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Characterization of coastal wetland soil organic matter: Implications for wetland submergence

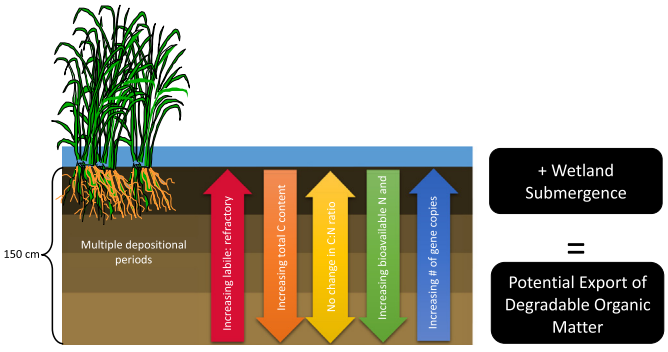
Havalend E. Steinmuller, Lisa G. Chambers *

Department of Biology, University of Central Florida, 4000 Central Florida Blvd., Orlando, FL 32816, United States of America

HIGHLIGHTS

- Ratios of labile: refractory carbon decreased with soil depth.
- Total soil carbon content increased with soil depth.
- High concentrations of bioavailable nitrogen and phosphorus are present at depth.
- Overall, high carbon quality down to 150 cm

GRAPHICAL ABSTRACT



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ABSTRACT

High rates of relative sea level rise can cause coastal wetland submergence, jeopardizing the stability of soil organic matter (SOM) sequestered within wetlands. Following submergence, SOM can be lost through mineralization, exported into the coastal ocean, or reburied within adjacent subtidal sediments. By combining measures of soil physicochemical properties, microbial community abundance, organic carbon fractionation, and stable isotope signatures, this study characterized subsurface SOM within a coastal wetland to inform its potential fate under altered environmental conditions. Nine soil cores were collected to a depth of 150 cm from a wetland currently experiencing rapid erosion and submergence within Barataria Bay, LA (USA), and were sectioned into 10 cm intervals. Each soil segment was analyzed to determine total carbon (C), nitrogen (N), phosphorus (P), and stable isotope ($\delta^{13}C$ and $\delta^{15}N$) content, as well as extractable ammonium (NH_4^+), nitrate (NO_3^-), and soluble reactive phosphorus (SRP). Extractable NH_4^+ and SRP concentrations increased 7× and 11×, respectively, between 0–10 cm and 130–140 cm. Through quantitative PCR, number of gene copies of bacteria and sulfate reduction genes were found to decrease with depth while there was no change in number of gene copies of archaea. This study also demonstrated only small decreases in labile: refractory C ratios with depth; by combining $\delta^{15}N$ data with labile:refractory C ratios and no observed change in C:N ratios with depth, we inferred the presence of minimally processed organic material within deep soils and high nutrient availability, challenging the applicability of the traditional theory of selective preservation and decreased soil quality with depth. As wetland submergence progresses and soils are exposed to oxygenated seawater, this relatively labile SOM and bioavailable N and P stored at depth has the potential for rapid mineralization and/or export into the coastal zone.

* Corresponding author.
E-mail address: lisa.chambers@ucf.edu (L.G. Chambers).

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1. Introduction

As one of the most productive ecosystem types, salt marsh soils sequester an average of 244.7 g carbon (C) m^{-2} y^{-1}, owing to high rates of primary productivity coupled with tidal flooding imposing anaerobic soil conditions that slow decomposition of organic matter (Amthor and Huston, 1998; Ouyang and Lee, 2014). These soil C stocks are vulnerable to coastal disturbances, such as sea level rise, which is occurring globally at a rate of 3.0 ± 0.4 mm y^{-1} (IPCC, 2013). Coastal wetlands can respond to sea level rise in multiple ways, including vertical accretion, landward transgression, and submergence, with the latter being the most extreme response and resulting in the conversion of the coastal wetland to open water (Kirwan and Megonigal, 2013). An estimated 22% of the areal extent of coastal wetlands are anticipated to be lost by 2100 (Nicholls et al., 1999). The long-term fate of submerged soil organic matter (SOM) is unknown, though studies have demonstrated that significant portions of previously sequestered SOM can be lost through increased mineralization within an aerobic water column (Steinmuller et al., 2019), export into the coastal ocean (Bianchi et al., 2008), or transported and reburied within adjacent sediments (Macreadie et al., 2013).

