Ecosystems
https://doi.org/10.1007/s10021-020-00554-z

ECOSYSTEMS

Mangrove Encroachment Alters Decomposition Rate in Saltmarsh Through Changes in Litter Quality

Loraé T. Simpson,[1,2,3,5]* Julia A. Cherry,[2] Rachel S. Smith,[4] and Ilka C. Feller[3]

[1]*Smithsonian Marine Station, Fort Pierce, Florida 34949, USA;* [2]*University of Alabama, Tuscaloosa, Alabama 35487, USA;* [3]*Smithsonian Environmental Research Center, Edgewater, Maryland 21037, USA;* [4]*University of Virginia, Charlottesville, Virginia 22903, USA;* [5]*Present address: Present Address: Florida Oceanographic Society, 890 NE Ocean Blvd, Stuart, Florida 34996, USA*

Abstract

Global climate change is driving the expansion of mangroves into saltmarsh habitat, which may alter the rate and magnitude of organic matter decomposition and nutrient cycling due to differences in the structural complexity, litter quality, and other ecophysiological traits of foundation species. This work quantified and compared aboveground litter decomposition of the range-expanding mangrove, *Avicennia germinans*, and resident saltmarsh cordgrass, *Spartina alterniflora*, and decomposition of a standard substrate belowground, in the saltmarsh and saltmarsh-mangrove ecotone habitat along the Atlantic coast of Florida, USA. Plant and soil fractions were tested for natural abundances of $\delta^{13}C$ and $\delta^{15}N$ stable isotopes to elucidate soil nutrient sources. Although aboveground decomposition rates differed between marsh and mangrove species due to differences in litter quality, decomposition rates did not vary between saltmarsh and ecotonal habitats. Decay rates were higher for *A. germinans* leaf litter ($0.007 \pm 0.0003\ k\ day^{-1}$) than for *S. alterniflora* ($0.004 \pm 0.0003\ k\ day^{-1}$) regardless of habitat, which suggests that increasing inputs of *A. germinans* litter with encroachment may increase nutrient availability through rapid turnover. Furthermore, belowground decomposition was similar between habitats ($0.015 \pm 0.0008\ k\ day^{-1}$), whereas soil $\delta^{13}C$ and $\delta^{15}N$ stable isotopes differed significantly. Collectively, these results suggest that mangrove encroachment may not modify the environmental factors driving decomposition, but alterations in foundation plant species may ultimately alter nutrient cycling within habitats through shifts in litter quality.

Key words: Decay rate; Litter quality; Stable isotopes; Mangrove encroachment; $\delta^{15}N$; Foundation species.

Highlights

- Changes in foundation species cover will alter aboveground decomposition rates.
- Species litter quality, not habitat structure, drives aboveground decomposition rates.
- Habitat structure did not affect belowground decomposition rates.

Received 22 June 2020; accepted 17 August 2020

Electronic supplementary material: The online version of this article (https://doi.org/10.1007/s10021-020-00554-z) contains supplementary material, which is available to authorized users.

Author's Contribution LTS and ICF designed the study; LTS performed the research; LTS and JAC analyzed the data; RSS contributed additional methods and data; LTS, JAC, RSS and ICF wrote the paper.

*Corresponding author; e-mail: lsimpson@floridaocean.org

Published online: 19 September 2020

Introduction

Climate change is shifting biome boundaries latitudinally and elevationally around the world (IPCC 2014). Given the magnitude and rate of global change, understanding how consequent ecological regime shifts will affect ecosystem properties and functions is critical for managing natural systems (Ellison and others 2005). Shifts among dominant plant species with different traits are likely to alter ecosystem properties and functions. Woody plant encroachment, defined here as the establishment, development, and spread of tree or shrub species, is one such species shift that has been documented worldwide in many ecosystems over the past 150 years (Archer and others 2017). In grasslands and savannahs, woody encroachment can modify microclimate, species diversity, and above- and belowground net primary productivity (Hughes and others 2006; Montané and others 2010; Ratajczak and others 2012; D'Odorico and others 2013). Moreover, woody encroachment can alter the quality and quantity of carbon (C) sources and thus may drive changes in nutrient flow through food webs (for example, Power and others 1996; Ehrenfeld 2010).

Mangrove expansion into saltmarshes is a case of woody encroachment, where low stature forbs and grasses are replaced by taller, woody vegetation (Saintilan and Rogers 2015). Woody encroachment of mangroves into saltmarsh at mangroves' latitudinal limits has been documented around the world, including the southeastern USA (Perry and Mendelssohn 2009; Cavanaugh and others 2014; Armitage and others 2015), southeastern Australia (Saintilan and Williams 1999), Asia (Lee and Yeh 2009; Durango-Cordero and others 2013) and South Africa (Saintilan and others 2014). Global climate change is driving the expansion of mangroves worldwide through increased atmospheric surface temperatures, changes in precipitation, fluxes of tidal nutrients, and disturbances that promote mangrove colonization (Eslami-Andargoli and others 2009; Doyle and others 2010; Cavanaugh and others 2014; Feher and others 2017). In North America, the ecotonal boundary between saltmarshes and mangroves is shifting northward in response to changing environmental conditions; cold-sensitive mangroves die back during freeze events and expand during warmer winters, creating a temporally and spatially dynamic ecosystem (Ross and others 2000; Stevens and others 2006; Rodriguez and others 2016; Osland and others 2017; Cavanaugh and others 2019). Changes of this magnitude to foundation plant species cover have the potential to significantly alter ecosystem structure and function (Guo and others 2017), with substantial consequences for the provision of ecosystem services.

Saltmarsh and mangrove both provide a wide range of critical ecosystem services, including coastal protection, water quality maintenance, nutrient retention and removal, fisheries habitat, and C sequestration (Barbier and others 2011). High rates of primary productivity and slow decomposition rates combine to generate high C accumulation (McLatchey and Reddy 1998), with organic matter decomposition slowly mineralizing C and nutrients back into the environment (Reddy and Delaune 2008; Ainley and Bishop 2015). Both systems act as important C sinks and sites of nutrient transformations, as well as sources of C and nutrients for adjoining communities. Hence, any changes in decomposition with shifts in habitat structure may have subsequent ramifications for nutrient cycling within and among ecosystems. Thus, understanding the decay of organic matter is of critical importance to both global C cycles and coastal and estuarine food web dynamics (Moore and others 2004).

Mangrove and saltmarsh vegetation are structurally and functionally distinct, with inherently different productivity rates (Yando and others 2018), C storage capacities (Duarte and others 2013; Alongi 2014), and C sequestration rates (Lovelock and others 2014). Differences in species tissue chemistry may drive differences in organic matter decomposition, as carbon:nitrogen (C:N) can be an important control of decay rates (for example, Valiela and others 1984; Jones and others 2016). Additionally, mangrove and saltmarsh roots have contrasting chemical qualities (Perry and Mendelssohn 2009) and physiological characteristics (McKee and others 1988; Skelton and Allaway 1996) that could drive differences in root exudate release (Bertin and others 2003) or radial oxygen loss (McKee and others 1988; Leopold and others 2013) to surrounding soils. Moreover, microbial community structure can differ between mangrove-dominated and saltmarsh-dominated habitats (Barreto and others 2018), and as such, mangrove encroachment may contribute to shifts in microbially mediated decomposition rates. Hence, mangrove encroachment into saltmarsh will likely have substantial effects on nutrient and C cycling and storage.

As foundation species shift, the relative contribution of their plant matter to soil nutrient cycling may change. Stable isotopes allow us to assess nutrient sources and biological transformations

that affect nutrient availability in ecosystems (McKee and others 2002). Isotopic signatures (for example, $\delta^{13}C$ and $\delta^{15}N$) can vary with plant photosynthetic pathways (Choi and others 2001), and environmental resource availability (for example, nutrients) or stress (for example, salinity) gradients (McKee and others 2002). Based on $\delta^{13}C$ values, Simpson and others (2019) found that soil organic C in a marsh-mangrove ecotone in Florida, USA, was derived mainly from saltmarsh plants, especially that of their belowground biomass. However, alterations to N cycling in response to mangrove encroachment have yet to be elucidated in these systems and understanding biomass N inputs is important when considering the implications of habitat shifts on biogeochemical cycles. For example, increased N mineralization rates due to shifts in dominant plant cover may lead to increased ^{15}N content in plant-available N pools, and hence, higher $\delta^{15}N$ values in plant tissues and soil organic matter (SOM). Consequently, conversion of dominant vegetation cover could dramatically alter biomass allocation and litter inputs to soil nutrient pools, ultimately altering the N cycle of the system.

