2009; Henry and Twilley, 2013; Yando et al., 2018; Raw et al., 2019), as mediated by climate setting, the C reservoir type being examined, and other contextual factors (Yando et al., 2016; Rogers and Krauss, 2019; Macy et al., 2020). Variation across the mangrove-saltmarsh ecotone in soil C storage is linked to patterns in soil enzyme activity, nutrient mineralization, decomposition, and dissolution (Lewis et al., 2014a; Charles et al., 2020; Simpson et al., 2020; Steinmuller et al., 2020). These depletive processes act on particular fractions of SOM (Grandy and Neff, 2008), and are carried out by soil microbial communities that differ phylogenetically and metabolically between mangrove and saltmarsh sediments (Barreto et al., 2018). The increased storage of soil C often observed with mangrove encroachment suggests that soil N and the potentially mobile fractions of both elements increase in parallel.

Mangrove, relative to saltmarsh, soil could store larger masses of potentially mobile C and N if they accumulate larger masses of SOM and fine mineral particles (silt and clay particles <53 μm). Both of these soil constituents retain potentially mobile material that might otherwise be exported. On sandy coastal hillslopes, for example, C and N are poorly retained and thus rapidly exported, whereas hillslopes with finer mineral particle sizes retain larger amounts of extractable C and N in situ (Castellano et al., 2013). Fine mineral sediments retain C and N by forming aggregates that encase and protect organic C and presumably its associated N (Six et al., 2004; Kleber et al., 2007), and by providing ion exchange sites that fix charged forms of N (Young and Aldag, 1982). This role of fine mineral particles in C and N protection is well-established in terrestrial soils (Hassink and Whitmore, 1997), and while it is less commonly examined in coastal wetlands, stable aggregate formation and the protection of organic C by fine mineral sediments do occur in coastal wetlands under a variety of plant taxa (Caravaca et al., 2005; Sun et al., 2019). Tidal inundation pumps sediment particles into mangrove forests where finer particles preferentially settle at slack tide (Furukawa and Wolanski, 1996), and sediment deposition onto soil surfaces is accordingly higher in mangrove forests than in the saltmarshes behind them (Adame et al., 2010). Carbon and N are principal constituents of SOM owing to its biological origin, so SOM may likewise hold large potentially mobile C and N fractions. The quality of SOM may differ between vegetation zones, however, so the relatively greater accumulation of soil C often observed in mangrove forests may not translate into larger mobile C fractions. Terrestrial soils can show this behavior. In some settings, for example, urban surface soils store more total N but similar masses of potentially mobile N as stored in nearby agricultural surface soils (Lewis et al., 2014c). In this study, we accordingly evaluate how surface-soil C and

N are allocated into fractions of various mobility across a mangrove-saltmarsh ecotone that is migrating in response to climate change and sea-level rise.

Here, we work across an ecotone in a region of well-documented mangrove range expansion (Raabe et al., 2012; Osland et al., 2013). Our objective is to investigate whether and why C and N pools and their potentially mobile fractions are greater in mangrove than in saltmarsh surface soils. Potentially mobile fractions of organic matter are most highly concentrated in the top 5–10 cm (Chen and Twilley, 1999; Kristensen et al., 2011). Surface accumulation of potentially mobile material results in part because the liberation of dissolved organic matter by tidally cyclic drying and rewetting of soils would be most expressed at the soil surface (Li et al., 2020), and in part because root mass, a source of organic exudates, is likewise concentrated at shallow depths (Barreto et al., 2018). Moreover, the increased soil C storage resulting from mangrove encroachment is particularly evident in the top 10 cm on account of rapid litter input (Simpson et al., 2019b). Encroaching plant propagules must first contend with this soil horizon, and it is the mobile fractions of this horizon that provide nutrients necessary for germination and early growth. Of course, far more C and N is stored throughout the full soil profile of coastal wetlands than what is found in the surficial soil layer (Donato et al., 2011) and aboveground biomass also stores abundant C and N. Much excellent work exists on full accountings of ecosystem C and N stocks in coastal wetlands (e.g., Liao et al., 2007; Wang et al., 2013; Charles et al., 2020; Macy et al., 2020; Alongi, 2020), so here we turn our attention to better understanding potentially mobile forms of C and N in the context of encroaching vegetation, orienting our focus on the surface horizon.

We test the hypothesis (1) that surface-soil accumulations of C, N, and their potentially mobile and non-mobile fractions are greater in mangrove than in saltmarsh owing to greater accumulations of C- and N-retaining soil constituents (organic matter and fine mineral particles) in the mangrove zone. This hypothesis is tested by evaluating whether surface-soil concentrations of C, N, and their various fractions correlate with concentrations of SOM and fine mineral particles, and whether these response and predictor variables are both greater in mangrove than in saltmarsh. We also test the hypothesis (2) that mangrove forests store larger fractions of potentially mobile C and N in surface soils simply on account of storing larger total C and N pools, versus the alternative that surface-soil C and N pools are inherently more or less mobile in mangrove forest. This hypothesis is tested by comparing mangrove and saltmarsh zones with regard to the proportions of their C and N pools that are potentially mobile. Finally, we test the hypothesis (3) that the biogeochemical cycling of C and N are coupled similarly in mangrove and saltmarsh surface soils. This hypothesis is tested by evaluating whether the stoichiometric ratios (C:N) of the total, non-mobile, and potentially mobile fractions are similar between the two vegetation zones.

2. Material and methods

2.1. Site description

We studied black mangrove (*Avicennia germinans*) dominated forest and black needlerush (*Juncus roemerianus*) saltmarsh along the Gulf of Mexico coastline in peninsular west-central Florida, USA (Fig. 1). This location has a humid subtropical climate with mean monthly temperatures ranging from 15.6 °C in January to 28.5 °C in August (1991–2020 monthly normals, U.S. NOAA National Centers for Environmental Information, station GHCND:USC00088824, Tarpon Springs, Florida), and annual precipitation of 1379 mm (annual mean 1991–2020, Tarpon Springs station). Precipitation falls as rain, with 60% falling during June through September, and 40% evenly distributed among other months. Monthly mean relative humidity ranges from 67% in April and May to 76% in August and September (1948–2018, U.S. NOAA Comparative Climate Data for the United States through 2018, station GHCND:

USW00012842, Tampa International Airport). Tides are semi-diurnal, with 0.57 m median amplitudes during the 12-month period prior to sampling (U.S. NOAA National Ocean Service, Clearwater Beach, Florida, station 8726724). Sea-level rise is 4.0 ± 0.6 mm per year (1973–2020 trend, mean \pm 95% confidence interval, NOAA NOS Clearwater Beach station). The *A. germinans* mangrove zone is either adjacent to water or fringed on the seaward side by a narrow band of red mangrove (*Rhizophora mangle*). A near-monoculture of *J. roemerianus* is often adjacent to and immediately landward of the *A. germinans* zone (see supplemental images S1–S5). The transition from the mangrove to the *J. roemerianus* zone is variable in our study area. An abrupt edge between closed-canopy mangrove and *J. roemerianus* monoculture may extend for up to several hundred meters in some locations, while other stretches of ecotone present a gradual transition where smaller, widely spaced trees are interspersed into the herbaceous marsh (cf. Yando et al., 2018; Steinmuller et al., 2020). *Juncus roemerianus* then extends landward to a high marsh patchwork of succulent halophytes (including *Salicornia bigelovii*, *Sesuvium* sp., and *Batis maritima*), scattered dwarf mangrove, and salt pans, followed in turn by upland vegetation that includes *Pinus* sp. and *Serenoa repens*. Other work in our study region (Osland et al., 2012) demonstrates that in the lower tidal frame where mangrove forests and graminoid marshes co-occur, soil pH is slightly acidic (6.0–6.8), while porewater salinity varies narrowly (30–33 ppt), does not differ between mangrove forest and graminoid marsh zones, and is uncorrelated with soil organic matter, C, N, and sediment particle size at 0–10 and 10–30 cm soil depths.

2.2. Field design and sample collection

We established three study sites spaced at approximately 5 km intervals along the western coastline of the central Florida peninsula (Figs. 1 and S3–S5). The sites consisted of the Salt Springs (28.3298°, –82.7274°), Energy Marine Center (28.2903°, –82.7278°), and Green Key (28.2530°, –82.7496°) sites on the Gulf of Mexico coastline in Pasco County, Florida, USA. At each site, we established three plot pairs, each consisting of one saltmarsh plot and one mangrove plot. Plots were 50 m² in size. Plots pairs within a site were separated by 230–1070 m, and the mangrove and saltmarsh plots composing a pair were 70–170 m apart. All plot pairs consisted of directly adjacent patches of mangrove forest and *J. roemerianus* saltmarsh, with the mangrove forests exhibiting a closed canopy and a tree architecture (height 4–6 m, crown width 1.5–3 m). Mangrove plots were located at approximately the midpoint between the seaward edge (water-mangrove interface) and landward edge (mangrove-saltmarsh interface) of the mangrove zone. Saltmarsh plots were located 20–25 m away from any mangrove trees and into the *J. roemerianus* zone (i.e., landward from the mangrove-saltmarsh interface). Plot pairs were coarsely similar in geomorphic setting, as all were located on the Gulf of Mexico coastline, rather than within major sheltering formations like Tampa Bay, and all plot pairs fit the tide-dominated domain of the Woodroffe (2002) classification, given their conspicuous semi-diurnal tides. There was nevertheless some geomorphic variation, as some plot pairs were directly open to the Gulf of Mexico while others sat behind keys and spits or along small tidal creeks (Figs. S3–S5). Our use of a plot-pair approach is intended to control for this geomorphic variation. Plot center elevations (cm above mean sea level, NAVD 88) were estimated by overlaying the plot locations determined with a global positioning system (Garmin GPS 60, Olathe, KS, USA) on a LiDAR-derived bare-earth digital elevation model (Dewberry, Inc., 2019). The digital elevation model had a vertical accuracy of ± 10 cm (95% CI) and a horizontal accuracy of ± 116 cm (95% CI).

Soil samples were collected via coring at low tide in June 2011. From each plot, we collected a composite soil sample consisting of three discrete 5.1-cm diameter soil cores taken at equidistant points to 7.6 cm depth. Cores were taken by tapping a sleeve into the soil until its top was flush with the soil surface, sliding a hand under the core, and lifting