In order to assess the fate of SOM stocks under wetland submergence scenarios, it is critical to understand the physical and chemical nature of the stored organic material, which is mediated by input characteristics and decomposition processes. While numerous studies have quantified the stocks of soil C in wetlands the physical and chemical formation and stabilization processes for SOM in wetland soils is less understood, and more detailed research is required (Chmura et al., 2003; Dodla et al., 2012a, 2012b; Lu et al., 2003; Mcleod et al., 2011; Mitra et al., 2005; Wang et al., 2011). This is in stark contrast to theoretical understanding of SOM preservation in terrestrial soils, which has recently experienced a dramatic increase in research focus (Castellano et al., 2015; Cotrufo et al., 2013; Lehmann and Kleber, 2015; Schmidt et al., 2011). Long-term accumulation of SOM in wetlands is attributed to anaerobic conditions, which is often the primary regulator of the balance between inputs (from autochthonous and allochthonous sources) and outputs (decomposition and export) (Reddy and DeLaune, 2008). Beyond redox chemistry, the generally accepted theory of decomposition within wetland soils centers around selective preservation, where inputs of organic matter are classified based on nutrient availability and molecular complexity, with each pool degrading at different rates throughout the decay continuum (Lützow et al., 2006; Melillo et al., 1989; Sollins et al., 1996). Labile components are defined as easily degradable, generally low molecular weight (LMW) compounds, examples of which include carbohydrates and proteins. Recalcitrant (or refractory) components require more energy to degrade and consist of high molecular weight (HMW) compounds such as lignin. As decomposition progresses, the selective preservation theory states that labile components will be preferentially degraded by heterotrophic microbes while refractory components will be preferentially preserved, resulting in a greater proportion of HMW compounds with increasing soil depth (Sollins et al., 1996, Fig. 1). This so called 'carbon quality,' a measure of elemental stoichiometry and/or molecular complexity of organic compounds, is considered a significant regulator of decomposition within soils (Aber et al., 1990; Cadisch and Giller, 1997; Melillo et al., 1989). Concomitant with carbon quality and environmental factors such as redox