In this study, we investigated above- and belowground decomposition in pure saltmarsh and in the saltmarsh-mangrove ecotone. By quantifying decomposition rates and soil $\delta^{15}N$ isotopic signatures in both habitats, our objective was to explore how changes in habitat structure with mangrove encroachment will alter decomposition and subsequent nutrient storage in these coastal ecosystems. We hypothesized that aboveground leaf litter decomposition would be greater in mangrove habitat than in saltmarsh habitat because contrasting species structures would differentially modify environmental conditions to stimulate the decay of high-quality litter in mangrove habitats. Mangroves modify microclimate relative to open saltmarsh in ways that are likely to promote decomposition. Mangrove canopies buffer temperatures and trap latent heat, thereby promoting warming under canopies during the winter, while also providing cooler temperatures in summer months (Devaney and others 2017; Guo and others 2017), whereas, in open saltmarsh plots, winds can accelerate heat loss from the surface to the overlying atmosphere (Chen and others 1993), thereby decreasing air and soil temperatures, and likely decomposition rates. We further postulated that belowground decomposition will be greater in mangrove habitat because the pneumatophores of *Avicennia germinans* (black mangrove) are efficient at translocating oxygen to the rhizosphere (McKee and others 1988; Comeaux and others 2012), which could increase decomposition by aerobic microorganisms (Barreto and others 2018). Species-specific differences in litter quality may also drive decomposition rates, as *A. germinans* leaf litter has a lower C:N than *Spartina alterniflora* (for example, Gallagher 1975; McKee and others 2007; Simpson and others 2013) and is likely to decay at a faster rate regardless of habitat structure. As a result, we proposed that $\delta^{15}N$ isotopic abundance would be greater in mangrove-dominated soils because greater decomposition of labile *A. germinans* litter would enrich soil N pools. Taken together, decomposition rates and stable isotope values give insight into biogeochemical changes under shifting foundation species regimes with implications for ecosystems worldwide.

Methods

Study Sites

Decomposition was assessed at five sites (28°–29° N) along the Atlantic coast of Florida, USA (Figure 1). These sampling sites allowed for quantification and comparison of decomposition dynamics in two types of vegetation structures (that is, habitats): pure saltmarsh and saltmarsh-mangrove ecotone. Within each of the five sites, there were six 10×10 m permanent plots, three in pure saltmarsh and three in saltmarsh-mangrove (hereafter, ecotone) habitat (Simpson and others 2017). In total, 30 plots were sampled across five sites. Pure saltmarsh plots contained monocultures or mixed stands of herbaceous graminoid or succulent saltmarsh species, including *Batis maritima, Distichlis spicata, Sarcocornia perennis*, and *S. alterniflora*. Ecotone plots were comprised of the same suite of saltmarsh species, as well as a mixture of *A. germinans*, *Laguncularia racemosa*, and/or *Rhizophora mangle* shrub mangroves, which migrated into saltmarsh in the mid-1980s (Cavanaugh and others 2014). At these study sites, mangroves are at the northern extent of their distribution and averaged 0.92 ± 0.03 m in height and had approximately 83.4 ± 11.19 pneumatophores per m^2 (Simpson and others 2017). Although these sites spanned a latitudinal gradient and the plots were comprised of contrasting habitats, the hydroedaphic conditions were similar across plots and sites (Table 1, Supplementary Table 1).

Because the dominant species differed between habitats, we measured a suite of site characteristics to determine whether there were environmental differences between habitat types (see

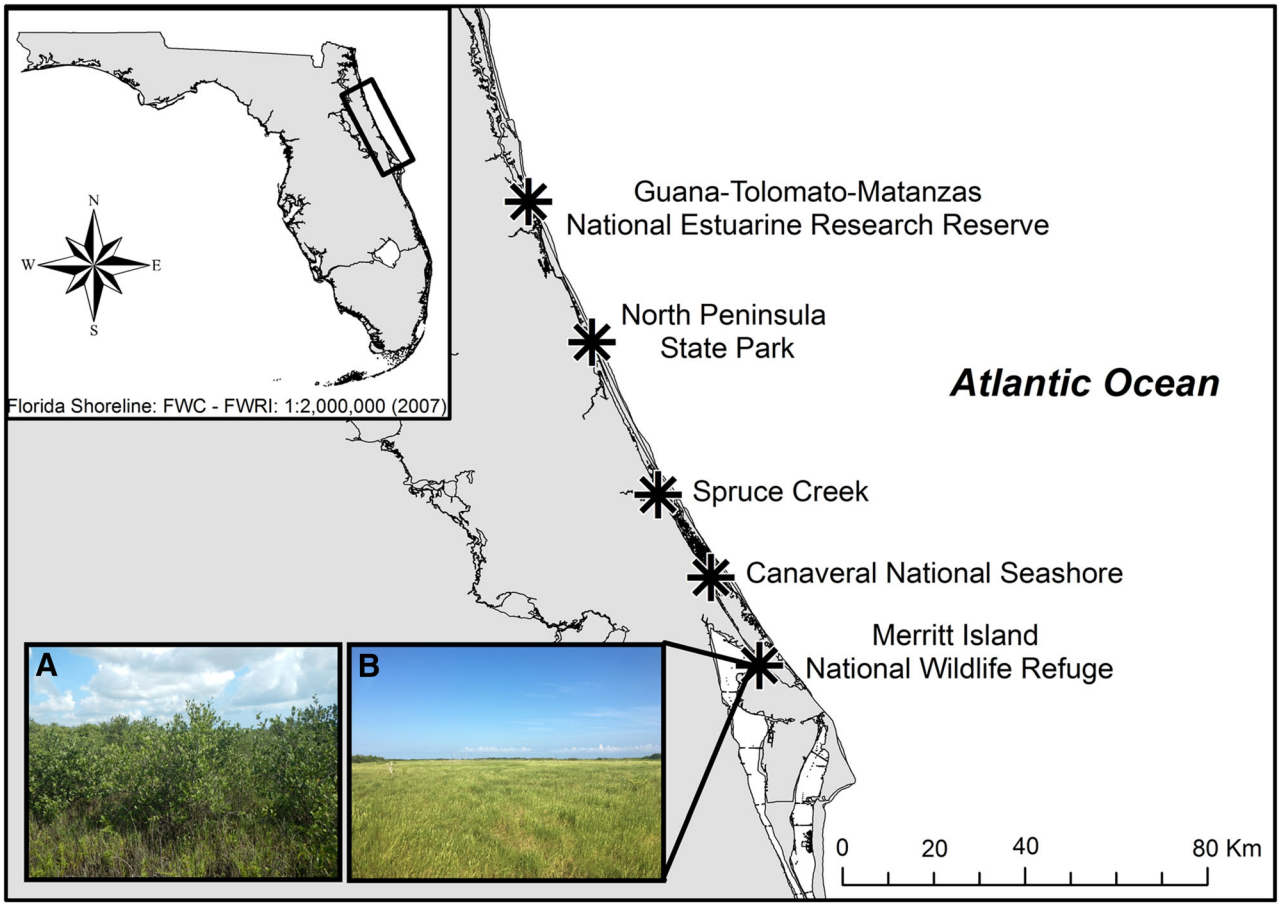

Figure 1. Site locations. Each site contains six plots, three in **a** the saltmarsh-mangrove ecotone and three in **b** pure saltmarsh. Plots at Merritt Island National Wildlife Refuge are pictured.

Simpson and others (2017) for methods). Across the latitudinal gradient we found no significant differences in elevation relative to mean sea level between saltmarsh (0.87 ± 0.02 m NAVD88) and ecotone (0.89 ± 0.02 m NAVD88) plots, which represents a proxy for flooding and inundation. Additionally, porewater salinity (32.8 ± 1.45) and pH (7.01 ± 0.06) were consistent across sites and between habitats. 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). Soil temperatures averaged 14.5 ± 0.76 °C in winter months and 28.0 ± 0.24 °C in summer months, and they did not vary between habitat types. See Supplementary Table 1 for site analyses. Thus, the experimental design isolated the effects of biotic (plant-mediated), not abiotic (environmental-mediated), conditions on decomposition, regardless of site location.

Litter Collection and Incubation

Decomposition bags were used to quantify aboveground decomposition rates over spatial and temporal scales. Decomposition bags (20 × 15 cm) were made of 1 mm^2 mesh, nylon-coated fiberglass screen material. Bags were separated into two compartments (10 × 15 cm each). One compartment was filled with 3 g of air-dried, senescent *A. germinans* leaf litter and the other was filled with 3 g of air-dried, senescent *S. alterniflora* leaf litter. Senescent *A. germinans* leaf litter was handpicked from mature trees and senescing *S. alterniflora* litter was collected from standing stocks in the field. Litter was not site-specific, but instead was collected from all sites and homogenized. Five sets of bags containing both litter types were deployed in October 2014 in each of the 30 plots, for a total of 150 bags. Bags were placed horizontally on the soil surface and staked into the ground with large plastic-coated paperclips. One set of bags per plot was retrieved in October 2014, January 2015, April 2015, July 2015, and October 2015 after 0, 3, 6, 9,