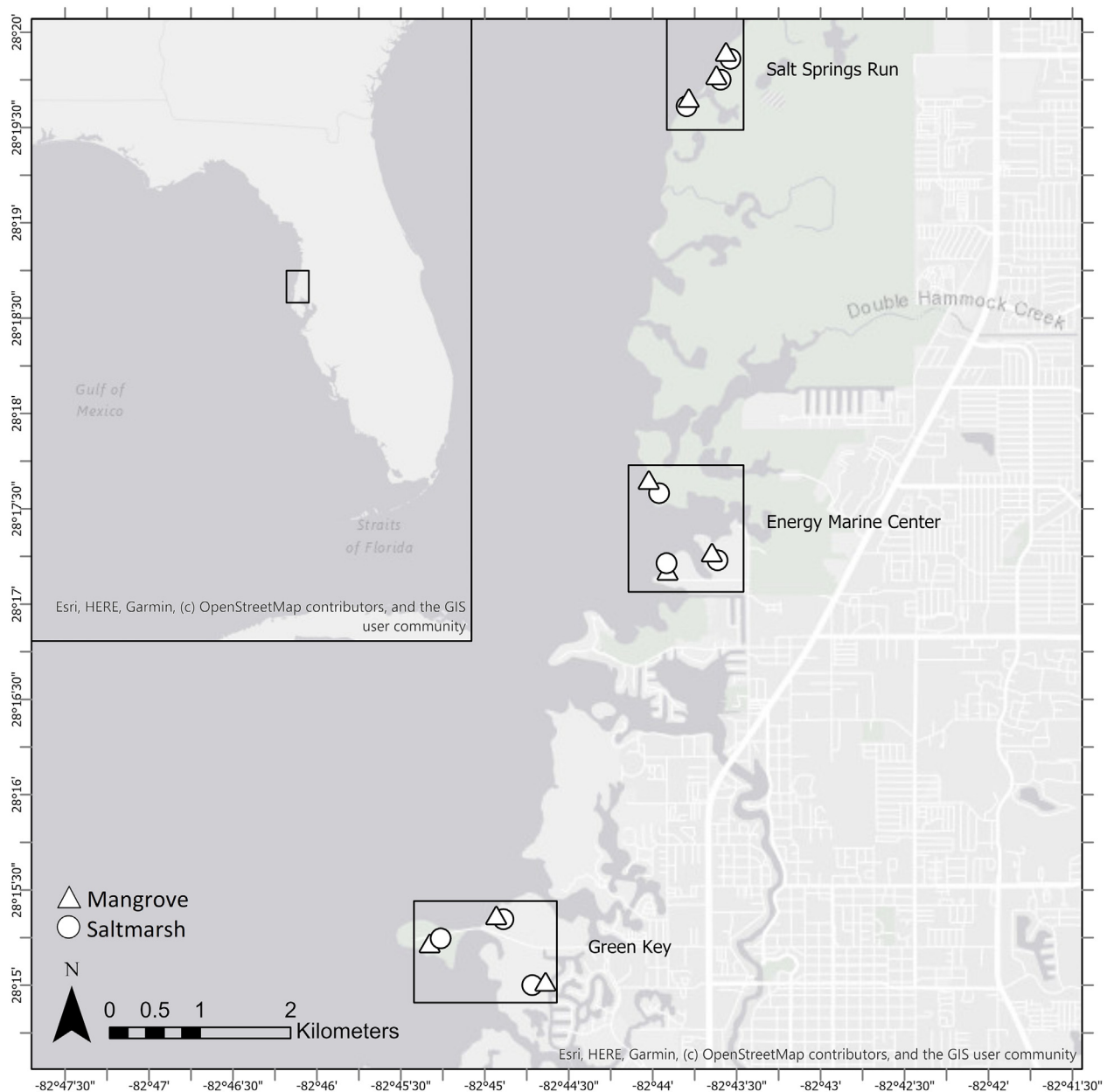


Fig. 1. Study region map.

Location of study sites on the west-central coast of the Florida, USA, peninsula. At each site, three plot pairs consisting of a mangrove forest (triangles) and saltmarsh (circles) plot were sampled. Aerial images of the sites are available in the supplemental material.

it up. Cores were then capped and transferred on ice to our laboratory at the University of South Florida (Tampa, Florida, USA), where they were combined in plastic zipper bags, and homogenized by hand into plot-level composite samples on the day they were collected. A damp soil subsample was immediately taken from each composite sample to initiate 1-y incubations for determination of active C and N (see below). The remainder of each composite sample was then placed in a drying oven (60 °C) for 1 week with frequent mixing of the soil to prevent aggregation and liberate water. Organic wetland soils are sometimes dried at 70 °C (Simpson et al., 2019b), however high drying temperatures can volatilize non-water liquids and oxidize and decompose organic matter, so 50 °C is also a common drying temperature for organic soils (Gardner, 1986); we accordingly chose 60 °C as a compromise between sufficient water removal and avoidance of non-water mass loss. Bulk density was determined as soil dry mass per core volume (adding back the dry mass equivalent of the damp subsample removed prior to drying). Dried subsamples were obtained for determination of

SOM, mineral texture composition, and extractable and total C and N within the following week.

2.3. Sample analyses

A dried subsample was apportioned from each composite sample to determine SOM as mass loss on ignition at 550 °C for 4 h. After organic matter was removed from soil via ignition, mineral particle size composition was determined using a combination of wet sieving and density separation in 49 mM (3%) sodium hexametaphosphate ((NaPO₃)₆) following procedures in Kettler et al. (2001). The percentage of dry soil mass composed of silt and clay particles (hereafter, fines) was calculated as the mass lost from dispersed mineral soil after sieving (0.053 mm mesh sieve). Fines could have been slightly underestimated if any clay particles were burned off during the preceding ignition of soil. An additional subsample was taken from each composite sample to determine extractable N and organic C concentrations via 0.5 M potassium

sulfate (K_2SO_4) extractions (as in Dail et al., 2001; Kaye et al., 2002; McDaniel et al., 2014). We combined soil and extractant (ratio of 1 g dry soil:5 mL extractant) in plastic bottles, reciprocally shook the slurry for 1 h at 120 rpm, and then gravity filtered it through Fisher G6 (1.6 μm pore size) glass fiber filters, followed by colorimetric detection of nitrite (NO_2^-) + nitrate (NO_3^-) and ammonium (NH_4^+) in the filtrate (Hood-Nowotny et al., 2010) using a microplate spectrophotometer (Biotek Epoch, Winooski, VT, USA). Filtrate was also analyzed for dissolved organic C (referred to hereafter as extractable organic C) and total dissolved N via combustion and oxidation followed by detection of the evolved CO_2 and N oxide gases on a Formacs HT TOC/TN analyzer (Skalar, Breda, The Netherlands). Extractable organic N was then computed as total dissolved N in filtrate minus extractable mineral N (itself the sum of extractable $\text{NH}_4\text{-N}$ and $\text{NO}_2\text{-N} + \text{NO}_3\text{-N}$). We determined soil total C and N from dried, milled subsamples subjected to elemental analysis (ECS 4010, Costech, Inc., Valencia, CA, USA) at the University of South Florida Stable Isotope Laboratory. Median concentration of inorganic C in unvegetated surface soil at our sites is 0.5% of soil mass (Anderson, 2019, via methods in Wang et al., 2011). Inorganic C concentrations are likely even lower in our samples from under vegetation, where organic matter would dilute the contribution of inorganic C to soil mass. Nevertheless, the presence of a small inorganic C pool in our soils may be counted in the total C values we report. Extractable organic C is necessarily of organic C origin given the method (sparging with HCl) used in detection.

Active C and N represent the fractions of organic C and N that are mineralizable by soil microorganisms under aerobic conditions in long-term soil incubations (Paul et al., 1999). To quantify active C and N, 60 g of field-moist soil were apportioned from each composite sample, placed in a filtration apparatus, and incubated in the dark at 25 °C and field capacity moisture for 365 d (as in Kaye et al., 2002; Lewis et al., 2014b, 2014c). Moisture levels were maintained by frequently weighing incubated soil and wetting them up to target mass. Daily CO_2 flux was quantified on 29 occasions at 0.5–3 week intervals during the incubation period (with shorter intervals earlier in the incubation), and these per-day flux rates were integrated over the 365-d period to compute an estimate of active C. Observations of per-day flux were made by sealing samples overnight in airtight chambers fitted with septa and quantifying headspace CO_2 accumulation by injecting headspace samples (obtained through the septa via needle and syringe) into an infrared gas analyzer (PP Systems EGM-4, Amesbury, MA, USA). To estimate active N, each incubated sample was leached with a C- and N-free, 35 psu solution containing micronutrients (Nadelhoffer, 1990) on 19 occasions at increasing 1–6 week intervals during the 365-d incubation, and then extracted in 0.5 M K_2SO_4 at the end of the incubation in order to remove any residual mineral N. Active N was then quantified as the total mass of mineral N leached and extracted. Mineral N in leached and extracted solutions was detected as $\text{NH}_4\text{-N}$ and $\text{NO}_2\text{-N} + \text{NO}_3\text{-N}$ via colorimetry as above. This incubation technique precludes new C and N inputs and persistently leaches mineral N, forcing microorganisms to meet demand by mineralizing existing pools, and thereby directly assays the potential activity of soil organic C and N pools present at the time of soil sampling (Robertson and Paul, 2000). Because this analysis commences with disrupting soil physical structure, it is biased toward higher estimates of active fractions.

2.4. Statistical analysis

Henceforth, in reference to our data, we will use the term *pools* when referring to the C and N concentrations determined via elemental analysis (total C and N), and will use the term *fractions* when referring to the various portions of these pools (extractable mineral N, extractable organic C and N, active C and N, and non-mobile C and N). Non-mobile C and N fractions were computed as total C and N concentrations minus the extractable and active fractions of each element. Surface-soil constituents (fines, SOM, and C and N pools and fractions) are reported in

areal units of mass per cm^2 to facilitate their comparison between zones. Areal concentrations were computed as $X \times D \times 7.6$, where X is the gravimetric concentration of a soil constituent (mass constituent/mass dry soil), D is soil bulk density ($\text{g dry soil} / \text{cm}^3$), and 7.6 is the sampling depth in cm. Gravimetric concentrations are reported for each zone in the supplemental information (Table S1). We also calculated each C and N fraction as a proportion of total C and N pools (e.g., mg active N / g total N). Finally, stoichiometric C:N ratios are reported on a molar basis for the extractable organic, active, and non-mobile fractions, and for total C and N pools.

We preliminarily used one-way ANOVA to investigate whether fines, SOM, or any soil C and N pools and fractions significantly differed between sites ($n = 18$ plots, 6 per site). We performed this analysis to address the possibility that any soil C or N correlation with fines or SOM (predicted by hypothesis 1) may be an outcome of a site-level effect on both response and predictor variables. Some variables were log or arcsin-square-root transformed to obtain normal distributions (confirmed with Shapiro-Wilk tests $p > 0.05$). Sample data for SOM were not normalized by transformation (Shapiro-Wilk $p = 0.021$), so SOM was compared among sites using a Kruskal-Wallis test. Three soil variables exhibiting unequal variance among sites (Bartlett test $p < 0.05$) were compared among sites using Welch's ANOVA. These modifications are noted in Tables S2 and S3.

To test hypothesis 1, that surface-soil C and N pools and fractions are greater in mangrove than in saltmarsh owing to greater accumulations of organic matter and fine mineral particles in the mangrove zone, we fit linear regressions ($n = 18$ plots) between soil C and N fractions and pools, on the one hand, and their hypothesized predictors of fines and SOM, on the other. Significance was determined using one-tailed tests predicting positive correlations. Active, non-mobile, and total N values were log-transformed for regression on either SOM or fines, while those of other variables remained in linear units. Residuals from all models were normally distributed (Shapiro-Wilk tests). We also conducted a paired t -test to determine whether the mean difference between zones in each soil constituent was zero ($n = 9$ paired mangrove and saltmarsh plots). Difference values (values in mangrove plots minus values in paired saltmarsh plots) were normally distributed (Shapiro-Wilk $p > 0.05$), except in the case of bulk density, for which a Wilcoxon signed-rank test was used to compare bulk density between zones. Significance was determined using one-tailed tests predicting greater concentrations in mangrove than in saltmarsh surface soil. This directional prediction is based on the growing understanding that mangroves store more soil organic matter and C than do other coastal wetland types (reviewed above), and on our interest in whether soil N and the fractions of soil C and N are entrained in this pattern. For fines, this directional prediction is based on the expectation that mangrove soil will receive greater deposition of fine mineral particles owing to the lower elevation of this zone and its closer proximity to open water. To seek auxiliary support for this expectation, we evaluated whether the difference in fines between plots in a pair was correlated with the elevation difference between plots (i.e., ρ of Δ fines between plots in a pair with Δ elevation between plots; $n = 9$ plot pairs). Hypotheses 2 (that mangrove surface soils hold larger fractions of potentially mobile C and N on account of storing larger total C and N pools) was tested with paired t -tests to determine whether there was zero difference between zones in the proportions of total C and N pools that are potentially mobile. Hypothesis 3 (that C and N biogeochemistry are coupled similarly in mangrove and saltmarsh surface soils) was likewise tested with paired t -tests to determine whether there was zero difference between zones in stoichiometric (C:N) ratios. Difference values (value in mangrove plot minus value in paired saltmarsh plot) for all variables examined under hypotheses 2 and 3 were normally distributed, with the two exceptions of extractable organic N as a proportion of total N, and total C:total N, which were compared between vegetation zones using a Wilcoxon signed-rank test. Significance was determined with two-tailed tests. In tests of surface-

soil differences between zones, and of correlations among surface-soil properties, we took p values ≤ 0.05 as significant and > 0.05 – 0.1 as marginally significant. Analyses were conducted using Matlab (R2018b and R2019a).