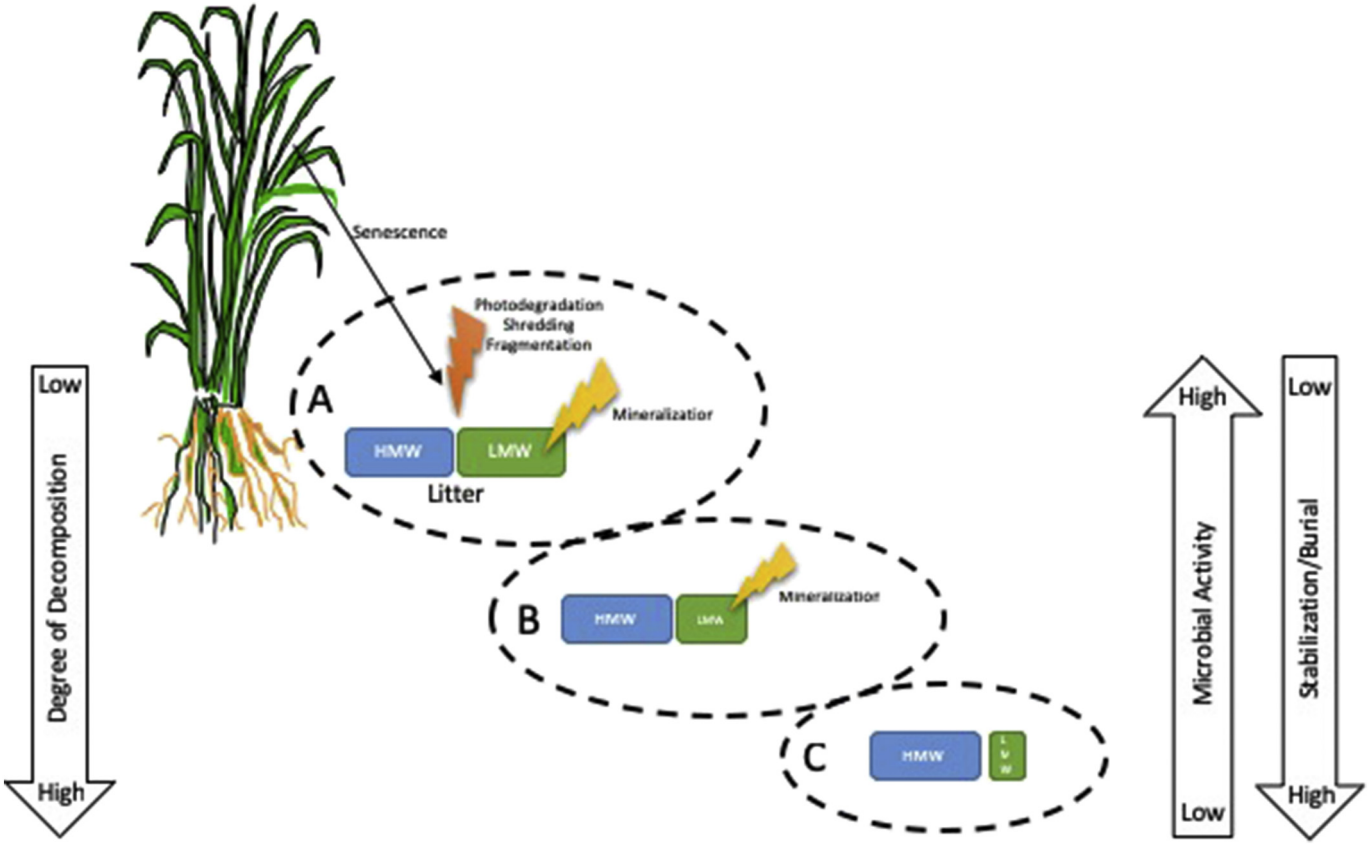

Fig. 1. Current paradigm of selective preservation and humification within wetland soils. A) As plants senesce, they deposit litter on the soil surface, which initially undergoes shredding from wetland fauna and microbial attack, targeting the low molecular weight (LMW) organic matter. B) As decomposition continues, LMW compounds continually undergo microbial degradation, reducing the size of the LMW pool. High molecular weight compounds require more energy to breakdown, thus the size of the pool remains generally the same. C) Decreases in microbial activity limit breakdown of the LMW pool resulting in an increase in the HMW pool, and a decrease in the LMW pool. Throughout this decay process, both degree of decomposition and stabilization/burial of organic matter increase, while microbial activity decreases with increasing depth.

status, decomposition and eventual SOM storage within wetlands is also regulated by microbial characteristics (i.e., microbial biomass, community structure, production of enzymes, etc.).

Following the decay continuum and selective preservation theory, SOM stored within wetlands is assumed to be increasingly decomposed with depth, with a concomitant increase in the relative abundance of HMW complex compounds resistant to further microbial catabolism and the possible formation of humified substances (i.e., Wang et al., 2011). However, there is limited empirical evidence to support these generally accepted theories, and new research may even contradict them (Kögel-Knabner et al., 1992; Schmidt et al., 2011). For example, in a bottle incubation study that exposed deep wetland soils (100 cm) to oxygen, Steinmuller et al. (2019) reported CO_2 production from the deep soils was roughly 4× greater than CO_2 production within surficial soils, indicating that a) organic material stored at depth can be *more* labile and decomposable than the surface, and b) even at depth, microbial communities remain present and can process organic material rapidly following a change in redox conditions.