Table 1. Characteristics of Sampling Sites Along the Atlantic Coast of Florida

Site	Latitude/longitude	Plot	Species dominance (%)	Pneumatophore density (m^{-2})	Salinity	pH	Elevation (m)
Guana Tolomato Matanzas NERR	N 29.72° W − 81.24°	Ecotone	Avi (100) Bat (61) Sar (48)	77.3 ± 16.0	34.1 ± 1.39	6.60 ± 0.79	0.91 ± 0.03
	N 29.73° W − 81.25°	Saltmarsh	Spr (80) Bat (10)	0.00	37.1 ± 1.57	6.63 ± 0.56	0.78 ± 0.05
North Peninsula State Park	N 29.41° W − 81.10°	Ecotone	Avi (100) Bat (5) Sar (4)	101.7 ± 15.0	45.0 ± 1.85	6.70 ± 0.11	1.21 ± 0.02
	N 29.42° W − 81.10°	Saltmarsh	Spr (58) Dis (42)	0.00	45.3 ± 2.13	6.23 ± 0.07	1.17 ± 0.01
Spruce Creek	N 29.08° W − 80.95°	Ecotone	Avi (74) Lag (15) Bat (13) Sar (5)	133.3 ± 17.8	28.4 ± 1.26	6.82 ± 0.11	1.30 ± 0.02
	N 29.08° W − 80.96°	Saltmarsh	Spr (58) Sal (10)	0.00	28.1 ± 1.14	7.01 ± 0.09	1.32 ± 0.01
Canaveral National Seashore	N 28.90° W − 80.84°	Ecotone	Avi (100) Bat (7) Sar (7)	64.0 ± 2.31	32.3 ± 2.13	6.79 ± 0.11	–
	N 28.90° W − 80.84°	Saltmarsh	Dis (99) Bat (1)	0.00	35.0 ± 1.85	6.76 ± 0.14	–
Merritt Island NWR	N 28.70° W − 80.73°	Ecotone	Lag (87) Avi (13) Bat (9) Sar (36)	40.7 ± 4.84	35.9 ± 2.05	6.60 ± 0.19	0.11 ± 0.03
	N 28.71° W − 80.74°	Saltmarsh	Dis (100)	0.00	32.9 ± 1.81	6.67 ± 0.18	0.24 ± 0.01

Values shown as mean ± 1 SE. n = 5. Salinity and pH values are averaged over the year. NERR = National Estuarine Research Reserve, NWR = National Wildlife Refuge. Avi = Avicennia germinans, Lag = Laguncularia racemosa, Bat = Batis maritima, Sar = Sarcocornia perennis Spr = Spartina alterniflora, Dis = Disticulus spicata. Sites did not differ in edaphic conditions (Supplementary Table 1).

and 12 months of incubation, respectively, to determine remaining mass (%) and decay rate (k). Control bags (0 month) were carried into the field and immediately retrieved.

Chemical Analysis and Mass Loss Determination of Aboveground Biomass

Oven-dried leaf material from control bags was ground and then pulverized to a powder in a ball-mill (Mixer/Mill 8000D, SPEX, Metuchen, New Jersey, USA) in preparation for total C (TC) and total N (TN) analyses. Concentrations of TC and TN were determined using a CE-440 elemental analyzer (Exeter Analytical, Inc., North Chelmsford, MA, USA) for both species.

After incubation in the field, litterbags were transported back to the laboratory where the remaining material was taken out of the bag, rinsed, and dried at 70 °C for 72 h to a constant weight. Initial weights were corrected for handling losses and initial moisture content to determine initial biomass. Correction factors were calculated from dried control bag biomass collected on day 0. Sediment contamination in field-incubated bags was negligible, and therefore samples were not ashed to determine ash-free dry mass remaining. Instead, litter mass loss was determined by weighing dried litter and subtracting the corrected initial weight. Decomposition rate (k) was calculated for each litterbag as percent dry mass remaining in the bags after 12 months, using the exponential decay model

$$y = y_0 e^{-kt} \quad (1)$$

where y = final biomass, y_0 = initial biomass, and t = time the bag was deployed in days.

Belowground Incubation and Mass Loss Determination

Given structural differences in habitat characteristics, we held substrate quality consistent by employing the TeaBag Index (TBI) protocol (Keuskamp and others 2013) to assess belowground decomposition rate (k). The TBI method is a simplified litterbag approach for characterizing the decomposition environment with a standard substrate so that k can be estimated, while isolating exogenous processes, without repeated sampling of decomposing material. Therefore, TBI isolated habitat-specific drivers of decay rather than the effects of species' litter quality. To test for belowground decomposition rate across habitats, two nylon tea bags (Lipton, Unilever, UK), one containing green tea (which represents the labile fraction) (EAN: 8 722700 055525) and one containing rooibos (which represents the recalcitrant fraction) (EAN: 8 722700 188438), were buried to a depth of 8 cm in April 2015. Rooibos tea decomposition is slower than green tea. Consequently, decomposition of labile material continues in rooibos tea after all labile material in green tea has been consumed and parts of the labile compounds in green tea have stabilized (Prescott 2010). Hence, stabilization (S) is measured by weight loss of the green tea, while initial decomposition rate (k) is measured by mass loss of the rooibos tea. The initial weight of teabag contents was determined by subtracting the mean weight of 10 empty bags (bag + string + label) from the weight of the intact tea bag prior to deployment (tea + bag + string + label). Triplicate sets of bags were deployed as pairs (one green and one rooibos) in each plot and were retrieved after 90 days of incubation.

Upon retrieval, tea bags were transported back to the laboratory, gently washed with DI water, and dried for 48 h at 70 °C. Tea bags were then opened, and remaining tea materials were carefully separated from fine roots and soil before being weighed. Mass remaining (%) was obtained and calculations for k followed Keuskamp and others (2013), using the following equations:

$$W_r(t) = a_r e^{-kt} + (1 - a_r) \quad (2)$$

$$S = 1 - a_g/H_g \quad (3)$$

$$a_r = H_r(1 - S) \quad (4)$$

where $W_r(t)$ describes the substrate weight of rooibos after incubation time (t in days), a_r is the labile fraction of the substrate, $1 - a_r$ is the recalcitrant fraction of the substrate, and k is the decomposition rate constant. S describes the stabilization factor, a_g is the decomposable fraction of green tea (based on the mass loss during incubation), and H_g is the hydrolysable fraction of green tea. The decomposable fraction of rooibos tea is calculated in Eq. (3) based on its hydrolysable fraction (H_r) and the stabilization factor S. With $W_r(t)$ and a_r known, k is calculated using Eq. (2).

Soil Analyses

At each plot, one 10 cm deep soil core was collected using an aluminum corer with a 5 cm inner diameter. Samples were systematically divided into 5 cm depth increments in the field, bagged, and placed in a cool box out of direct sunlight prior to

being returned to the laboratory for analysis. In the laboratory, soil samples were dried at 70 °C until they reached a constant weight and were then ground prior to analysis. Bulk density (BD) (g cm^3) of each sample was calculated by dividing the oven-dried mass by the volume of the sample. Samples were then homogenized using zirconium beads in a Mixer/Mill 8000D ball mill (SPEX, Metuchen, New Jersey, USA) to ensure homogeneity prior to analysis for TC, TN, loss-on-ignition (LOI), and stable isotope (δ^{13}C and δ^{15}N) measurements. Homogenized soils were subsampled and combusted using a Costech ECS 4010 CHNS-O elemental analyzer (Costech Analytical Technologies, Inc., Valencia, CA, USA) for TC and TN. Another set of subsamples were combusted at 500 °C for 4 h in a Lindberg/Blue MTM MoldathermTM box furnace (Thermo Fischer Scientific, Waltham, Massachusetts, USA) for LOI measurements, which measure SOM pools. Organic C (OC %) was calculated with the following equation (Kauffman and Donato 2012):

$$\text{Organic C}\,(\%) = 0.415 * \text{LOI}\% + 2.89 \qquad (5)$$

A third subsample was then analyzed for δ^{13}C and δ^{15}N at the Light Stable Isotope Mass Spec Lab at the University of Florida (Gainesville, FL, USA) using a continuous flow isotope ratio mass spectrometer (Thermo Electron) model Finnigan DeltaPlusXL (Thermo Scientific Corporation, USA). The δ^{13}C and δ^{15}N isotopic ratios of the sample gas were measured relative to a laboratory reference CO_2 gas. Stable isotope values were reported in delta (δ) notation in parts per thousand (‰) relative to international standards (USGS 40) that have been certified relative to Vienna Peedee Belemnite (VPDB). Precision of samples was estimated to be 0.15 permil based on measurement of 12 USGS40 standards run with samples. Delta (δ) notation in parts per thousand (‰) relative to the international standards was determined as follows:

$$\delta^{13}\text{C}\ (‰) = \left(R^{\text{sample}}/R_{\text{standard}} - 1\right) \times 1000 \qquad (6)$$

$$\delta^{15}\text{N}\ (‰) = \left(R_{\text{sample}}/R_{\text{standard}} - 1\right) \times 1000 \qquad (7)$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or $R = {}^{15}\text{N}/{}^{14}\text{N}$.