3. Results

3.1. Regional and site-level variation

Surface-soil C and N pools and fractions all exhibited notable variation, although the potentially mobile (extractable and active) fractions varied more than the non-mobile fractions and total pool sizes did. Potentially mobile fractions varied approximately 3-fold across all 18 plots, while the non-mobile fractions and total pools varied approximately 2-fold. Extractable mineral, extractable organic, and active N concentrations varied over ranges of 32.4–102.3, 108–340, and 450–1619 $\mu\text{g N} / \text{cm}^2$ ground surface area (integrated to 7.6 cm depth), respectively, while non-mobile N concentrations spanned the proportionally narrower range of 15.1–31.1 $\text{mg N} / \text{cm}^2$ (Table S2). Likewise, extractable organic and active C concentrations varied over ranges of 0.98–2.84 and 11.6–35.7 mg / cm^2 , respectively, while non-mobile C concentrations spanned the range 205–390 $\text{mg C} / \text{cm}^2$ (Table S2).

Surface-soil C and N pools and fractions also varied among plots within sites. Within-site patterns of variation mimicked study-wide patterns. Potentially mobile fractions (extractable mineral N, extractable organic C and N, active C and N) varied among plots within a site (coefficient of variation [CV] = 0.11–0.50 depending on site and fraction) more than non-mobile C and N fractions and total C and N pools did (CV = 0.08–0.27). Among-plot variation was dampened at one site (Energy Marine Center, Table S2), where all the various C and N pools and fractions we quantified exhibited among-plot CV values in the range 0.08–0.32. Conversely, among-plot CV in C and N pools and fractions were in the higher ranges of 0.12–0.47 at the Green Key site, and 0.21–0.50 at the Salt Springs site. Surface-soil C and N pools and fractions, and their predictor variables (SOM and fines), did not differ between sites (ANOVA, Welch's ANOVA, or Kruskal-Wallis $p > 0.1$), with the exception of active C, which was greater at the Green Key site than at the other sites (ANOVA $p = 0.010$) (Table S2). Detrending active C of this "site effect" did not alter its distinction between zones or relationships (or lack thereof) with SOM and fines, so we used the original active C data in subsequent analyses. Because soil C and N pools and fractions, SOM, and fines generally do not vary among sites, correlations among these soil properties (reported in Section 3.3) do not result from site effects on these variables.

3.2. Differences between mangrove and saltmarsh zones

To varying degrees, and with varying statistical significance, areal concentrations of all soil C and N fractions and pools were more concentrated in mangrove than in saltmarsh surface soil (Table 1). Extractable organic C and N concentrations exhibited large differences between vegetation zones, as extractable organic C was 39% greater in mangrove than in saltmarsh surface soil ($p = 0.019$), while extractable organic N showed even greater difference, being 45% more concentrated in mangrove than in saltmarsh surface soil ($p = 0.031$; Fig. 2). Extractable mineral N ($p = 0.086$) and active C ($p = 0.054$) were both 18% (and statistically marginally; $p < 0.1$) greater in mangrove than in saltmarsh soil. Active N (by 8%), total N (by 14%), and total C (by 9%) were greater in mangrove surface soil, but not at statistical significance. Mangrove surface soil had 18% greater SOM ($p = 0.011$) and 29% greater fines ($p = 0.027$) concentrations than did saltmarsh surface soils, although bulk density of surface soil did not statistically differ between vegetation zones ($p = 0.5$) (Fig. 3, Table 1). In sum, the potentially mobile fractions of extractable organic C and N and, marginally, extractable mineral N and active C exhibited greater concentrations in mangrove surface

Table 1

Concentration by zone.

Differences between zones in concentrations of surface-soil constituents (mean \pm 95% C.I., $n = 9$ per zone).

Soil constituent	Saltmarsh	Mangrove	p -Value
Bulk density (g dry soil / cm^3)	0.174 \pm 0.023	0.199 \pm 0.051	0.500
Soil organic matter (mg / cm^2)	494 \pm 34	582 \pm 75	0.011
Fines (mg / cm^2)	192 \pm 31	248 \pm 48	0.027
Elevation (cm a.m.s.l. NAVD 88)	50.7 \pm 9.8	34.1 \pm 10.2	0.023
Extractable mineral N (mg / cm^2)	0.0519 \pm 0.0124	0.0610 \pm 0.0145	0.086
Extractable organic N (mg / cm^2)	0.165 \pm 0.048	0.239 \pm 0.058	0.031
Active N (mg / cm^2)	0.776 \pm 0.272	0.837 \pm 0.132	0.312
Non-mobile N (mg / cm^2)	19.2 \pm 3.0	21.9 \pm 4.3	0.112
Total N (mg / cm^2)	20.2 \pm 3.1	23.0 \pm 4.4	0.111
Extractable organic C (mg / cm^2)	1.52 \pm 0.30	2.12 \pm 0.37	0.019
Active C (mg / cm^2)	18.7 \pm 5.5	22.1 \pm 4.3	0.054
Non-mobile C (mg / cm^2)	255 \pm 21	276 \pm 47	0.139
Total C (mg / cm^2)	275 \pm 24	300 \pm 48	0.118

Notes: Abbreviations—a.m.s.l., above mean sea level. Areal concentrations reported here are integrated through the sampling depth of 7.6 cm. The p -value reports result of a one-tailed paired t -test of the null hypothesis that values are similar between zones, versus the alternative that values are greater in mangrove forest than in saltmarsh surface soil.

soils than in saltmarsh soils, as did the soil properties (SOM and fines) expected to contribute to the retention of these potentially mobile C and N fractions. Total C and N pools and the non-mobile fractions that dominated them did not statistically differ between zones ($p > 0.1$), although exhibited a trend of being greater in mangrove than in saltmarsh surface soil.

The range in elevation among the nine saltmarsh plots was 30–70 cm (\pm 10 cm, 95% CI) above mean sea level, while elevation range among the nine mangrove plots was 12–51 cm (\pm 10 cm). Elevation tended to be higher for saltmarsh plots than for mangrove plots (Fig. 3, Table 1). However, the mangrove plot was higher than the saltmarsh plot at two, and elevation was nearly equal between vegetation zones at one, of the nine plot pairs. The elevation difference between plots within a pair ranged from -16 cm (mangrove plot higher) to $+41$ cm (saltmarsh plot higher).

3.3. Soil C and N correlations with SOM and fines

The surface-soil concentrations of several C and N fractions and pools correlated with surface-soil concentrations of SOM (Fig. 4). The strongest relationship was between total C and SOM. If the intercept of this relationship is set to zero (which is within the intercept CI), the slope is 0.53 ± 0.03 (estimate \pm 95% CI), suggesting that C composes about half the mass of SOM, as expected. Total N also exhibited a strong positive relationship with SOM. Setting the intercept of this relationship to zero (within intercept CI), the slope of the total N-SOM relationship is 0.040 ± 0.004 (estimate \pm 95% CI), suggesting that N constitutes about 4% of the mass of SOM. Total C and total N were primarily composed of their non-mobile fractions (see below), so non-mobile C and N fractions also exhibited strong positive relationships with SOM. Among the potentially mobile fractions, active N and extractable organic C and N scaled significantly ($p < 0.05$), and extractable mineral N scaled marginally ($p = 0.067$), with SOM (Fig. 4). The 77% increase in SOM across the range we observed (448–792 mg / cm^2 ; Table S2) corresponded with a proportionally similar increase (77%) in least-squares-predicted extractable organic C, a proportionally greater (93%) increase in extractable organic N, and a 54% increase in active N. Active C did not appear to correlate with SOM.

Extractable organic C and N concentrations exhibited positive relationships with concentrations of fine (silt + clay) mineral particles (Fig. 5). The 170% increase in the concentration of surface-soil fines across the range we observed (125–337 mg / cm^2 ; Table S2) corresponded with a near doubling (90–100% increases) in least-squares-predicted extractable organic C and N. Total and non-mobile

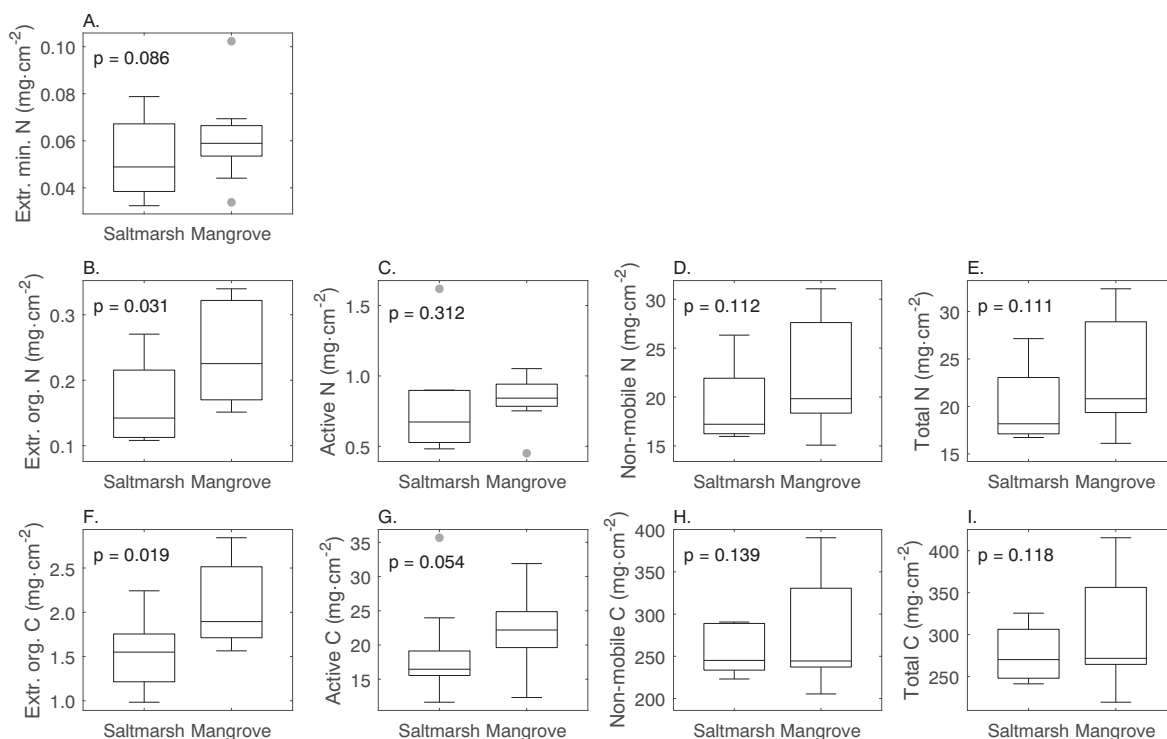


Fig. 2. C and N fractions and pools by zone.

Variation in fractions and total pools of C and N in surface soils of saltmarsh and mangrove forest vegetation zones. Data are presented using standard box plots in units of mg element per cm^2 integrated through the sampling depth of 7.6 cm. The p values report results of paired t -tests comparing soil properties between vegetation zones.

C also scaled positively with fines, increasing by 31% across the fines concentration gradient. Active C and N fractions did not significantly correlate with fines, nor did extractable mineral, non-mobile, or total N concentrations.