The goal of this study was to address the apparent discrepancy between the assumption that SOM quality (defined here as nutrient availability and molecular complexity) decreases with depth, and the observed high rates of potential respiration at depth (Steinmuller et al., 2019). This was accomplished by evaluating the potential degradability of SOM (to a depth of 150 cm) within a submerging coastal wetland through, 1) chemical fractionation of SOM, 2) evaluation of total and bioavailable nutrient pools to support decomposition, 3) stable isotope profiles of SOM, and 4) quantification of microbial community with depth. Together, these four approaches can be leveraged for both assessing the stability of SOM during sea level rise and quantifying potential export of C, N, and P from submerging wetland soils into the coastal ocean. We hypothesized that SOM quality will not decrease with depth and total C content will increase with depth. Additionally, we hypothesize that bacterial abundance (16S) and sulfate reducers will decrease with depth, while Archaea increases with depth.

2. Methods

2.1. Site selection and soil sampling

The island selected for sampling was located within Barataria Bay, LA, a shallow open water basin located west of the Mississippi River Delta (29°26′36.77″ N, 89°53′59.28″ W, Fig. 2). The site experiences diurnal tides, with a salinity of 6–22 ppt (Levine et al., 2017; Rakocinski et al., 1992). The combination of shallow topography, lack of regular sediment inputs, tectonic subsidence, and high wind and wave energy within the bay contributes to an abnormally high erosion rate of 25.9 $km^2\ y^{-1}$ (Penland et al., 2000). More specifically, the erosion rate at this site was 141.6 ± 24.4 cm y^{-1} (Sapkota and White, in review). The dominant vegetation at this site at the time of sampling was *Spartina alterniflora*.

In June 2018, soil cores were collected along three transects, roughly 1 m apart, that consisted of three points: the coastal fringe (0 m inland), 1 m inland, and 2 m inland. Soil cores were collected in polycarbonate tubes via the push core method to a depth of 150 cm, and field-