Statistical Analysis

To identify differences in environmental conditions between habitats, we tested the main effects of habitat type (saltmarsh and ecotone), blocked by site (random factor) along the latitudinal gradient, on salinity, pH, and soil temperature using a one-way analysis of variance (ANOVA). Annual average atmospheric temperature was analyzed using a one-way ANOVA by latitudinal gradient region. A linear model was created to examine differences in elevation between habitats across sites, using habitat (ecotone and saltmarsh) as a fixed effect and site as a random effect. Initial litter chemistry (C:N) for *A. germinans* and *S. alterniflora* was analyzed for differences between species using a one-way ANOVA. The main effects of litter type (*A. germinans* and *S. alternilfora*) and habitat (saltmarsh and ecotone) on litter mass remaining (%) were tested with a two-way ANOVA. Litter type and habitat were independent variables and were blocked by site (random). The main effects of habitat type (saltmarsh and ecotone), time (0, 3, 6, 9, 12 months) and their interaction on aboveground litter mass remaining (%) and k were tested using two-way ANOVAs. Habitat type and time were fixed factors within the models, which were blocked by site (random) to account for potential differences along the latitudinal gradient. Differences in mass remaining and k after 12 months between species litter (fixed factor) were analyzed with one-way ANOVAs. Belowground mass remaining (%) and k were analyzed with one-way ANOVAs, blocked by site, to test for differences between habitat types. Soil parameters (BD, LOI, TC, TN, C:N and stable isotopes values) were analyzed down the soil profile with a two-way ANOVA with depth and habitat as fixed factors. The model was blocked by site (random) to account for potential differences along the latitudinal gradient. When depth was insignificant, the factor was removed and values were reanalyzed for the main effect of habitat using a one-way ANOVA.

The 'lme4' package in R (version 3.5.2) (Bates and others 2015; Team 2017) was used to test for differences in habitat elevation and the 'DHARMa' package was used to ensure that model assumptions were met (Hartig 2017). Normality of the data used in ANOVAs 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 assumptions for linear models as noted in the results (Supplementary Table 2). If assumptions failed under transformation, the Kruskal–Wallis nonparametric test was used (Supplementary Table 2). When significant differences

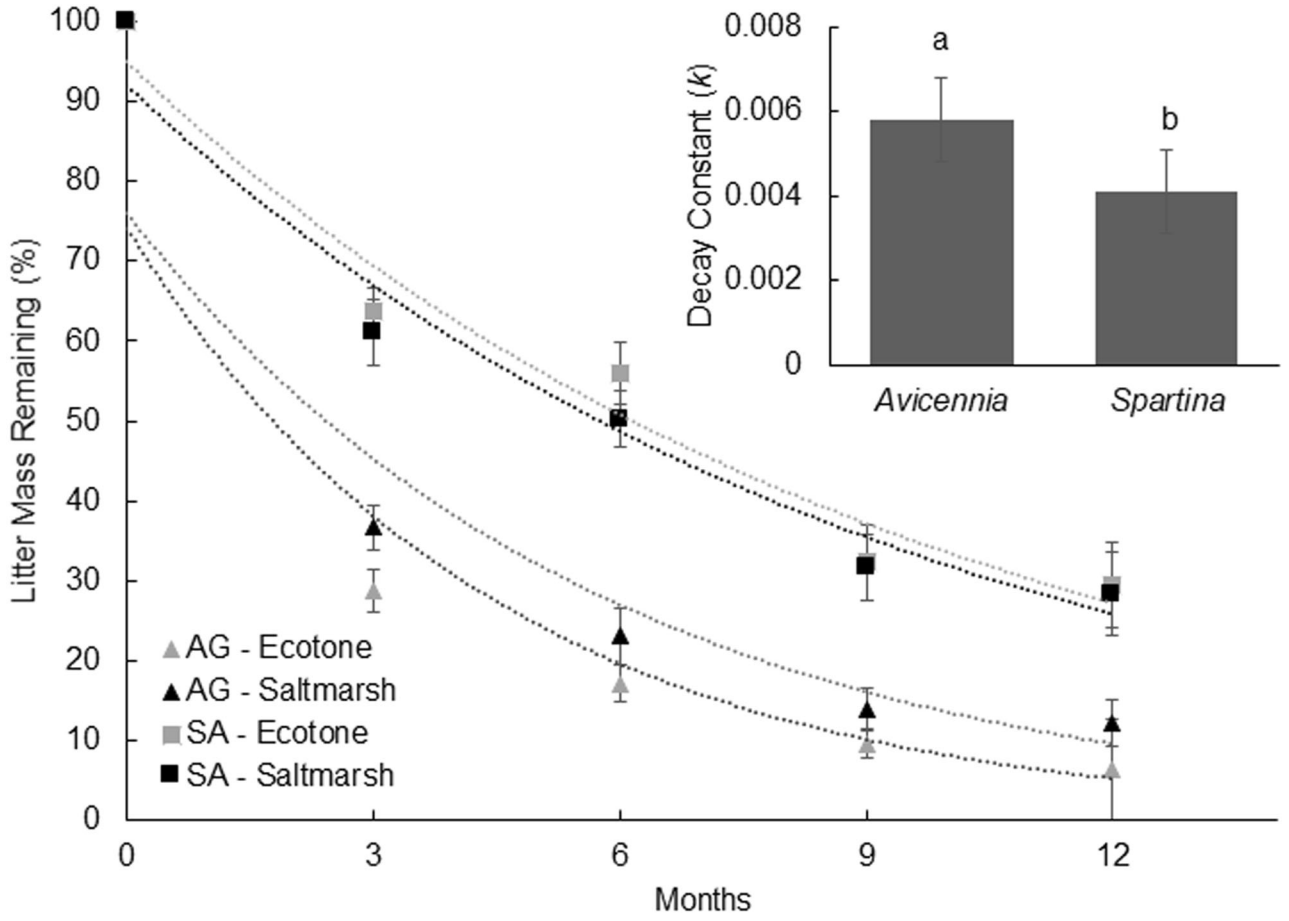

Figure 2. Mass remaining (%) of *Avicennia germinans* (AG) and *Spartina alterniflora* (SA) leaf litter after 12 months of aboveground incubation (n = 15). Dashed lines signify the exponential decay curves. Triangles denote *A. germinans* litter; black are saltmarsh plots (R^2 = 0.92) and gray are ecotone plots (R^2 = 0.95). Squares signify *S. alterniflora* litter; black are saltmarsh plots (R^2 = 0.96) and gray are ecotone plots (R^2 = 0.96). Values are means with + 1 SE. Inset graph portrays differences between species litter decay constants (n = 30). Different letters signify statistical difference.

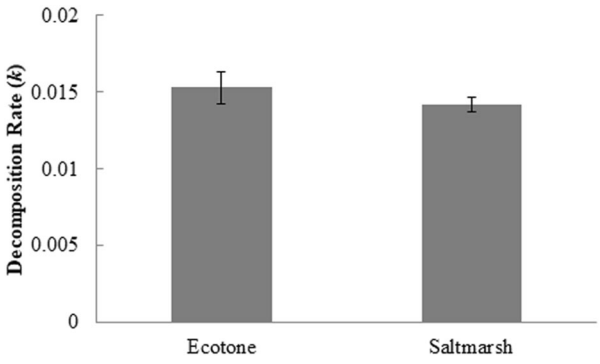

Figure 3. Decay constant (k) of teabags after 3 months of belowground incubation (n = 90). There is no significant difference between the habitats (p = 0.93).

among treatments were found, pair-wise comparisons were explored with Tukey's honestly significant differences test with alpha (α) set at 0.05. Analyses (except for elevation) were performed using JMP 14.0 (S.A.S. Inc., Cary, North Carolina, USA). Data are reported as mean ± 1 standard error (SE) throughout the manuscript.

Results

Aboveground Decomposition

Leaf litter decomposition differed between species after 12 months ($F_{1,292}$ = 49.1, $p \leq 0.0001$), regardless of habitat ($F_{1,292}$ = 0.43, p = 0.53). Differences in species decomposition rates are replete within the literature; hence individual models were used for each litter type (*A. germinans* and *S. alterniflora*) to isolate the effect of habitat type on aboveground decomposition rates. The mass of *A. germinans* leaf litter decreased over time ($F_{4,140}$ = 88.1, $p \leq 0.0001$), with no significant difference in mass remaining ($F_{1,140}$ = 8.28,

Table 2. Soil Properties Down Profile and Across Habitats

	n	Depth (cm)	Ecotone	Saltmarsh
Bulk density (g/cm^3)	15	0–5	1.17 ± 0.14	0.62 ± 0.10
	15	5–10	1.17 ± 0.16	0.67 ± 0.13
LOI (%)	15	0–5	28.6 ± 5.00	38.6 ± 6.95
	15	5–10	31.9 ± 6.05	37.1 ± 6.35
OC (%)	15	0–5	14.6 ± 2.08	18.9 ± 2.90
	15	5–10	16.2 ± 2.51	18.3 ± 2.63
Total C (%)	15	0–5	9.77 ± 1.43	13.6 ± 3.13
	15	5–10	9.70 ± 1.95	14.1 ± 3.56
Total N (%)	15	0–5	0.63 ± 0.09	1.23 ± 0.31
	15	5–10	0.85 ± 0.25	1.41 ± 0.34
C:N	15	0–5	15.2 ± 0.32	12.1 ± 0.64
	15	5–10	14.6 ± 0.86	13.7 ± 0.67
δ^{13}C	15	0–5	− 25.9 ± 0.27	− 21.3 ± 0.57
	15	5–10	− 24.3 ± 0.69	− 22.5 ± 0.67
δ^{15}N	15	0–5	1.54 ± 0.40	2.63 ± 1.26
	15	5–10	2.23 ± 0.27	2.70 ± 0.37

Values shown as mean ± 1 SE.