In relationships of C and N with SOM (Fig. 4) and fines (Fig. 5), both predictor and response variables tended to be lower in saltmarsh than in mangrove surface soils. Accordingly, the strength of these relationships is revealed through pooling data from both vegetation zones. In

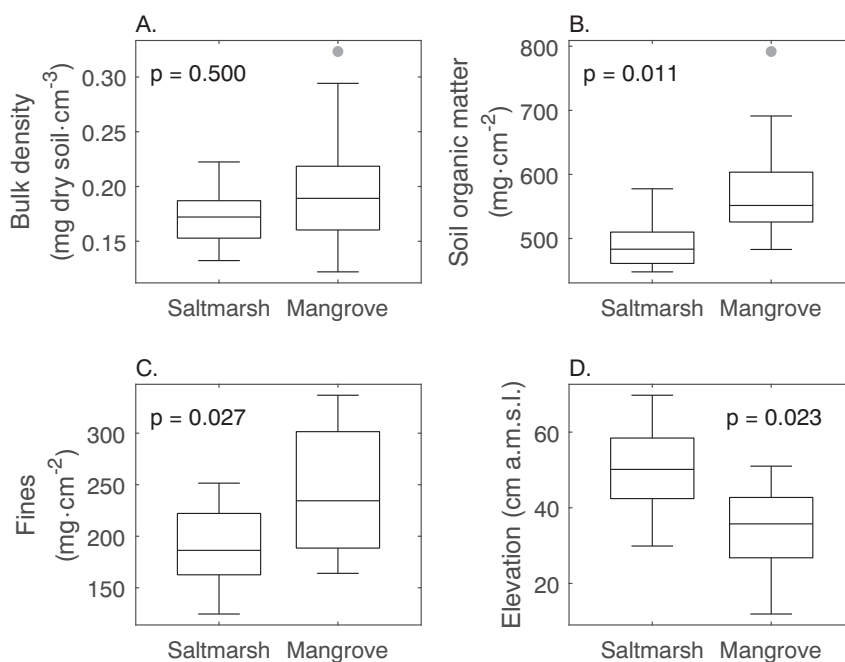


Fig. 3. Bulk density, SOM, fines, and elevation by zone.

Variation in surface-soil bulk density, SOM, and fines, and in elevation, of saltmarsh and mangrove forest vegetation zones. Data are presented using standard box plots. SOM and fines concentrations are integrated through the sampling depth of 7.6 cm. The p values report results of paired t -tests (or a Wilcoxon signed-rank test for bulk density) comparing soil properties between vegetation zones.

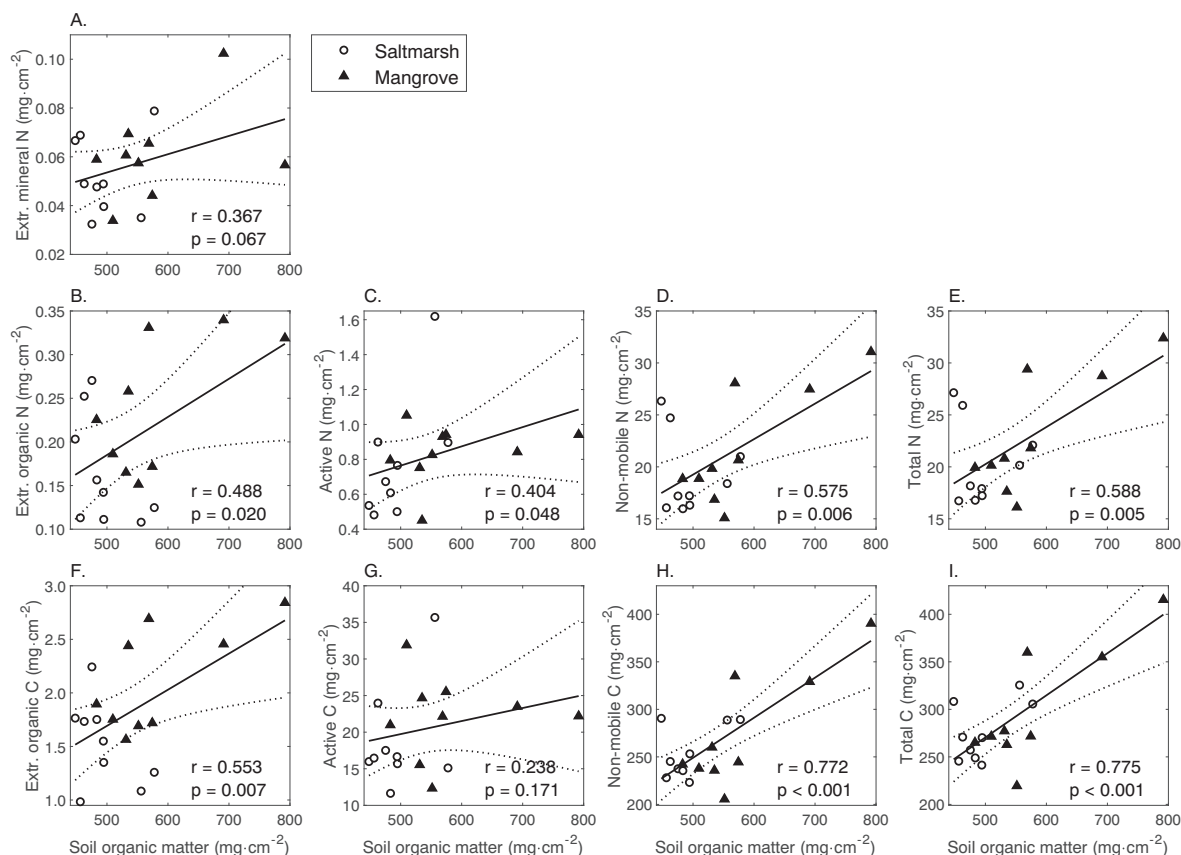


Fig. 4. C and N pools and fractions vs. SOM.

Correlations of C and N fractions and pools with SOM in surface soil. Units are mg element or SOM per cm² integrated through the sampling depth of 7.6 cm. Least-square fits (solid lines) are to data from both vegetation zones pooled. Dotted lines bound 95% confidence intervals. The correlation statistics (*r* and *p* values) for active, non-mobile, and total N were determined with these variables log transformed to normalize regression residuals, although they are plotted in linear units for consistency with other variables.

some cases, the global relationship is recapitulated within one of the vegetation zones. For example, the relationships of total C and N with SOM (Fig. 4) are also evident within the mangrove, but not the saltmarsh, zone (Table S4). Conversely, the relationship between total C and fines (Fig. 5) is not independently evident in either zone taken alone (Table S4).

Surface-soil concentrations of fine mineral particles appear to respond to soil-surface elevation. In seven of the nine plot pairs, the lower plot had a greater fines concentration. Fines concentrations differed more dramatically between paired plots that were more widely separated in elevation (Fig. 6). Fines concentration was greater in the higher-elevation plot in one pair, and was nearly indistinguishable between plots in the one instance where the paired plots sat at about the same elevation. In two plot pairs where the saltmarsh plot was at a lower elevation than the mangrove plot, the saltmarsh plots had greater fines concentrations in the surface soil.

3.4. Fraction allocation and stoichiometry

Extractable organic C makes up a larger share of the total C pool in mangrove surface soil than it does in saltmarsh surface soil. In mangrove surface soil, the proportional concentration of extractable organic C was 7.1 mg / g total C, whereas it was 5.6 mg extractable organic C / g total C in saltmarsh surface soil (Table 2). As expected, non-mobile fractions constituted the majority of total C and N pools. However, the total N pool was more heavily dominated by its non-mobile fraction (0.91–0.97 g non-mobile N / g total N) than was the total C pool (0.88–0.95 g non-mobile C / g total C) (Table S3). Expressed as fractions of their total element pool sizes, non-mobile N exceeded non-mobile C

in 17 of 18 plots, and was similar in one plot, (paired *t*-test *p* < 0.001, *n* = 18) indicating greater potential mobility of surface-soil C than of N.

The C and N stoichiometric ratios did not differ between the surface soil of mangrove and the surface soil of saltmarsh (Table 2). The molar C:N ratio of the total C and N pools was 16.2 ± 1.7 (mean \pm 95% CI) in saltmarsh and 15.4 ± 0.7 in mangrove surface soil, not a significant difference. The stoichiometric ratios of the various fractions (extractable organic, active, and non-mobile) likewise did not differ significantly between vegetation zones.

4. Discussion

Temperature and hydrological changes that symptomize climate change are rearranging plant distributions with potential impacts on carbon and nutrient cycles. Associations between vegetation form and biogeochemical processes under a changing climate are particularly important in coastal wetlands, where temperature warming and sea-level rise are provoking woody mangrove encroachment into herbaceous saltmarshes across a landscape with highly concentrated pools of soil C and N. Effects of vegetation change on the size and mobility of these large pools have implications for C and N exports to the atmosphere and coastal open waters, and for the productivity and ecosystem services of coastal wetlands. We accordingly examined the total and potentially mobile fractions of C and N, as well as properties that promote C and N retention, in surface soils (top 7.6 cm) of mangrove and saltmarsh vegetation zones.

We tested three hypotheses. Our findings suggest that in the surface-soil horizon, mangrove forests store larger masses of extractable organic C and N than do saltmarshes owing to greater accumulations of

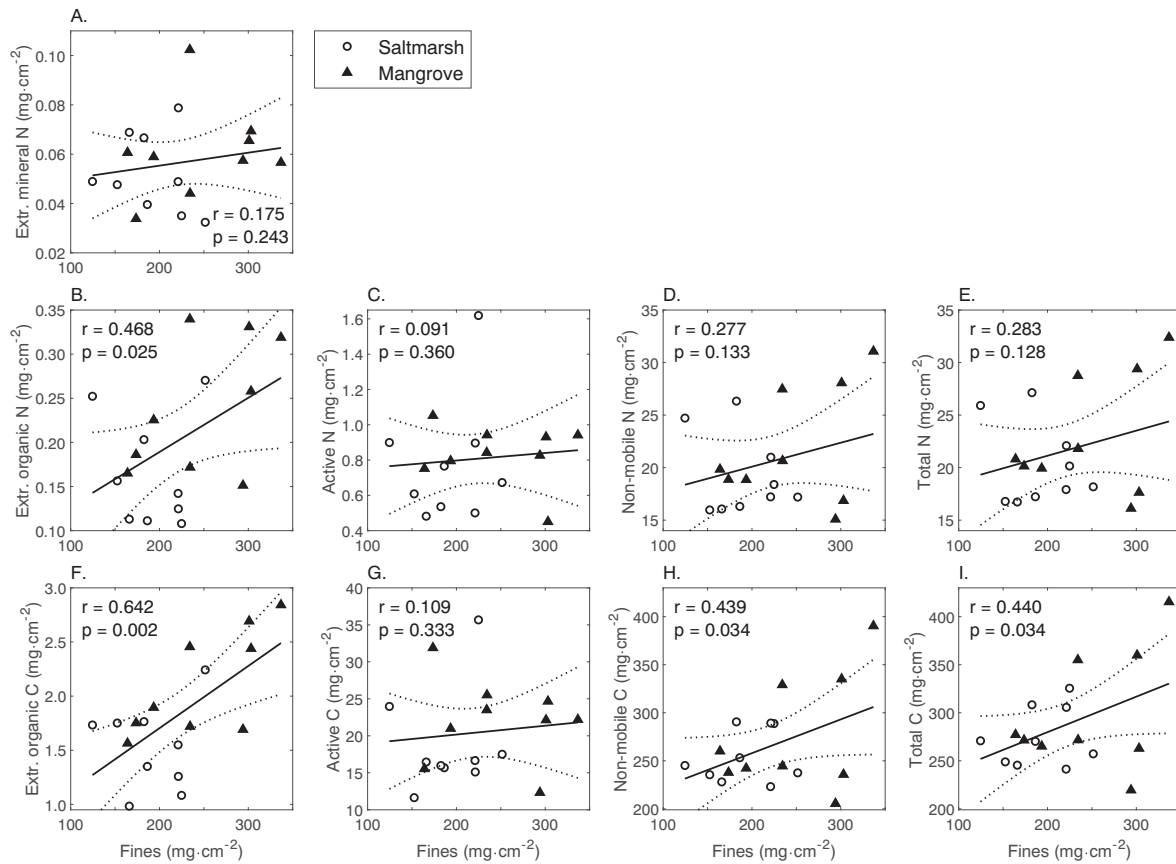


Fig. 5. C and N pools and fractions vs. fines.

Correlations of C and N fractions and pools with fines in surface soil. Units are mg element or fines per cm² integrated through the sampling depth of 7.6 cm. Least-square fits (solid lines) are to data from both vegetation zones pooled. Dotted lines bound 95% confidence intervals. The correlation statistics (r and p values) for active N were determined with this variable log transformed to normalize regression residuals, although it is plotted in linear units for consistency with other variables.

fine mineral sediments at the soil surface under mangroves (hypothesis 1). The extractable organic C fraction represents a larger share of the total C pool in mangrove than in saltmarsh surface soils, suggesting that mangrove surface soils store a larger mass of extractable organic C in part because mangrove surface soils simply have a larger reservoir of SOM, yet also because that material is allocated differently among

fractions that vary in potential mobility (hypothesis 2). The coupling of C and N in surface soils, insofar as stoichiometric ratios of stored material indicate, does not appear to differ between mangrove and saltmarsh zones, as molar C:N is similar between the two zones for total pools and all fractions of C and N (hypothesis 3).