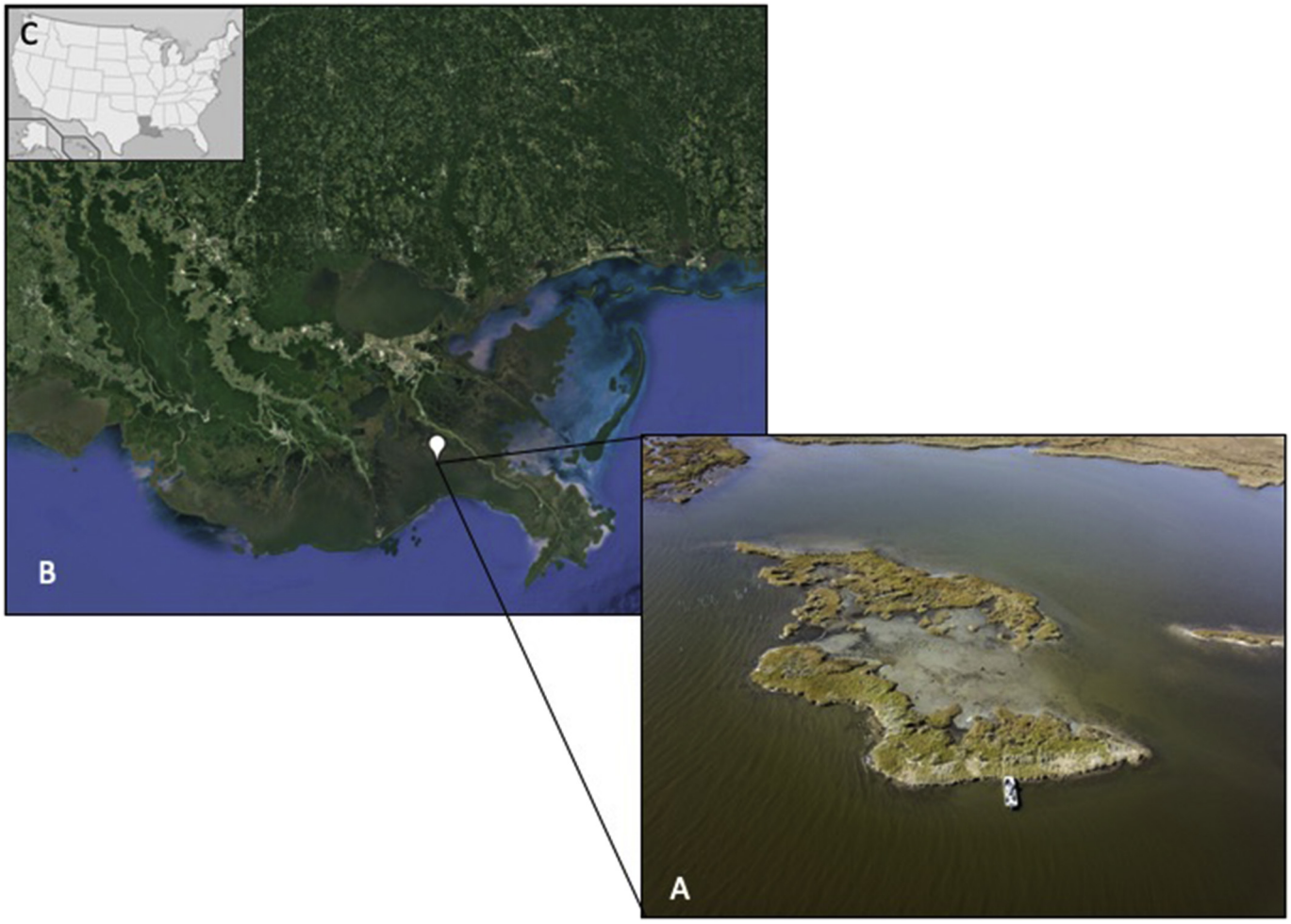

Fig. 2. Drone photo of sampling location (A) within the larger context of both coastal Louisiana (B), and the USA (C). Drone photo courtesy of Eddie Weeks and Yadav Sapkota.

Table 1
Forward and reverse primer sequences and names for each functional gene selected, as well as annealing temperatures used in qPCR analysis.

Gene	Forward primer	Sequence (5′-3′)	Reverse primer	Sequence (5′-3′)	Annealing temperature (°C)
dsrA	dsrA_290F	CGGCGTTGCGCATTTYCAYACVVT	dsrA_660R	GCCGGACGATGCAGHTCRTCCTGRWA	60
16S	Eub338	ACTCCTACGGGAGGCAGCAG	Eub518	ATTACCGCGGCTGCTGG	55.5
Arch	Arch967F	AATTGGCGGGGGAGCAC	Arch-1060R	GGCCATGCACCWCCTCTC	59

extruded into 15 separate 10-cm intervals. Soils were stored in polyethylene bags on ice and immediately transported back to the laboratory, where they were kept at 4 °C until sample analysis was complete.

2.2. Soil physicochemical properties

Soil samples were homogenized upon return to the laboratory, and subsamples were dried at 70 °C until a constant weight was achieved to determine moisture content and bulk density. Dried samples were then ground on a SPEX Sample Prep 8000M Mixer Mill (Metuchen, NJ, USA). Total C and nitrogen (N) content was determined on dried, ground subsamples by use of a Vario Micro Cube CN Analyzer (Elementar Americas Inc., Mount Laurel, NJ, USA). Subsamples of dried, ground material were digested with 50 mL of 1 N HCl at 100 °C for 30 min, then filtered through Whatman #41 filter paper for analysis of total phosphorus (P) (Andersen, 1976), which was determined colorimetrically on an AQ2 Automated Discrete Analyzer (Seal Analytical, Mequon, WI; EPA method 365.1 Rev.2).