Table 3. Two-Way ANOVA Summaries Performed on Soil Variables

	Bulk density (g/cm^3)	LOI (%)	Organic C (%)	Total N (%)	Total C (%)	CN	δ^{13}C	δ^{15}N
Habitat	24.61***	0.556	0.021	1.700	0.039	11.28**	30.48***	4.635*
Depth	0.015	0.002	1.526	0.007	0.575	1.316	0.092	1.126
Habitat × depth	0.021	0.080	0.167	1.162	0.0007	1.512	6.213***	0.729

Habitat (ecotone, saltmarsh); Depth (0–5, 5–10). LOI = loss-on-ignition. N = 15 cores per habitat, N = 30 samples per depth. Values are F-statistics
**p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.0001.*

$p = 0.09$) or decay rates after 12 months ($F_{1,23} = 3.43$, $p = 0.08$) between habitats (Figure 2). Similarly, the mass of *S. alterniflora* litter decreased over time ($F_{4,140} = 92.3$, $p \leq 0.0001$), with no significant differences in mass remaining ($F_{1,140} = 0.92$, $p = 0.34$) or decay rates ($F_{1,23} = 0.01$, $p = 0.90$) between habitats (Figure 2). When analyzed as a fixed factor, there was significantly more *S. alterniflora* litter remaining after 12 months than *A. germinans* litter, regardless of habitat ($F_{1,58} = 20.5$, $p \leq 0.0001$). In addition, *A. germinans* decomposed at a faster rate than *S. alterniflora* ($F_{1,52} = 15.3$, $p = 0.0003$) (Figure 2). The C:N of *S. alterniflora* (36.7 ± 2.26) was significantly higher than that of *A. germinans* (25.8 ± 0.76) ($F_{1,47} = 37.08$, $p \leq 0.0001$).

Belowground Decomposition

The belowground decay constant (k) (Figure 3) and stabilization factor (S) did not differ between ecotone and saltmarsh plots ($F_{1,66} = 0.01$, $p = 0.93$, $F_{1,71} = 0.28$, $p = 0.60$; respectively). k averaged 0.014 ± 0.0005 and S averaged − 0.045 ± 0.015 across habitats. After 3 months, the green and rooibos tea bags stabilized at 82.2 ± 1.08 ($F_{1,71} = 0.31$, $p = 0.58$) and 41.7 ± 0.71 ($F_{1,78} = 0.62$, $p = 0.43$) % mass remaining, respectively, regardless of habitat.

Soil Analyses

Soil TN, TC, LOI and OC were not significantly different across habitats or down soil profile (Tables 2 and 3). Bulk density and C:N were greater in ecotonal soils but did not vary down the soil profile (Tables 2 and 3). There were no significant differences in δ^{13}C ($p = 0.68$) or δ^{15}N ($p = 0.57$) stable isotopes or C:N ($p = 0.46$) down the soil profiles of either habitat. However, δ^{13}C (‰) was significantly lower in ecotone plots (− 25.1 ± 0.37) than in saltmarsh plots (− 21.8 ± 0.44) and soil δ^{15}N (‰) was greater in ecotone plots (2.67 ± 0.24) than in saltmarsh plots

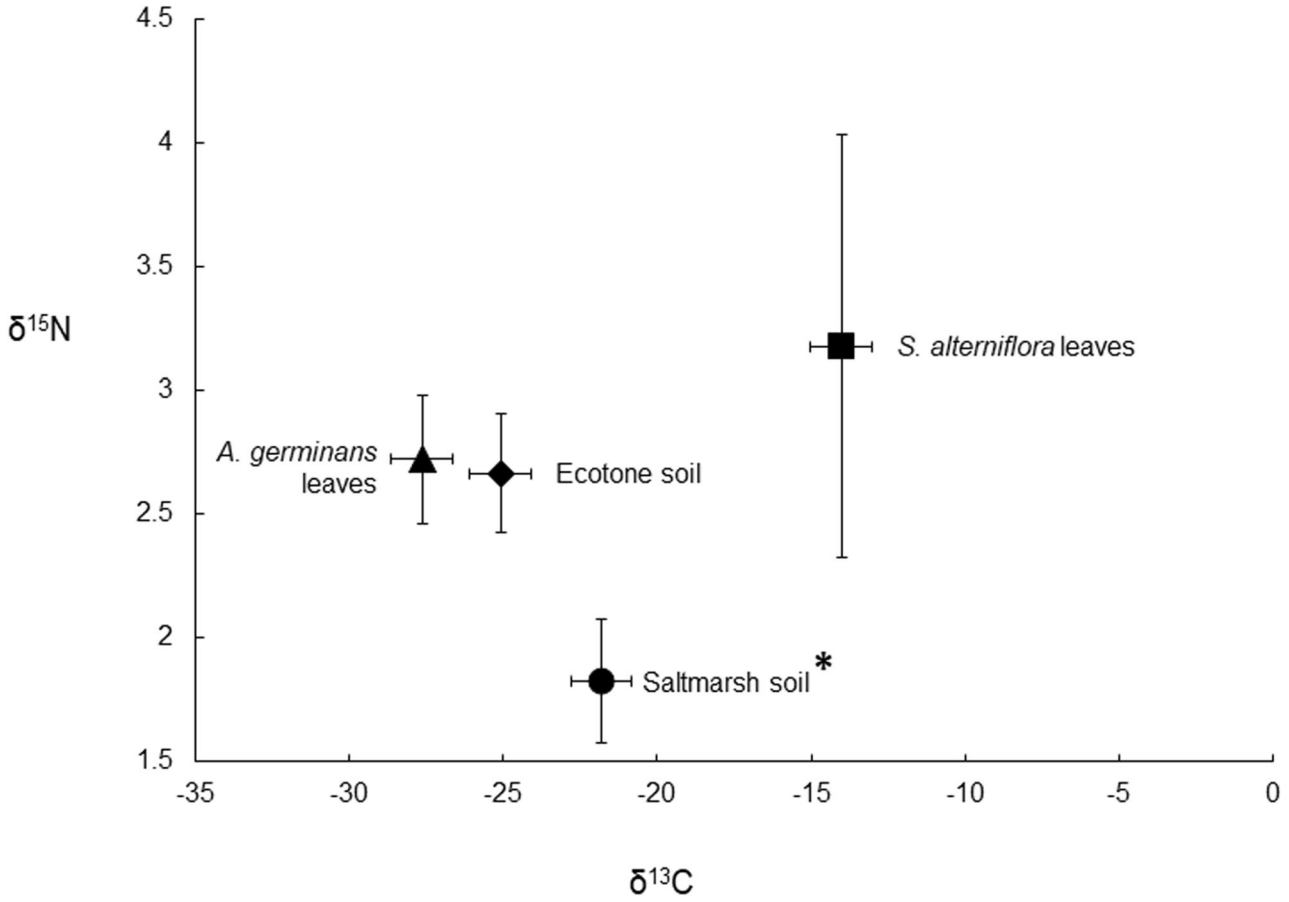

Figure 4. Biplot of δ^{15}N and δ^{13}C stable isotopes values for habitat soils and vegetation. Markers represent means ± 1 SE. Asterisk denotes δ^{15}N of saltmarsh soil is significantly different from ecotonal soils and species biomass. *Spartina* leaves (n = 6), *Avicennia* leaves (n = 20), ecotonal soil (n = 30), saltmarsh soil (n = 30).

(1.85 ± 0.27) (Table 3, Figure 4). There were no differences in species leaf litter δ^{15}N (‰) values ($F_{1,24}$ = 0.48, p = 0.49), but δ^{13}C (‰) fractions were significantly greater in *S. alterniflora* (C_4) leaf litter than in *A. germinans* (C_3) leaf litter ($F_{1,25}$ = 34.1, $p \leq 0.0001$) (Figure 4).

Discussion

Aboveground litter decomposition rates in habitats experiencing mangrove encroachment were driven by differences in species litter quality, not that of habitat structure. Furthermore, δ^{15}N isotope values were lower in saltmarsh soils than in ecotone soils, even though belowground decomposition was similar between habitats. Taken together, these results suggest that mangrove encroachment into saltmarsh habitat will drive changes in decomposition rates through changes in the quality of litter provided by mangrove and marsh foundation species, rather than differences in environmental conditions between habitats.

Differences in decomposition rates of aboveground tissues in this study reflected initial litter chemistry, not the environment in which decomposition occurred. C:N can be an important control for decomposition (Valiela and others 1984; Enríquez and others 1993); plant matter with high C:N ratios (refractory, low quality) generally decomposes more slowly than material with low C:N ratios (labile, high quality) (Webster and Benfield 1986; Enriquez and others 1993). Although all species lost a significant fraction of litter mass in the first few months of the study, *S. alterniflora* had more mass remaining after 12 months (369 days), likely due to its high C:N. These findings corroborate and expand on previous work demonstrating that *A. germinans* leaves decomposed significantly faster than *S. alterniflora* after 69 (Perry and Mendelssohn 2009), and 214 days (Smith and others 2018) of aboveground incubation. The longer incubation period of this study, which encompassed annual temperature differences, confirmed that *A. germinans* decom-

posed faster than *S. alterniflora*, regardless of habitat. The quick turnover of *A. germinans* litter relative to that of marsh species suggests that mangrove encroachment will increase the ecosystem's overall decomposition rate through the input of highly labile plant material. Increases in the inputs of labile C should also increase the release of nutrients from that litter, thereby altering the formation of SOM (Berg and McClaugherty 2003) and nutrient cycling in the system.