4.1. Faster turnover in mangrove soils?

We found that surface-soil C and N tend to be greater in mangrove forest populated by *A. germinans* than in the adjacent, landward *J. roemerianus* saltmarsh zone. Total C and N pools and their large non-

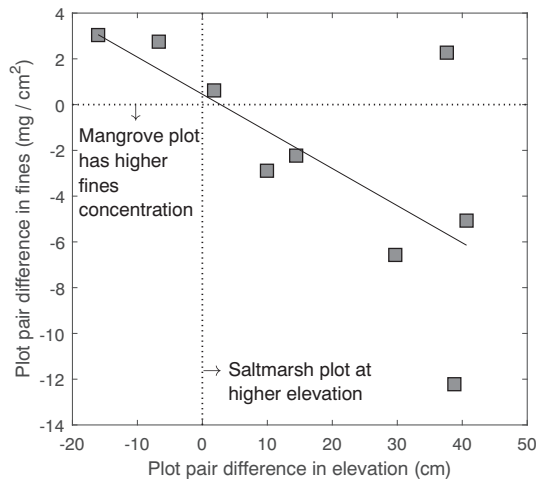


Fig. 6. Delta fines vs delta elevation.

Plots within a plot pair that differed more in elevation tended to also differ more dramatically in fine (silt + clay) mineral particles stored in surface soil. Each data point represents one plot pair. Correlation $r = -0.671$ ($p = 0.024$). Without the outlier in the upper right, $r = -0.909$, $p < 0.001$. Trendline is fit to all $n = 9$ points.

Table 2

Fractionation and stoichiometry by zone.

Comparison between zones in C and N fractions as proportions of total pools, and in stoichiometric molar ratios of discrete fractions and pools (mean \pm 95% C.I., $n = 9$ per zone).

Variable	Saltmarsh	Mangrove	p -Value
Extractable mineral N (mg / g total N)	2.6 \pm 0.6	2.7 \pm 0.7	0.787
Extractable organic N (mg / g total N)	8.2 \pm 2.3	10.4 \pm 1.6	0.164 [†]
Active N (mg / g total N)	38.9 \pm 13.2	37.6 \pm 7.5	0.793
Non-mobile N (g / g total N)	0.95 \pm 0.01	0.95 \pm 0.01	0.814
Extractable organic C (mg / g total C)	5.6 \pm 1.3	7.1 \pm 0.8	0.029
Active C (mg / g total C)	67.6 \pm 15.6	75.3 \pm 17.1	0.143
Non-mobile C (g / g total C)	0.93 \pm 0.02	0.92 \pm 0.02	0.085
C:N Extractable organic fractions	11.3 \pm 1.5	10.7 \pm 1.0	0.461
C:N Active fractions	29.6 \pm 5.6	32.3 \pm 10	0.581
C:N Non-mobile fractions	15.8 \pm 1.7	14.8 \pm 0.7	0.308
C:N Total pools	16.2 \pm 1.7	15.4 \pm 0.7	0.203 [†]

Note: The p value reports result of a two-tailed paired t -test of the null hypothesis that values are similar between zones, versus the alternative that values are not.

[†] Wilcoxon signed-rank test used in lieu of paired t -test.

mobile fractions were 8–14% greater in mangrove than in saltmarsh surface soils, although statistically, these differences were not significant. Potentially mobile fractions differed more clearly between zones. Extractable organic C and N and active C fractions were larger in mangrove than in saltmarsh surface soils. Likewise, our previous work showed that the instantaneously available (i.e., in situ soil respiration) and the rapidly mineralizable (via 7-d incubation) fractions of soil organic C were larger in the surface of mangrove soil than in saltmarsh soil (Lewis et al., 2014a). These findings collectively suggest that the small yet rapidly cycled mobile fractions of C and possibly N are larger in mangrove than in saltmarsh surface soil. They accord with the presence of a microbial community in mangrove surface soil that is more efficient at consuming labile substrates than are saltmarsh microbes (Barreto et al., 2018), and suggest that biogeochemical turnover could speed up in saltmarsh areas replaced by encroaching mangroves. More generally, shifts to soil C with shorter residence times are also observed with terrestrial woody plant encroachment into herbaceous plant communities (Liao et al., 2006).

Extractable organic C and N, insofar as they are soluble fractions, are potentially mobile in both a biological and a geological sense. Dissolution of organic material is an important step toward acquisition of its constituent elements by biota (Schimel and Bennett, 2004). Moreover, extractable organic C and N can be hydrologically mobilized and possibly exported from coastal wetlands in pore seepage and tidal water, where they contribute to dissolved organic matter budgets in open water (Ray et al., 2018). The allocation we observed of C and N into extractable organic fractions (approximately 5–10 mg extractable organic C or N / g total C or N) is on the large side. This allocation is similar to or somewhat greater than soluble fractions typically seen across diverse ecosystems such as tropical tidal wetlands with 0.5–3.8, 0.6–6.4, and 2.4–4.4 mg dissolved organic C (DOC) / g total sediment organic C (Alongi et al., 1996; Feng et al., 2019; and Wang et al., 2015, respectively), temperate forests with 1.7–1.9 and 2.4–8.2 mg dissolved organic N (DON) / g total soil N (Perakis and Hedin, 2001 and Lewis et al., 2014b, respectively), and freshwater wetlands with 0.7–2.1 mg DON / g total soil N (Lewis and Feit, 2015), although these studies use varied extraction or porewater sampling approaches so comparisons should be taken qualitatively. Nevertheless, the rather large allocations of soil C and N to extractable organic fractions that we observed are relevant at ecosystem levels because leaching loss of dissolved organic matter can effectively perpetuate nutrient limitation of ecosystem primary production (Vitousek et al., 1998). Accordingly, the larger absolute sizes of extractable organic C and N fractions, and the greater proportional allocation of total C into its extractable organic fraction, in mangrove forests suggests that mangrove replacement of saltmarsh could impact a functionally meaningful mass of potentially mobile C and N.

The active fractions are also potentially mobile, as they represent the material susceptible to mineralization by microorganisms. They were larger than the extractable organic fractions, with the active N pool about 4× the size of the extractable organic N pool, and the active C pool about 11× the size of the extractable organic C pool. This larger size of active pools is not surprising, as they consist of all the C and N released in a year-long incubation, rather than instantaneously extracted. Yet, the active C and N we observed constituted a relatively small fraction of total C and N pools when compared with findings from terrestrial soils. Here, active N represented <40 mg / g total N (Table 2). By contrast, proportional concentrations of active N are 60–110 mg / g total N in urbanizing desert soils (Lewis et al., 2014c), 60–80 mg active N / g total N in temperate forested ridge soils (Lewis et al., 2014b), and approximately 200 mg active N / g total N in temperate grassland plains soils (Kaye et al., 2002) using equivalent methods. Similarly, while we detected 68–75 mg active C / g total C, this fraction had proportional concentrations of 110–150, 270–290, and 210–280 mg active C / g total C in the urbanizing, forested, and grassland settings, respectively. This smaller allocation of C and N into active fractions of coastal wetland soils is somewhat surprising, as the organic matter of wetland soils is

often portrayed as otherwise bioavailable material protected by anoxia. But when our wetland soil was aerated (the method for determining active fractions), large proportions of the soil C and N pools were not consumed, perhaps owing to the absence of key enzymes. This finding suggests that coastal wetland C and N pools, at least in surface soil, are more non-mobile than the C and N pools of terrestrial ecosystems, and that their exports, while large, are not as large as might be expected from the sizes of their total C and N pools.

4.2. Potential drivers of mangrove-saltmarsh soil differences

Our findings suggest that potentially mobile C and N accumulates more in the surface of mangrove than of saltmarsh soils on account of greater surface accumulations of organic matter and fine mineral particles in mangrove soils. Extractable organic fractions provide the clearest evidence of this linkage. Concentrations of extractable organic C and N were substantially greater in mangrove than in saltmarsh surface soil. They differed between zones by a proportionally greater magnitude (39–45% greater in mangrove than in saltmarsh surface soil) than exhibited by other C and N fractions. Additionally, concentrations of extractable organic C and N correlated steeply with SOM and fines, showing large proportional increases per unit increase in SOM and fines. Finally, SOM and fines concentrations in surface soils were greater in mangrove than in saltmarsh, matching the zonation patterns exhibited by the extractable organic fractions. Active C and extractable mineral N were 18% greater in mangrove than in saltmarsh surface soil, but their concentrations were not correlated with SOM or fines concentrations, suggesting some other mechanism for their greater accumulation under mangroves.

Fine mineral textures in coastal wetland soils may retain C and N by binding potentially soluble organic molecules on exchange sites, and through organo-mineral interactions that protect organic matter from microbial attack (Cotrufo et al., 2013; Sun et al., 2019). The former mechanism may be more operative in the soil we examined. Our extractable organic fractions consist of organic molecules liberated from soil via ion-exchange and dissolution during vigorous shaking, so likely reveal the fraction of organic molecules retained via ionic bonding. Our active fractions are quantified in a year-long aerobic incubation to reveal the C and N that microorganisms can access. The extractable organic, but not active, fractions correlated with fines, so it seems reasonable that fine particles were retaining potentially mobile and exportable C and N through chemical binding rather than through protection of organic matter from microorganisms. Fine particles and their retained C and N may accumulate more in the mangrove than the saltmarsh zone because mangrove sites tend to sit at lower elevations (Fig. 2D), which hold greater concentrations of fines (Fig. 6), perhaps due to prolonged deposition during longer tidal inundations. Conversely, adjacent mangrove and saltmarsh zones in another Gulf of Mexico location accrete sediment and build vertically at similar rates (McKee and Vervaeke, 2018), although that study is not entirely analogous to ours, as it examined shorter-statured shrub mangroves that sat at a higher elevation than the saltmarsh zone.

Larger SOM reservoirs in mangrove than in saltmarsh surface soils may also contribute to the greater concentrations of extractable organic C and N that we observed in mangrove soil. Larger reservoirs of SOM may hold greater concentrations of extractable organic C and N simply because SOM is the source of these fractions. Additionally, the organic matter of mangrove surface soils may be proportionally enriched in these fractions. Extractable organic C represented a larger share of the total C pool in mangrove surface soils than it did in saltmarsh surface soils. This finding runs contrary to our null second hypothesis that C pools of the two zones were similarly apportioned into the various fractions.

Besides C and N retention by fine mineral particles and SOM, alternative or complementary explanations for C and N differences between mangrove and saltmarsh surface soils may include functional traits of

the vegetation and spatial zonation. The saltmarsh we investigated was *J. roemerianus* marsh. This plant is a rush with hardened foliage and a subsurface biomass composed primarily of rhizomes (de la Cruz and Hackney, 1977) with densely-packed, cutin-covered cataphylls and suberized tissue (Eleuterius, 1976), so could be a poor source of soluble organic matter. Moreover, mangrove trees produce abundant litter that can decompose faster than saltmarsh litter does (Simpson et al., 2020), so may yield more leachable organic material per unit of detritus. Additionally, mangrove surface soils might accumulate more soluble organic matter owing to their spatial position between open water and the more inland saltmarsh, allowing them to receive allochthonous organic matter subsidies in both flood and ebb flows (Sasmitho et al., 2020) and relatively more autochthonous plant detritus from storm damage (Smith et al., 2009). Finally, soil porewaters differ between mangrove and marsh soils in a wide variety of electrochemical and dissolved mineral properties (Patterson and Mendelssohn, 1991; Comeaux et al., 2012), possibly affecting the binding of extractable constituents on soil.