However, the formation of SOM is mediated by the decomposition of both above- and belowground biomass. Although we did not measure species-specific differences in root litter quality and decay, Perry and Mendelssohn (2009) found that *A. germinans* roots degraded faster than *S. alterniflora* roots. Globally, mangrove roots decay faster than saltmarsh roots, which is driven by species identity and root stoichiometry rather than the abiotic environment (Ouyang and others 2017). However, by holding substrate quality consistent using the TBI protocol, we isolated the abiotic effects of habitat on belowground decomposition. There were no differences in salinity, pH, soil temperature and flooding (that is, plot elevation) between habitat types. These similarities in habitat characteristics could explain the consistent belowground decomposition rates across habitats when litter quality is held consistent, which was also seen in Mueller and others (2018) and Perry and Mendelssohn (2009). Decomposition proceeds slowly as soil moisture content increases (Reddy and Delaune 2008) and redox potential decreases (Van der Valk and Attiwill 1983; Mendelssohn and others 1999). Although *A. germinans* has pneumatophores that facilitate oxygen transport to roots, this species occurs in waterlogged conditions that could override the benefits of an oxygenated rhizosphere (Ouyang and others 2017). Thus, the slow decay rate of belowground tissues likely reflects the inhibitory effect of flooding and anaerobic soil conditions that are commonplace in wetland ecosystems, which could ultimately contribute to SOM accumulation.

Although fractions of aboveground litter and dead roots are both microbially mineralized, the relative contribution of shoot versus root litter to the soil C pool will be disproportionate due to species- and tissue-specific differences in litter quality, regardless of habitat. In this study, only 10–30% of aboveground litter remained after 1 year, which is likely an overestimation due to the litterbag method employed. Leaf litter is, to varying extents, exported by tides or shredded by crabs (Lee and others 2014) and other detritivores, the effects of which were not documented in this study. Consequently, leaf litter likely contributes relatively little to SOM formation in this system, with the relative contributions by species differing based on litter quality. Additionally, belowground decomposition is significantly slower than aboveground decomposition (for example, Reddy and Delaune 2008), suggesting that greater resource allocation to the production of roots and rhizomes, through the encroachment of mangroves, would stimulate organic matter accumulation. Middleton and McKee (2001) found that it took 10 years for 90% turnover of mangrove roots in a Belizean forest, whereas 90% turnover of leaf litter biomass took about 1 year in this study. Furthermore, mangrove leaf litter decomposed more rapidly than roots in other mangrove ecosystems (McKee and Faulkner 2000; Middleton and McKee 2001), and fine roots contributed the most material ($> 90\%$) to SOM accumulation in four different mangrove forest types (Liu and others 2017). This pattern of root-driven inputs to SOM is supported by $\delta^{13}C$ values of ecotone and saltmarsh soils, which suggest that all buried organic matter is from roots, not leaves (Simpson and others 2019). Because roots and organic matter are produced and accumulate under anaerobic conditions (Webster and Benfield 1986), an increase in production of belowground tissues, whether through shifts in biomass allocation or foundation species cover, should lead to the accumulation of slowly decaying material, which can then contribute to SOM accretion and C storage.

Although above- and belowground decomposition rate did not vary with differences in habitat structure, changes in species litter quantity and quality, coupled with disparate microbial community structure, may induce changes in ecosystem nutrient cycling. There were no differences in natural $\delta^{15}N$ abundance of species' leaves, due in part to the large variability of $\delta^{15}N$ in *S. alterniflora*, which can vary depending on the stage at which the leaf was collected (for example, Currin and others 1995) and the environmental conditions in which it was growing (Wigand and others 2007; Bannon and Roman 2008). However, microbial community structure has been shown to differ between mangrove and saltmarsh dominated systems (Barreto and others 2018), suggesting that transformations and mineralization of plant biomass nutrients may vary between habitats, regardless of resulting TN and TC. Although the variability *S. alterniflora* $\delta^{15}N$ biomass abundance is hard to elucidate in this study, soils are a good integrator of biomass variance, and soil $\delta^{15}N$ values

reflect the net effect of N-cycling processes as influenced by the biotic and abiotic environment (Liao and others 2006). At the ecosystem level, soil δ^{15}N values are influenced by a number of factors, such as quality and quantity of organic matter inputs, soil N sources, and isotopic fractionation resulting from N transformations (Nadelhoffer and others 1996; Piccolo and others 1996).

Natural δ^{15}N abundance in bulk soil is related to the degree of organic matter humification, increasing with a higher degree of decomposition (Turner and others 1983). Soil N is an important component of SOM, and greatly influences SOM decomposition and humification rates. Habitats in this study did not differ in TN, and therefore SOM or OC, supporting prior research documenting N-limitation in mangroves along the Atlantic Coast of Florida (Feller and others 2007, 2009; Dangremond and others 2019) as well as in saltmarshes under high salinity regimes (for example, Crain 2007). Under N-limited conditions, isotopic fractionation is expected to be low, because all N is used, regardless of isotopic ratio (Montoya and Mccarthy 1995; Evans and others 1996). δ^{15}N values in this study were within the range of δ^{15}N values found in the N-limited mangrove dominated soils in Belize (McKee and others 2002; Wooller and others 2003) and Brazil (Reis and others 2017), as well as N-limited saltmarsh dominated soils of Massachusetts (Kinney and Valiela 2013) and Portugal (Castro and others 2007). Because all abiotic variables were similar between habitats, litter quality of *A. germinans*, coupled with habitat specific microbial community, could drive the difference in soil δ^{15}N abundance seen in this study. Turner and others (1983) found that δ^{15}N increased in soils treated with plant material rich in N. In addition, low δ^{15}N fractionation was found in the phosphorous-limited mangroves of the Florida Everglades (Mancera and others 2009) and the nutrient limited mangroves of Belize (McKee and others 2002). Although the mechanisms underlying δ^{15}N accumulation are not well understood, it is thought to be the result of microbial heterotroph metabolism (Nadelhoffer and Fry 1994). Hence, differences in natural δ^{15}N abundance between habitats, without accompanying differences in habitat SOM, suggest that the microbial decomposer community had limited energy to break down more complex components of SOM, with saltmarsh plots being more limited than ecotonal plots. Collectively, the work presented here suggests that mangrove encroachment may alter nutrient cycling indirectly by providing higher quality, N-enriched organic matter sources to the system. By increasing N availability through a labile C source (for example, *A. germinans* leaves), mangrove biomass production may increase, and if there is no change in decomposition rate, especially belowground, this may ultimately cause an increase in the belowground C accumulation in the system.

Conclusions

Woody encroachment may not modify the environmental factors driving decomposition, but changes in foundation plant species cover may ultimately alter nutrient cycling within habitats through shifts in the quality of litter input. Shifts from herbaceous to woody species have altered nutrient cycling though changes in litter quality input in mountain grasslands (Montané and others 2010), tallgrass prairies (Norris and others 2001), and subtropical savannahs (Boutton and others 2009) suggesting that alterations in litter dynamics may alter regional biogeochemical processes globally. In this study, ecotonal and saltmarsh habitats displayed similar belowground decay rates, whereas species litter quality drove differences in aboveground decomposition rate over time, regardless of habitat. Increases in *A. germinans* litter input with mangrove encroachment should introduce more labile material into the system, which may increase nutrient availability and further facilitate encroachment (Dangremond and others 2019). However, due to the waterlogged, anaerobic conditions of these systems, belowground decomposition will be slower regardless of vegetation and may not change with encroachment. The belowground C fractions in this system originate mainly from root organic matter (Simpson and others 2019), suggesting that although leaves decompose faster and will provide more readily available nutrients to the system, the long-term soil C fraction will be composed of slowly decomposed roots. If there is no change in decomposition rate, but an increase in a labile C source (for example, *A. germinans* leaves) and belowground root growth with encroachment, this may lead to an increase in the belowground C accumulation in the system. As woody expansion into grasslands continues with climate change, understanding the factors that influence decomposition is of critical importance to ecosystem maintenance and stability.

Acknowledgements

This research was funded by the National Aeronautics and Space Administration (NASA) Climate and Biological Response program (NNX11AO94G)

and the National Science Foundation (NSF) MacroSystems Biology program (EF1065821). The authors would like to thank Florida State Parks, the Merritt Island National Wildlife Refuge, Guana Tolomato Matanzas National Estuarine Research Reserve, and Canaveral National Seashore for permits and unabridged access to their parks. We also thank K.V. Curtis for laboratory nutrient analysis and T.Z. Osborne, L.J. Duckett, M.H. Lehmann and Z.R. Foltz for field and technical assistance. We sincerely thank the three anonymous reviewers for their edits and suggestions, which greatly improved this manuscript. This is Contribution No. 1144 of the Smithsonian Marine Station.

REFERENCES

Ainley LB, Bishop MJ. 2015. Relationships between estuarine modification and leaf litter decomposition vary with latitude. Estuar Coast Shelf Sci 164:244–52.

Alongi DM. 2014. Carbon cycling and storage in Mangrove forests. Ann Rev Mar Sci 6:195–219.