Although the potentially mobile fractions we quantified can be removed from soil via ion-exchange and dissolution (extractions) and via amplifying microbial activity (incubations), it is important to recognize that these fractions are extant in soil. It may thus be tempting to infer that, by retaining larger masses of these fractions, mangrove surface soils export less C and N than do saltmarshes. Yet on the contrary, faster rates of evasive CO₂ efflux have been observed from the soil surface of mangroves than of saltmarsh (Lewis et al., 2014a; Simpson et al., 2019b) and mangroves export greater masses of particulate and dissolved organic C to adjacent waters (Alongi, 2020). Accordingly, the replacement of saltmarshes by mangrove forests may result in both more C and N storage within, and export from, the coastal wetland environment. Mangrove surface soils, and mangrove ecosystems in general, may accumulate large C and N pools that accrue through non-steady-state budgets in which high input rates sustain large stocks against large exports.

5. Conclusions

The subtropical ecotone between mangrove forests and saltmarshes is migrating both poleward and landward as the global climate warms and sea levels rise, eliciting widespread interest in how and where this shift will affect ecosystem C storage. Here we highlight the parallel need to understand how mangrove encroachment will influence the potentially mobile fractions of soil C and N that are ecologically important because they can yield C and N outfluxes to the atmosphere and adjacent open waters, and because they support high rates of coastal wetland productivity. In comparing mangrove forest populated primarily by *A. germinans* with the adjacent, more landward *J. roemerianus* saltmarsh, we observed a trend of larger C and N pools and fractions in surface soils (top 7.6 cm). Extractable organic C and N were particularly more concentrated in mangrove than in saltmarsh surface soil, likely because of a greater mass and solubility of source material, and more opportunities for retention via binding to fine mineral particles. Though rapidly cycled C and N in surface soils are small fractions of total C and N pools, their larger concentration in mangrove than in saltmarsh surface soils may account for greater exports from mangrove forests.

CRedit authorship contribution statement

David Bruce Lewis: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Funding acquisition. **Kristine L. Jimenez:** Conceptualization, Methodology, Investigation, Data curation, Project administration. **Amr Abd-Elrahman:** Conceptualization, Methodology, Investigation, Funding acquisition. **Michael G. Andreu:** Conceptualization, Methodology, Investigation, Writing – review & editing, Funding acquisition. **Shawn M. Landry:**

Conceptualization, Investigation, Writing – review & editing. **Robert J. Northrop:** Conceptualization, Methodology, Investigation, Funding acquisition. **Cassandra Campbell:** Conceptualization, Visualization, Writing – review & editing. **Hilary Flower:** Conceptualization, Writing – review & editing. **Mark C. Rains:** Conceptualization, Writing – review & editing. **Christina L. Richards:** Conceptualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Jewel Brown, Trista Brophy, Carolyn Cheatham Rhodes, Sharon Feit, Nicole Hewitt, Ralph Perkerson, and Ping Wang for technical assistance, and are grateful to Mark Butler and the staff of the Energy Marine Center (Pasco County Schools) for facilitating access to that site. We thank three reviewers for suggestions that improved the manuscript. Raw data reported in this article are available from the Environmental Data Initiative data repository (data package DOI:<https://doi.org/10.6073/pasta/0e08cbe07c84488cb7b9dd16669946d0>). This material is based upon work supported by the U.S. National Science Foundation under grant numbers 1059236 and 1930451.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.149328>.

References

- Adame, M.F., Neil, D., Wright, S.F., Lovelock, C.E., 2010. Sedimentation within and among mangrove forests along a gradient of geomorphological settings. *Estuar. Coast. Shelf Sci.* 86, 21–30. <https://doi.org/10.1016/j.ecss.2009.10.013>.
- Adams, D.A., 1963. Factors influencing vascular plant zonation in North Carolina saltmarshes. *Ecology* 44, 445–456. <https://doi.org/10.2307/1932523>.
- Alongi, D.M., 2020. Carbon balance in saltmarsh and mangrove ecosystems: a global synthesis. *J. Mar. Sci. Eng.* 8. <https://doi.org/10.3390/jmse8100767>.
- Alongi, D.M., Clough, B.F., Dixon, P., Tirendi, F., 2003. Nutrient partitioning and storage in arid-zone forests of the mangroves *Rhizophora stylosa* and *Avicennia marina*. *Trees* 17, 51–60. <https://doi.org/10.1007/s00468-002-0206-2>.
- Alongi, D.M., Tirendi, F., Goldrick, A., 1996. Organic matter oxidation and sediment chemistry in mixed terrigenous-carbonate sands of Ningaloo Reef, Western Australia. *Mar. Chem.* 54, 203–219. [https://doi.org/10.1016/0304-4203\(96\)00037-0](https://doi.org/10.1016/0304-4203(96)00037-0).
- Alongi, D.M., Trott, L.A., Wattayakorn, G., Clough, B.F., 2002. Below-ground nitrogen cycling in relation to net canopy production in mangrove forests of southern Thailand. *Mar. Biol.* 140, 855–864. <https://doi.org/10.1007/s00227-001-0757-6>.
- Anderson, B.D., 2019. The distribution and biogeochemistry of subtropical intertidal microbial mats. University of South Florida, Tampa, FL, USA.
- Anderson, I.C., Tobias, C.R., Neikirk, B.B., Wetzell, R.L., 1997. Development of a process-based nitrogen mass balance model for a Virginia (USA) *Spartina alterniflora* saltmarsh: implications for net DIN flux. *Mar. Ecol. Prog. Ser.* 159, 13–27. <https://doi.org/10.3354/meps159013>.
- Archer, S.R., Andersen, E.M., Predick, K.L., Schwinning, S., Steidl, R.J., Woods, S.R., 2017. Woody plant encroachment: causes and consequences. In: Briske, D.D. (Ed.), *Rangeland Systems: Processes, Management and Challenges*. Springer Series on Environmental Management, pp. 25–84. https://doi.org/10.1007/978-3-319-46709-2_2.
- Augustinus, P.G.E.F., 1995. Geomorphology and sedimentology of mangroves. In: Perillo, G.M.E. (Ed.), *Geomorphology and Sedimentology of Estuaries*. Developments in Sedimentology. 53. Elsevier, Amsterdam, pp. 333–357. [https://doi.org/10.1016/S0070-4571\(05\)80032-9](https://doi.org/10.1016/S0070-4571(05)80032-9).
- Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. *Ecol. Monogr.* 81, 169–193. <https://doi.org/10.1890/10.1510.1>.
- Barreto, C.R., Morrissey, E.M., Wykoff, D.D., Chapman, S.K., 2018. Co-occurring mangroves and saltmarshes differ in microbial community composition. *Wetlands* 38, 497–508. <https://doi.org/10.1007/s13157-018-0994-9>.
- Bianchi, T.S., Allison, M.A., Zhao, J., Li, X., Comeaux, R.S., Feagin, R.A., et al., 2013. Historical reconstruction of mangrove expansion in the Gulf of Mexico: linking climate change with carbon sequestration in coastal wetlands. *Estuar. Coast. Shelf Sci.* 119, 7–16. <https://doi.org/10.1016/j.ecss.2012.12.007>.

- Blank, R.R., 2008. Biogeochemistry of plant invasion: a case study with downy brome (*Bromus tectorum*). *Invasive Plant Science and Management* 1, 226–239. <https://doi.org/10.1614/ipsm-07-026.1>.
- Boto, K.G., Wellington, J.T., 1988. Season variations in concentrations and fluxes of dissolved organic and inorganic materials in a tropical, tidally-dominated mangrove waterway. *Mar. Ecol. Prog. Ser.* 50, 151–160. <https://doi.org/10.3354/meps050151>.
- Bouillon, S., Borges, A.V., Castaneda-Moya, E., Diele, K., Dittmar, T., Duke, N.C., et al., 2008. Mangrove production and carbon sinks: a revision of global budget estimates. *Glob. Biogeochem. Cycles* 22, GB2013. <https://doi.org/10.1029/2007gb003052>.
- Caravaca, F., Aiguacil, M.M., Torres, P., Roldan, A., 2005. Plant type mediates rhizospheric microbial activities and soil aggregation in a semiarid Mediterranean saltmarsh. *Geoderma* 124, 375–382. <https://doi.org/10.1016/j.geoderma.2004.05.010>.
- Castellano, M.J., Lewis, D.B., Kaye, J.P., 2013. Response of soil nitrogen retention to the interactive effects of soil texture, hydrology, and organic matter. *J. Geophys. Res. Biogeosci.* 118, 280–290. <https://doi.org/10.1002/jgrg.20015>.
- Chapman, S.K., Langley, J.A., Hart, S.C., Koch, G.W., 2006. Plants actively control nitrogen cycling: uncorking the microbial bottleneck. *New Phytol.* 169, 27–34. <https://doi.org/10.1111/j.1469-8137.2005.01571.x>.
- Charles, S.P., Kominoski, J.S., Armitage, A.R., Guo, H.Y., Weaver, C.A., Pennings, S.C., 2020. Quantifying how changing mangrove cover affects ecosystem carbon storage in coastal wetlands. *Ecology* 101, e02916. <https://doi.org/10.1002/ecy.2916>.
- Chen, R.H., Twilley, R.R., 1999. A simulation model of organic matter and nutrient accumulation in mangrove wetland soils. *Biogeochemistry* 44, 93–118. <https://doi.org/10.1023/a:1006076405557>.
- Childers, D.L., Day Jr., J.W., McKellar Jr., H.N., 2002. Twenty more years of marsh and estuarine flux studies: revisiting Nixon (1980). In: Weinstein, M.P., Kreger, D.A. (Eds.), *Concepts and Controversies in Tidal Marsh Ecology*. Springer, Dordrecht, pp. 391–424. https://doi.org/10.1007/0-306-47534-0_18.
- Comeaux, R.S., Allison, M.A., Bianchi, T.S., 2012. Mangrove expansion in the Gulf of Mexico with climate change: implications for wetland health and resistance to rising sea levels. *Estuar. Coast. Shelf Sci.* 96, 81–95. <https://doi.org/10.1016/j.ecss.2011.10.003>.
- Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Deneff, K., Paul, E., 2013. The microbial efficiency-matrix stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Glob. Chang. Biol.* 19, 988–995. <https://doi.org/10.1111/gcb.12113>.
- Craft, C., Megonigal, P., Broome, S., Stevenson, J., Freese, R., Cornell, J., et al., 2003. The pace of ecosystem development of constructed *Spartina alterniflora* marshes. *Ecol. Appl.* 13, 1417–1432. <https://doi.org/10.1890/1027-0086>.
- Cui, B.S., He, Q.A., An, Y.A., 2011. Community structure and abiotic determinants of saltmarsh plant zonation vary across topographic gradients. *Estuar. Coasts* 34, 459–469. <https://doi.org/10.1007/s12237-010-9364-4>.
- Dail, D.B., Davidson, E.A., Chorover, J., 2001. Rapid abiotic transformation of nitrate in an acid forest soil. *Biogeochemistry* 54, 131–146. <https://doi.org/10.1023/a:1010627431722>.
- de la Cruz, A.A., Hackney, C.T., 1977. Energy value, elemental composition, and productivity of belowground biomass of a juncus tidal marsh. *Ecology* 58, 1165–1170. <https://doi.org/10.2307/1936938>.
- Dittmar, T., Hertkorn, N., Kattner, G., Lara, R.J., 2006. Mangroves, a major source of dissolved organic carbon to the oceans. *Glob. Biogeochem. Cycles* 20. <https://doi.org/10.1029/2005GB002570>. doi:10.2959/2005gb002570.
- Donato, D.C., Kauffman, J.B., Murdiyarso, D., Kurnianto, S., Stidham, M., Kanninen, M., 2011. Mangroves among the most carbon-rich forests in the tropics. *Nat. Geosci.* 4, 293–297. <https://doi.org/10.1038/ngeo1123>.
- Dontis, E.E., Radabaugh, K.R., Chappel, A.R., Russo, C.E., Moyer, R.P., 2020. Carbon storage increases with site age as created saltmarshes transition to mangrove forests in Tampa Bay, Florida (USA). *Estuar. Coasts* 43, 1470–1488. <https://doi.org/10.1007/s12237-020-00733-0>.
- Doughty, C.L., Langley, J.A., Walker, W.S., Feller, I.C., Schaub, R., Chapman, S.K., 2016. Mangrove range expansion rapidly increases coastal wetland carbon storage. *Estuar. Coasts* 39, 385–396. <https://doi.org/10.1007/s12237-015-9993-8>.
- Eleuterius, L.N., 1976. Vegetative morphology and anatomy of the saltmarsh rush, *Juncus roemerianus*. *Gulf Res. Rep.* 5, 1–10. <https://doi.org/10.18785/grr.0502.01>.
- Fagherazzi, S., Kirwan, M.L., Mudd, S.M., Guntenspergen, G.R., Temmerman, S., D'Alpaos, A., et al., 2012. Numerical models of saltmarsh evolution: ecological, geomorphic, and climatic factors. *Rev. Geophys.* 50. <https://doi.org/10.1029/2011rg000359>.
- Feng, J.X., Wang, S.G., Wang, S.J., Ying, R., Yin, F.M., Jiang, L., et al., 2019. Effects of invasive *Spartina alterniflora* loisel. and subsequent ecological replacement by *Sonneratia apetala* Buch.-Ham. on soil organic carbon fractions and stock. *Forests* 10, 171. <https://doi.org/10.3390/f10020171>.
- Furukawa, K., Wolanski, E., 1996. Sedimentation in mangrove forests. *Mangroves Salt Marshes* 1, 3–10. <https://doi.org/10.1023/A:1025973426404>.
- Gardner, W.H., 1986. Water content. In: Klute, A. (Ed.), *Methods of Soil Analysis: Part 1 Physical and Mineralogical Methods*, 5.1, Second edition Soil Science Society of America, Madison, WI, USA, pp. 493–544. <https://doi.org/10.2136/sssabookser5.1.2ed.c21>.
- Grandy, A.S., Neff, J.C., 2008. Molecular C dynamics downstream: the biochemical decomposition sequence and its impact on soil organic matter structure and function. *Sci. Total Environ.* 404, 297–307. <https://doi.org/10.1016/j.scitotenv.2007.11.013>.
- Haines, E., Chalmers, A., Hanson, R., Sherr, B., 1977. Nitrogen pools and fluxes in a Georgia saltmarsh. In: Wiley, M. (Ed.), *Estuarine Processes, Volume II: Circulation, Sediments, and Transfer of Material in the Estuary*. Academic Press, New York, pp. 241–254. <https://doi.org/10.1016/B978-0-12-751802-2.50025-4>.
- Hassink, J., Whitmore, A.P., 1997. A model of the physical protection of organic matter in soils. *Soil Sci. Soc. Am. J.* 61, 131–139. <https://doi.org/10.2136/sssaj1997.03615995006100010020x>.
- Henry, K.M., Twilley, R.R., 2013. Soil development in a coastal Louisiana wetland during a climate-induced vegetation shift from saltmarsh to mangrove. *J. Coast. Res.* 29, 1273–1283. <https://doi.org/10.2112/COASTRES-D-12-00184.1>.
- Hood-Nowotny, R., Hinko-Najera Umana, N., Inselbacher, E., Oswald-Lachouani, P., Wanek, W., 2010. Alternative methods for measuring inorganic, organic, and total dissolved nitrogen in soil. *Soil Sci. Soc. Am. J.* 74, 1018–1027. <https://doi.org/10.2136/sssaj2009.0389>.
- Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A., Vitousek, P.M., 1990. Effects of soil resources on plant invasion and community structure in californian serpentine grassland. *Ecology* 71, 478–491. <https://doi.org/10.2307/1940302>.
- Kaye, J., Barrett, J., Burke, I., 2002. Stable nitrogen and carbon pools in grassland soils of variable texture and carbon content. *Ecosystems* 5, 461–471. <https://doi.org/10.1007/s10021-002-0142-4>.
- Kelleway, J.J., Saintilan, N., Macreadie, P.I., Baldock, J.A., Ralph, P.J., 2017. Sediment and carbon deposition vary among vegetation assemblages in a coastal saltmarsh. *Biogeochemistry* 14, 3763–3779. <https://doi.org/10.5194/bg-14-3763-2017>.
- Kelleway, J.J., Saintilan, N., Macreadie, P.I., Skillebeck, C.G., Zawadzki, A., Ralph, P.J., 2016. Seventy years of continuous encroachment substantially increases "blue carbon" capacity as mangroves replace intertidal saltmarshes. *Glob. Chang. Biol.* 22, 1097–1109. <https://doi.org/10.1111/gcb.13158>.
- Kettler, T.A., Doran, J.W., Gilbert, T.L., 2001. Simplified method for soil particle-size determination to accompany soil-quality analyses. *Soil Sci. Soc. Am. J.* 65, 849–852. <https://doi.org/10.2136/sssaj2001.653849x>.
- Kirwan, M.L., Guntenspergen, G.R., 2012. Feedbacks between inundation, root production, and shoot growth in a rapidly submerging brackish marsh. *J. Ecol.* 100, 764–770. <https://doi.org/10.1111/j.1365-2745.2012.01957.x>.
- Kleber, M., Sollins, P., Sutton, R., 2007. A conceptual model of organo-mineral interactions in soils: self-assembly of organic molecular fragments into zonal structures on mineral surfaces. *Biogeochemistry* 85, 9–24. <https://doi.org/10.1007/s10533-007-9103-5>.
- Krauss, K.W., Cormier, N., Osland, M.J., Kirwan, M.L., Stagg, C.L., Nestlerode, J.A., et al., 2017. Created mangrove wetlands store belowground carbon and surface elevation change enables them to adjust to sea-level rise. *Sci. Rep.* 7. <https://doi.org/10.1038/s41598-017-01224-2>.
- Krauss, K.W., From, A.S., Doyle, T.W., Doyle, T.J., Barry, M.J., 2011. Sea-level rise and landscape change influence mangrove encroachment onto marsh in the ten Thousand Islands region of Florida, USA. *J. Coast. Conserv.* 15, 629–638. <https://doi.org/10.1007/s11852-011-0153-4>.
- Kristensen, E., Mangion, P., Tang, M., Flindt, M.R., Holmer, M., Ulomi, S., 2011. Microbial carbon oxidation rates and pathways in sediments of two Tanzanian mangrove forests. *Biogeochemistry* 103, 143–158. <https://doi.org/10.1007/s10533-010-9453-2>.
- Kulmatiski, A., Beard, K.H., Stevens, J.R., Cobbold, S.M., 2008. Plant-soil feedbacks: a meta-analytical review. *Ecol. Lett.* 11, 980–992. <https://doi.org/10.1111/j.1461-0248.2008.01209.x>.
- Lamont, K., Saintilan, N., Kelleway, J.J., Mazumder, D., Zawadzki, A., 2020. Thirty-year repeat measures of mangrove above- and below-ground biomass reveals unexpectedly high carbon sequestration. *Ecosystems* 23, 370–382. <https://doi.org/10.1007/s10021-019-00408-3>.
- Lewis, D.B., Brown, J.A., Jimenez, K.L., 2014a. Effects of flooding and warming on soil organic matter mineralization in *Avicennia germinans* mangrove forests and *Juncus roemerianus* saltmarshes. *Estuar. Coast. Shelf Sci.* 139, 11–19. <https://doi.org/10.1016/j.ecss.2013.12.032>.
- Lewis, D.B., Castellano, M.J., Kaye, J.P., 2014b. Forest succession, soil carbon accumulation, and rapid nitrogen storage in poorly remineralized soil organic matter. *Ecology* 95, 2687–2693. <https://doi.org/10.1890/13-2196.1>.
- Lewis, D.B., Feit, S.J., 2015. Connecting carbon and nitrogen storage in rural wetland soil to groundwater abstraction for urban water supply. *Glob. Chang. Biol.* 21, 1704–1714. <https://doi.org/10.1111/gcb.12782>.
- Lewis, D.B., Kaye, J.P., Kinzig, A.P., 2014c. Legacies of agriculture and urbanization in labile and stable organic carbon and nitrogen in Sonoran Desert soils. *Ecosphere* 5, art59. <https://doi.org/10.1890/es13-00400.1>.
- Li, J.Y., Qu, W.D., Han, G.X., Lu, F., Zhou, Y.F., Song, W.M., et al., 2020. Effects of drying-rewetting frequency on vertical and lateral loss of soil organic carbon in a tidal saltmarsh. *Wetlands* 40, 1433–1443. <https://doi.org/10.1007/s13157-020-01286-5>.
- Liao, C.Z., Luo, Y.Q., Jiang, L.F., Zhou, X.H., Wu, X.W., Fang, C.M., et al., 2007. Invasion of *Spartina alterniflora* enhanced ecosystem carbon and nitrogen stocks in the Yangtze estuary, China. *Ecosystems* 10, 1351–1361. <https://doi.org/10.1007/s10021-007-9103-2>.
- Liao, J.D., Boutton, T.W., Jastrow, J.D., 2006. Organic matter turnover in soil physical fractions following woody plant invasion of grassland: evidence from natural ^{13}C and ^{15}N . *Soil Biol. Biochem.* 38, 3197–3210. <https://doi.org/10.1016/j.soilbio.2006.04.004>.
- Macy, A., Osland, M.J., Cherry, J.A., Cebrian, J., 2020. Changes in ecosystem nitrogen and carbon allocation with black mangrove (*Avicennia germinans*) encroachment into *Spartina alterniflora* saltmarsh. *Ecosystems* <https://doi.org/10.1007/s10021-020-00565-w>.
- Matthijs, S., Tack, J., van Speybroeck, D., Koedam, N., 1999. Mangrove species zonation and soil redox state, sulphide concentration and salinity in Gazi Bay (Kenya), a preliminary study. *Mangroves Salt Marshes* 3, 243–249. <https://doi.org/10.1023/a:1009971023277>.
- McDaniel, M.D., Grandy, A.S., Tiemann, L.K., Weintraub, M.N., 2014. Crop rotation complexity regulates the decomposition of high and low quality residues. *Soil Biol. Biochem.* 78, 243–254. <https://doi.org/10.1016/j.soilbio.2014.07.027>.
- McKee, K.L., 1993. Soil physicochemical patterns and mangrove species distribution – reciprocal effects? *J. Ecol.* 81, 477–487. <https://doi.org/10.2307/2261526>.
- McKee, K.L., Cahoon, D.R., Feller, I.C., 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Glob. Ecol. Biogeogr.* 16, 545–556. <https://doi.org/10.1111/j.1466-8238.2007.00317.x>.