Archer SR, Anderson EM, Predick KI, Schwimming S, Steidl RJ, Woods SR. 2017. Rangeland Systems: processes, management and challenges. (Burdick DM, editor.). New York: Springer

Armitage AR, Highfield WE, Brody SD, Louchouarn P. 2015. The contribution of mangrove expansion to salt marsh loss on the Texas Gulf Coast. PLoS ONE 10:1–17. https://doi.org/10.1371/journal.pone.0125404.

Bannon RO, Roman CT. 2008. Using stable isotopes to monitor anthropogenic nitrogen inputs to estuaries. Ecol Appl 18:22–30.

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR. 2011. The value of estuarine and coastal ecosystem services. Ecol Monogr 81:169–93.

Barreto CR, Morrissey EM, Wykoff DD, Chapman SK. 2018. Co-occurring mangroves and salt marshes differ in microbial community composition. Wetlands 38:497–508.

Bates D, Mächler M, Bolker BM, Walker SC. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–43.

Berg B, McClaugherty C. 2003. Plant litter decomposition, humus formation, carbon sequestration. Berlin: Springer.

Bertin C, Yang X, Weston LA. 2003. The role of root exudates and allelochemicals in the rhizosphere. Plant Soil 256:67–83.

Boutton TW, Liao JD, Filley TR, Archer SR. 2009. Belowground carbon storage and dynamics accompanying woody plant encroachment in a subtropical savanna. In: Soil carbon sequestration and the greenhouse effect, vol 57, pp 181–205.

Castro P, Valiela I, Freitas H. 2007. Eutrophication in Portuguese estuaries evidenced by δ15N of macrophytes. Mar Ecol Prog Ser 351:43–51.

Cavanaugh KC, Dangremond EM, Doughty CL, Park Williams A, Parker JD, Hayes MA, Rodriguez W, Feller IC. 2019. Climate-driven regime shifts in a mangrove–salt marsh ecotone over the past 250 years. Proc Natl Acad Sci USA 116:21602–8.

Cavanaugh KC, Kellner JR, Forde AJ, Gruner DS, Parker JD, Rodriguez W, Feller IC. 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. Proc Natl Acad Sci USA 111:723–7.

Chen J, Franklin JF, Spies TA. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. Agric For Meteorol 63:219–37.

Choi Y, Hsieh Y, Wang Y. 2001. Vegetation succession and carbon sequestration in a coastal wetland in northwest Florida: evidence from carbon isotopes. Global Biogeochem Cycles 15:311–19.

Comeaux RS, Allison MA, Bianchi TS. 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.

Crain C. 2007. Shifting nutrient limitation and Eutrophication effects in marsh vegetation across estuarine salinity gradients. Estuar Coasts 30:26–34.

Currin CA, Newell SY, Paerl HW. 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. Mar Ecol Prog Ser 121:99–116.

D'Odorico P, He Y, Collins S, De Wekker SFJ, Engel V, Fuentes JD. 2013. Vegetation-microclimate feedbacks in woodland-grassland ecotones. Glob Ecol Biogeogr 22:364–79.

Dangremond EM, Simpson LT, Osborne TZ, Feller IC. 2019. Nitrogen enrichment accelerates mangrove range expansion in the temperate–tropical ecotone. Ecosystems 23:703–14.

Devaney JL, Lehmann M, Feller IC, Parker JD. 2017. Mangrove microclimates alter seedling dynamics at the range edge. Ecology 98:2513–20.

Doyle TW, Krauss KW, Conner WH, From AS. 2010. Predicting the retreat and migration of tidal forests along the northern Gulf of Mexico under sea-level rise. For Ecol Manag 259:770–7.

Duarte CM, Losada IJ, Hendriks IE, Mazarrasa I, Marbà N. 2013. The role of coastal plant communities for climate change mitigation and adaptation. Nat Clim Chang 3:961–8.

Durango-Cordero J, Satyanarayana B, Zhang B. 2013. Vegetation structure at Zhangiang Mangrove National Nature Reserve (ZMNNR), P.R. China: acomparison between original and non-original trees using ground truthing, remote sensing and GIS techniques.

Ehrenfeld JG. 2010. Ecosystem consequences of biological invasions. Annu Rev Ecol Evol Syst 41:59–80.

Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J, Orwig DA, Rodenhouse NL, William V, Stinson KA, Stone JK, Swan CM, Thompson J, Holle V, Webster JR, Ellisonl AM, Bank MS, Clinton BD, Colburnm EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J, Orwig DA, Rodenhouse NL, Sobczak WV, Stinson KA, Stone JK, Swan CM, Thompson J, Von Holle B, Webster JR. 2005. Loss of foundation species: consequences for the structure and dynamics of forest ecosystems. Front Ecol Environ 3:479–86.

Enríquez S, Duarte CM, Sand-Jensen K. 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. Oecologia 94:457–71.

Eslami-Andargoli L, Dale P, Sipe N, Chaseling J. 2009. Mangrove expansion and rainfall patterns in Moreton Bay, Southeast Queensland, Australia. Estuar Coast Shelf Sci 85:292–8. https://doi.org/10.1016/j.ecss.2009.08.011.

Evans RD, Bloom AJ, Sukrapanna SS, Ehleringer JR. 1996. Nitrogen isotope composition of tomato (*Lycopersicon esculen-*

tum Mill. cv. T-5) grown under ammonium or nitrate nutrition. Plant Cell Environ 19:1317–23.

Feher LC, Osland MJ, Griffith KT, Grace JB, Howard RJ, Stagg CL, Enwright NM, Krauss KW, Gabler CA, Day RH, Rogers K. 2017. Linear and nonlinear effects of temperature and precipitation on ecosystem properties in tidal saline wetlands. Ecosphere 8:2–23.

Feller IC, Lovelock CE, McKee KL. 2007. Nutrient addition differentially affects ecological processes of *Avicennia germinans* in nitrogen versus Phosphorus limited mangrove ecosystems. Ecosystems 10:347–59. https://doi.org/10.1007/s10021-007-9025-z. Last accessed 02/08/2011

Feller IC, Lovelock CE, Piou C. 2009. Growth and nutrient conservation in Rhizophora mangle in response to fertilization along latitudinal and tidal gradients. Smithson Contrib Mar Sci 38:345–58.

Gallagher JL. 1975. Effect of an ammonium nitrate pulse on the growth and elemental composition of natural stands of *Spartina alterniflora* and *Juncus roemerianus*. Am J Bot 62:644–8.

Guo H, Weaver C, Charles SP, Whitt A, Dastidar S, D'Odorico P, Fuentes JD, Kominoski JS, Armitage AR, Pennings SC. 2017. Coastal regime shifts: Rapid responses of coastal wetlands to changes in mangrove cover. Ecology 98:762–72.

Hartig F. 2017. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.1, 5(5).

Hughes RF, Archer SR, Asner GP, Wessman CA, McMurtry C, Nelson J, Ansley RJ. 2006. Changes in aboveground primary production and carbon and nitrogen pools accompanying woody plant encroachment in a temperate savanna. Glob Change Biol 12:1733–47.

IPCC. 2014. Climate change 2014: Synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. (Pachauri RK, Meyer LA, editors.). Geneva: IPCC

Jones JA, Cherry JA, McKee KL. 2016. Species and tissue type regulate long-term decomposition of brackish marsh plants grown under elevated CO2 conditions. Estuar Coast Shelf Sci 169:38–45. https://doi.org/10.1016/j.ecss.2015.11.033.

Kauffman JB, Donato DC. 2012. Protocols for the measurement, monitoring and reporting of structure, biomass and carbon stocks in mangrove forests. Cent Int For Res 86:40. http://www.amazonico.org/speclab/SiteAssets/SitePages/Methods/Mangrove-biomass-CIFOR.pdf

Keuskamp JA, Dingemans BJJ, Lehtinen T, Sarneel JM, Hefting MM. 2013. Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems. Methods Ecol Evol 4:1070–5.

Kinney EL, Valiela I. 2013. Changes in δ15 N in salt marsh sediments in a long-term fertilization study. Mar Ecol Prog Ser 477:41–52.

Lee SY, Primavera JH, Dahdouh-Guebas F, Mckee K, Bosire JO, Cannicci S, Diele K, Fromard F, Koedam N, Marchand C, Mendelssohn I, Mukherjee N, Record S. 2014. Ecological role and services of tropical mangrove ecosystems: a reassessment. Glob Ecol Biogeogr 23:726–43.

Lee TM, Yeh HC. 2009. Applying remote sensing techniques to monitor shifting wetland vegetation: a case study of Danshui River estuary mangrove communities. Taiwan. Ecol Eng 35:487–96.

Leopold A, Marchand C, Deborde J, Chaduteau C, Allenbach M. 2013. Influence of mangrove zonation on CO_2 fluxes at the sediment-air interface (New Caledonia). Geoderma 202–203:62–70.

Liao JD, Boutton TW, Jastrow JD. 2006. Organic matter turnover in soil physical fractions following woody plant invasion of grassland: Evidence from natural 13C and 15N. Soil Biol Biochem 38:3197–210.