- McKee, K.L., Vervaeke, W.C., 2018. Will fluctuations in saltmarsh-mangrove dominance alter vulnerability of a subtropical wetland to sea-level rise? *Glob. Chang. Biol.* 24, 1224–1238. <https://doi.org/10.1111/gcb.13945>.
- McLeod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., et al., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Front. Ecol. Environ.* 9, 552–560. <https://doi.org/10.1890/110004>.
- Morris, J.T., Sundareshwar, P.V., Nietch, C.T., Kjerfve, B., Cahoon, D.R., 2002. Responses of coastal wetlands to rising sea level. *Ecology* 83, 2869–2877. <https://doi.org/10.2307/3072022>.
- Nadelhoffer, K.J., 1990. Microlysimeter for measuring nitrogen mineralization and microbial respiration in aerobic soil incubations. *Soil Sci. Soc. Am. J.* 54, 411–415. <https://doi.org/10.2136/sssaj1990.03615995005400020019x>.
- Nedwell, D.B., Blackburn, T.H., Wiebe, W.J., 1994. Dynamic nature of the turnover of organic carbon, nitrogen and Sulphur in the sediments of a jamaican mangrove forest. *Mar. Ecol. Prog. Ser.* 110, 223–231. <https://doi.org/10.3354/meps110223>.
- Nellemann, C., Corcoran, E., Duarte, C.M., Valdés, L., De Young, C., Fonseca, L., Grimsditch, G., 2009. Blue Carbon. A Rapid Response Assessment. United Nations Environment Programme. GRID-Arendal 978-82-7701-060-1 <https://www.grida.no/publications/145>.
- Osland, M.J., Enwright, N., Day, R.H., Doyle, T.W., 2013. Winter climate change and coastal wetland foundation species: saltmarshes vs. mangrove forests in the southeastern United States. *Glob. Chang. Biol.* 19, 1482–1494. <https://doi.org/10.1111/gcb.12126>.
- Osland, M.J., Gabler, C.A., Grace, J.B., Day, R.H., McCoy, M.L., McLeod, J.L., et al., 2018. Climate and plant controls on soil organic matter in coastal wetlands. *Glob. Chang. Biol.* 24, 5361–5379. <https://doi.org/10.1111/gcb.14376>.
- Osland, M.J., Spivak, A.C., Nestlerode, J.A., Lessmann, J.M., Almario, A.E., Heitmüller, P.T., et al., 2012. Ecosystem development after mangrove wetland creation: plant–soil change across a 20-year chronosequence. *Ecosystems* 15, 848–866. <https://doi.org/10.1007/s10021-012-9551-1>.
- Patterson, C.S., Mendelsohn, I.A., 1991. A comparison of physicochemical variables across plant zones in a mangal/saltmarsh community in Louisiana. *Wetlands* 11, 139–161. <https://doi.org/10.1007/BF03160845>.
- Paul, E.A., Harris, D., Collins, H.P., Schultess, U., Robertson, G.P., 1999. Evolution of CO₂ and soil carbon dynamics in biologically managed, row-crop agroecosystems. *Appl. Soil Ecol.* 11, 53–65. [https://doi.org/10.1016/S0929-1393\(98\)00130-9](https://doi.org/10.1016/S0929-1393(98)00130-9).
- Pennings, S.C., Callaway, R.M., 1992. Saltmarsh plant zonation: the relative importance of competition and physical factors. *Ecology* 73, 681–690. <https://doi.org/10.2307/1940774>.
- Perakis, S.S., Hedin, L.O., 2001. Fluxes and fates of nitrogen in soil of an unpolluted old-growth temperate forest, southern Chile. *Ecology* 82, 2245–2260. [https://doi.org/10.1890/0012-9658\(2001\)082\[2245:FAFONI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[2245:FAFONI]2.0.CO;2).
- Perry, C.L., Mendelsohn, I.A., 2009. Ecosystem effects of expanding populations of *Avicennia germinans* in a Louisiana saltmarsh. *Wetlands* 29, 396–406. <https://doi.org/10.1672/08-100.1>.
- Raabe, E.A., Roy, L.C., McIvor, C.C., 2012. Tampa Bay coastal wetlands: nineteenth to twentieth century tidal marsh-to-mangrove conversion. *Estuar. Coasts* 35, 1145–1162. <https://doi.org/10.1007/s12237-012-9503-1>.
- Ramos e Silva, C.A., Oliveira, S.R., Rego, R.D.P., Mozeto, A.A., 2007. Dynamics of phosphorus and nitrogen through litter fall and decomposition in a tropical mangrove forest. *Mar. Environ. Res.* 64, 524–534. <https://doi.org/10.1016/j.marenvres.2007.04.007>.
- Raw, J.L., Julie, C.L., Adams, J.B., 2019. A comparison of soil carbon pools across a mangrove-saltmarsh ecotone at the southern african warm-temperate range limit. *S. Afr. J. Bot.* 127, 301–307. <https://doi.org/10.1016/j.sajb.2019.11.005>.
- Ray, R., Michaud, E., Aller, R.C., Vantrepotte, V., Gleixner, G., Walcker, R., et al., 2018. The sources and distribution of carbon (DOC, POC, DIC) in a mangrove dominated estuary (French Guiana, South America). *Biogeochemistry* 138, 297–321. <https://doi.org/10.1007/s10533-018-0447-9>.
- Reed, D.J., 1995. The response of coastal marshes to sea-level rise: survival or subsidence? *Earth Surf. Process. Landf.* 20, 39–48. <https://doi.org/10.1002/esp.3290200105>.
- Robertson, A.L., Alongi, D.M., Boto, K.G., 1992. Food chains and carbon fluxes. In: Robertson, A.L., Alongi, D.M. (Eds.), *Tropical Mangrove Ecosystems. Coastal and Estuarine Studies Book Series 41*. American Geophysical Union, Washington, D.C., USA, pp. 293–326. <https://doi.org/10.1029/CE041p0293>.
- Robertson, G.P., Paul, E.A., 2000. Decomposition and soil organic matter dynamics. In: Sala, O.E., Jackson, R.B., Mooney, H.A., Howarth, R.W. (Eds.), *Methods in Ecosystem Science*. Springer, New York, pp. 104–116. https://doi.org/10.1007/978-1-4612-1224-9_8.
- Rogers, K., Krauss, K.W., 2019. Moving from generalisations to wpecificity about mangrove-saltmarsh dynamics. *Wetlands* 39, 1155–1178. <https://doi.org/10.1007/s13157-018-1067-9>.
- Saintilan, N., Wilson, N.C., Rogers, K., Rajkaran, A., Krauss, K.W., 2014. Mangrove expansion and saltmarsh decline at mangrove poleward limits. *Glob. Chang. Biol.* 20, 147–157. <https://doi.org/10.1111/gcb.12341>.
- Sanderman, J., Hengl, T., Fiske, G., Solvik, K., Adame, M.F., Benson, L., et al., 2018. A global map of mangrove forest soil carbon at 30 m spatial resolution. *Environ. Res. Lett.* 13, 055002. <https://doi.org/10.1088/1748-9326/aabe1c>.
- Sasmith, S.D., Kuzyakov, Y., Lubis, A.A., Murdiyarso, D., Hutley, L.B., Bachri, S., et al., 2020. Organic carbon burial and sources in soils of coastal mudflat and mangrove ecosystems. *Catena* 187, 104414. <https://doi.org/10.1016/j.catena.2019.104414>.
- Scheffell, W.A., Heck, K.L., Johnson, M.W., 2018. Tropicalization of the northern Gulf of Mexico: impacts of saltmarsh transition to black mangrove dominance on faunal communities. *Estuar. Coasts* 41, 1193–1205. <https://doi.org/10.1007/s12237-017-0334-y>.
- Schimel, J.P., Bennett, J., 2004. Nitrogen mineralization: challenges of a changing paradigm. *Ecology* 85, 591–602. <https://doi.org/10.1890/03-8002>.
- Sherman, R.E., Fahey, T.J., Howarth, R.W., 1998. Soil-plant interactions in a neotropical mangrove forest: iron, phosphorus and sulfur dynamics. *Oecologia* 115, 553–563. <https://doi.org/10.1007/s004420050553>.
- Simpson, L.T., Lovelock, C.E., Cherry, J.A., Feller, I.C., 2020. Short-lived effects of nutrient enrichment on *Avicennia germinans* decomposition in a saltmarsh-mangrove ecotone. *Estuar. Coast. Shelf Sci.* 235, 106598. <https://doi.org/10.1016/j.ecss.2020.106598>.
- Simpson, L.T., Osborne, T.Z., Feller, I.C., 2019a. Wetland soil CO₂ efflux along a latitudinal gradient of spatial and temporal complexity. *Estuar. Coasts* 42, 45–54. <https://doi.org/10.1007/s12237-018-0442-3>.
- Simpson, L.T., Stein, C.M., Osborne, T.Z., Feller, I.C., 2019b. Mangroves dramatically increase carbon storage after 3 years of encroachment. *Hydrobiologia* 834, 13–26. <https://doi.org/10.1007/s10750-019-3905-z>.
- Six, J., Bossuyt, H., Degryze, S., Denef, K., 2004. A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. *Soil Tillage Res.* 79, 7–31. <https://doi.org/10.1016/j.still.2004.03.008>.
- Smith, T.J., Anderson, G.H., Balentine, K., Tiling, G., Ward, G.A., Whelan, K.R.T., 2009. Cumulative impacts of hurricanes on Florida mangrove ecosystems: sediment deposition, storm surges, and vegetation. *Wetlands* 29, 24–34. <https://doi.org/10.1672/08-40.1>.
- Steinmüller, H.E., Foster, T.E., Boudreau, P., Hinkle, C.R., Chambers, L.G., 2020. Tipping points in the mangrove march: characterization of biogeochemical cycling along the mangrove-saltmarsh ecotone. *Ecosystems* 23, 417–434. <https://doi.org/10.1007/s10021-019-00411-8>.
- Sun, H.M., Jiang, J., Cui, L.N., Feng, W.T., Wang, Y.G., Zhang, J.C., 2019. Soil organic carbon stabilization mechanisms in a subtropical mangrove and saltmarsh ecosystems. *Sci. Total Environ.* 673, 502–510. <https://doi.org/10.1016/j.scitotenv.2019.04.122>.
- Teal, J.M., 1962. Energy flow in the saltmarsh ecosystem of Georgia. *Ecology* 43, 614–624. <https://doi.org/10.2307/1933451>.
- Twilley, R.R., Chen, R.H., Hargis, T., 1992. Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water Air Soil Pollut.* 64, 265–288. <https://doi.org/10.1007/bf00477106>.
- Van de Broek, M., Vandendriessche, C., Poppelmonde, D., Merckx, R., Temmerman, S., Govers, G., 2018. Long-term organic carbon sequestration in tidal marsh sediments is dominated by old-aged allochthonous inputs in a macrotidal estuary. *Glob. Chang. Biol.* 24, 2498–2512. <https://doi.org/10.1111/gcb.14089>.
- van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T., et al., 2013. Plant-soil feedbacks: the past, the present and future challenges. *J. Ecol.* 101, 265–276. <https://doi.org/10.1111/1365-2745.12054>.
- Vitousek, P.M., Hedin, L.O., Matson, P.A., Fownes, J.H., Neff, J., 1998. Within-system element cycles, input-output budgets, and nutrient limitation. In: Pace, M.L., Groffman, P.M. (Eds.), *Successes, Limitations, and Frontiers in Ecosystem Science*. Springer, New York, pp. 432–451. https://doi.org/10.1007/978-1-4612-1724-4_18.
- Wang, G., Guan, D.S., Peart, M.R., Chen, Y.J., Peng, Y.S., 2013. Ecosystem carbon stocks of mangrove forest in Yingluo Bay, Guangdong Province of South China. *For. Ecol. Manag.* 310, 539–546. <https://doi.org/10.1016/j.foreco.2013.08.045>.
- Wang, G., Guan, D., Zhang, Q., Peart, M.R., Chen, Y., Peng, Y., 2015. Distribution of dissolved organic carbon and KMnO₄-oxidizable carbon along the low-to-high intertidal gradient in a mangrove forest. *J. Soils Sediments* 15, 2199–2209. <https://doi.org/10.1007/s11368-015-1150-2>.
- Wang, Q.R., Li, Y.C., Wang, Y., 2011. Optimizing the weight loss-on-ignition methodology to quantify organic and carbonate carbon of sediments from diverse sources. *Environ. Monit. Assess.* 174, 241–257. <https://doi.org/10.1007/s10661-010-1454-z>.
- Woodroffe, C.D., 2002. *Coasts: Form, Process and Evolution*. Cambridge University Press 9780521011839 623p.
- Yando, E.S., Osland, M.J., Hester, M.W., 2018. Microspatial ecotone dynamics at a shifting range limit: plant-soil variation across saltmarsh-mangrove interfaces. *Oecologia* 187, 319–331. <https://doi.org/10.1007/s00442-018-4098-2>.
- Yando, E.S., Osland, M.J., Willis, J.M., Day, R.H., Krauss, K.W., Hester, M.W., 2016. Saltmarsh-mangrove ecotones: using structural gradients to investigate the effects of woody plant encroachment on plant-soil interactions and ecosystem carbon pools. *J. Ecol.* 104, 1020–1031. <https://doi.org/10.1111/1365-2745.12571>.
- Young, J.L., Aldag, R.W., 1982. Inorganic forms of nitrogen in soil. In: Stevenson, F.J. (Ed.), *Nitrogen in Agricultural Soils*. Agronomy Monograph. 22. American Society of Agronomy, Madison, WI, USA, pp. 43–66. <https://doi.org/10.2134/agronmonogr22.c2>.