Liu X, Xiong Y, Liao B. 2017. Relative contributions of leaf litter and fine roots to soil organic matter accumulation in mangrove forests. Plant Soil 421:493–503.

Lovelock CE, Adame MF, Bennion V, Hayes M, O'Mara J, Reef R, Santini NS. 2014. Contemporary rates of carbon sequestration through vertical accretion of sediments in mangrove forests and saltmarshes of South East Queensland, Australia. Estuaries and Coasts 37:763–71.

Mancera JE, Twilley RR, Rivera-monroy VH. 2009. Carbon (Δ13C) and nitrogen (Δ15 N) isotopic discrimination in mangroves in Florida Coastal Everglades as a function of environmental stress. Contrib Mar Sci 38:109–29.

McKee KL, Faulkner PL. 2000. Mangrove peat analysis and reconstruction of vegetation history at the Pelican Cays, Belize. Atoll Res Bull 468:47–58.

McKee KL, Feller IC, Popp M, Wanek W. 2002. Mangrove isotopic (δ15 N and δ13C) fractionation across a nitrogen vs. phosphorus limitation gradient. Ecology 83:1065–75.

McKee KL, Mendelssohn IA, Hester MW. 1988. Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of Rhizophora mangle and *Avicennia germinans*. Am J Bot 75:1352–9.

McKee KL, Rooth JE, Feller IC. 2007. Mangrove recruitment after forest disturbance is facilitated by herbaceous species in the Caribbean. Ecol Appl 17:1678–93.

McLatchey GP, Reddy KR. 1998. Regulation of organic matter decompostion and nutrient release in a wetland soil. J Environ Qual 27:1268–74.

Mendelssohn IA, Sorrell BK, Brix H, Schierup HH, Lorenzen B, Maltby E. 1999. Controls on soil cellulose decomposition along a salinity gradient in a Phragmites australis wetland in Denmark. Aquat Bot 64:381–98.

Middleton BA, McKee KL. 2001. Degradation of mangrove tissues and implications for peat formation in Belizean island forests. J Ecol 89:818–28.

Montané F, Romanyà J, Rovira P, Casals P. 2010. Aboveground litter quality changes may drive soil organic carbon increase after shrub encroachment into mountain grasslands. Plant Soil 337:151–65.

Montoya JP, Mccarthy JJ. 1995. Isotopic fractionation during nitrate uptake by phytoplankton grown in continuous culture. J Plankton Res 17:439–64.

Moore T, Blodau C, Turunen J, Roulet N, Richard PJH. 2004. Patterns of nitrogen and sulfur accumulation and retention in ombrotrophic bogs, eastern Canada. Glob Chang Biol 11:356–67.

Mueller P, Schile-Beers LM, Mozdzer TJ, Chmura GL, Dinter T, Kuzyakov Y, De Groot AV, Esselink P, Smit C, D'Alpaos A, Ibáñez C, Lazarus M, Neumeier U, Johnson BJ, Baldwin AH, Yarwood SA, Montemayor DI, Yang Z, Wu J, Jensen K, Nolte S. 2018. Global-change effects on early-stage decomposition processes in tidal wetlands-implications from a global survey using standardized litter. Biogeosciences 15:3189–202.

Nadelhoffer KJ, Fry B. 1994. Nitrogen isotope studies in forest ecosystems. In: Stable isotopes in ecology and environmental science (Lajtha K, Michener R, editors), pp 23–44.

Nadelhoffer K, Shaver G, Fry B, Giblin A, Johnson L, Mckane R. 1996. 15N natural abundances and use by tundra plants. Oecologia 107:386–94.

Norris MD, Blair JM, Johnson LC. 2001. Land cover change in eastern kansas: Litter dynamics of closed-canopy eastern redcedar forests in tallgrass prairie. Can J Bot 79:214–22.

Osland MJ, Feher LC, Griffith KT, Cavanaugh KC, Enwright NM, Day RH, Stagg CL, Krauss KW, Howard RJ, Grace JB, Rogers K. 2017. Climatic controls on the global distribution, abundance, and species richness of mangrove forests. Ecol Monogr 87:341–59.

Ouyang X, Lee SY, Connolly RM. 2017. The role of root decomposition in global mangrove and saltmarsh carbon budgets. Earth-Science Rev 166:53–63. https://doi.org/10.1016/j.earscirev.2017.01.004.

Perry CL, Mendelssohn IA. 2009. Ecosystem effects of expanding populations of *Avicennia germinans* in a Louisiana salt marsh. Wetlands 29:396–406.

Piccolo MC, Neill C, Melillo JM, Cerri CC, Steudler PA. 1996. 15N natural abundance in forest and pasture soils of the Brazilian Amazon Basin. Plant Soil 182:249–58.

Power ME, Parker MS, Wootton JT. 1996. Disturbance and food chain lengths in rivers. Boston, MA: Springer.

Prescott CE. 2010. Litter decomposition: What controls it and how can we alter it to sequester more carbon in forest soils? Biogeochemistry 101:133–49.

Ratajczak Z, Nippert JB, Collins SL. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Ecology 93:697–703.

Reddy KR, Delaune RD. 2008. Biogeochemisty of Wetlands. Boca Raton: CRC Press.

Reis CRG, Nardoto GB, Rochelle ALC, Vieira SA, Oliveira RS. 2017. Nitrogen dynamics in subtropical fringe and basin mangrove forests inferred from stable isotopes. Oecologia 183:841–8.

Rodriguez W, Feller IC, Cavanaugh KC. 2016. Spatio-temporal changes of a mangrove–saltmarsh ecotone in the northeastern coast of Florida, USA. Glob Ecol Conserv 7:245–61. https://doi.org/10.1016/j.gecco.2016.07.005.

Ross MS, Meeder JF, Sah JP, Ruiz PL, Telesnicki GJ. 2000. The Southeast saline Everglades revisited: 50 years of coastal vegetation change. J Veg Sci 11:101–12.

Saintilan N, Rogers K. 2015. Woody plant encroachment of grasslands: a comparison of terrestrial and wetland settings. New Phytol 205:1062–70.

Saintilan N, Williams RJ. 1999. Mangrove transgression into saltmarsh environments in south-east Australia. Glob Ecol Biogeogr 8:117–24. https://doi.org/10.1046/j.1365-2699.1999.00133.x

Saintilan N, Wilson NC, Rogers K, Rajkaran A, Krauss KW. 2014. Mangrove expansion and salt marsh decline at mangrove poleward limits. Glob Chang Biol 20:147–57.

Simpson LT, Feller IC, Chapman SK. 2013. Effects of competition and nutrient enrichment on *Avicennia germinans* in the salt marsh-mangrove ecotone. Aquat Bot 104:55–9.

Simpson LT, Osborne TZ, Duckett LJ, Feller IC. 2017. Carbon Storages along a Climate Induced Coastal Wetland Gradient. Wetlands 37:1023–35.

Simpson LT, Stein CM, Osborne TZ, Feller IC. 2019. Mangroves dramatically increase carbon storage after 3 years of encroachment. Hydrobiologia 0123456789:1–14. https://doi.org/10.1007/s10750-019-3905-z

Skelton NJ, Allaway WG. 1996. Oxygen and pressure changes measured in situ during flooding in roots of the Grey Mangrove *Avicennia marina* (Forssk.) Vierh. Aquat Bot 54:165–75.

Smith RS, Blaze JA, Osborne TZ, Byers JE. 2018. Facilitating your replacement? Ecosystem engineer legacy affects establishment success of an expanding competitor. Oecologia 188:251–62. https://doi.org/10.1007/s00442-018-4184-5.

Stevens PW, Fox SL, Montague CL. 2006. The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. Wetl Ecol Manag 14:435–44.

Team R. 2017. R: a language and Environment for Statistical Computing, Vienna, Austria. https://www.R-project.org.

Turner GL, Bergersen FJ, Tantala H. 1983. Natural enrichment of 15N during decomposition of plant material in soil. Soil Biol Biochem 15:495–7.

Valiela I, Wilson J, Buchsbaum R, Rietsma C, Bryant D, Foreman K, Teal J. 1984. Importance of chemical composition of salt marsh litter on decay rates and feeding by detritivores. Bull Mar Sci 35:261–9.

Van der Valk AG, Attiwill PM. 1983. Above-and below-ground litter decomposition in an Australian salt marsh. Aust J Ecol 8:441–7.

Webster JR, Benfield EF. 1986. Vascular plant breakdown in freshwater ecosystems. Annu Rev Ecol Evol Syst 17:567–94.

Wigand C, McKinney RA, Cole ML, Thursby GB, Cummings J. 2007. Varying stable nitrogen isotope ratios of different coastal marsh plants and their relationships with wastewater nitrogen and land use in New England, USA. Environ Monit Assess 131:71–81.

Wooller M, Smallwood B, Jacobson M, Fogel M. 2003. Carbon and nitrogen stable isotopic variation in *Laguncularia racemosa* (L.) (white mangrove) from Florida and Belize: implications for trophic level studies. Hydrobiologia 499:13–23.

Yando ES, Osland MJ, Hester MW. 2018. Microspatial ecotone dynamics at a shifting range limit: plant–soil variation across salt marsh–mangrove interfaces. Oecologia 187:319–31. https://doi.org/10.1007/s00442-018-4098-2.