2.3. Extractable nutrients

Subsamples of field-moist soil (2.5 g) were weighed into centrifuge tubes containing 20 mL of 2 M KCl. Samples were placed on a longitudinal shaker in the dark for 1 h, then centrifuged at 4000 rpm for 10 min at 10 °C. The supernatant was decanted into 0.45 μL Supor membrane filters and filtered through vacuum filtration, then acidified to a pH of <2 with double-distilled H_2SO_4. Within 21 days, samples were analyzed on an AQ2 Automated Discrete Analyzer (Seal Analytical, Mequon, WI) for nitrate (NO_3^-), ammonium (NH_4^+), and soluble reactive phosphorus (SRP) (EPA methods 231-A Rev. 0, 210-A Rev. 1, and 204-A Rev. 0).

2.4. Organic matter fractionation

To determine fractions of organic matter (indicators of molecular complexity), dried, ground subsamples were subjected to sequential extraction with H_2SO_4, following Rovira and Vallejo (2002) and Oades et al. (1970), with modifications. The first fraction is referred to hereafter as Labile Pool 1 (LP1) and consists of either plant- or microbially-derived non-cellulosic polysaccharides, including hemicellulose. Labile Pool 1 was extracted by adding 20 mL of 5 N H_2SO_4 into a 50 mL flask containing 0.5 g of soil. The solution was heated for 30 min at 105 °C and subsequently allowed to cool. Samples were then filtered through Whatman #41 filters to separate particulates from the solution, and then diluted to a final volume of 50 mL. Labile Pool 2 (LP2), which consists of cellulose, was determined by adding 2 mL of 26 N H_2SO_4 to 0.5 g of dried, ground soil. Samples were shaken at 100 rpm for 16 h, then diluted to a final concentration of 2 N H_2SO_4 with deionized water. Samples were heated for 3 h at 105 °C, then filtered in the same manner as LP1. Determinations of LP1 and LP2 concentrations were conducted by use of a Shimadzu TOC-L (Shimadzu, Kyoto, Japan). The refractory pool was calculated as total soil C minus the sum of the labile pools. All pools were normalized to total soil C content.

2.5. Stable isotope analysis ($\delta^{13}C$)

Stable isotope analysis was performed at the Stable Isotope Mass Spectroscopy Laboratory, Department of Geological Sciences at the University of Florida. Dried, ground subsamples from only the 1 m inland cores were initially combusted on a Carlo Erba NA1500 CNS elemental analyzer. Following the removal of oxygen and water from the sample gas, the stream was passed through a 0.7 m GC column (120 °C), which separated the N_2 gas from CO_2. Effluent then passed into a ConFlo II system, and into a Thermo Electron Delta V Advantage isotope ratio mass spectrometer, where sample gas was measured in relation to laboratory reference gases. C isotope results are expressed in relation to Vienna PDB, in standard delta notation.

2.6. DNA extraction, quantification, and qPCR

Following removal of samples from the field, subsets of field-moist samples from only the 1 m inland cores were frozen at −22 °C and transported back to the laboratory. Samples were allowed to thaw at 4 °C for 24 h before being sieved through a 2 mm mesh sieve to remove particulate plant material (Schneegurt et al., 2003). Samples were then centrifuged at 4000 rpm and 25 °C for 1 min and excess water was decanted. DNA was extracted from 0.25 g subsamples using a DNAeasy PowerSoil Extraction Kit (QIAGEN, Hilden, Germany). DNA quantification was performed by use of a Take3 micro-volume plate analyzed with a BioTek Synergy HTX (BioTek Instruments, Inc., Winooski, VT, USA). Extracted DNA was stored at −22 °C until qPCR analysis was performed.

Primers were selected to amplify specific taxonomic and functional genes of interest: sμfate reduction (dsrA), all bacteria (16S), and all archaea (Arch) within the samples (Table 1). Genomic DNA from *Desulfobacterium autotrophicum* (Strain DSM 3382 (HRM2), ATCC, Manassas, VA, USA) was used to establish standard curves for both amplification of the 16S gene and the dsrA gene, while *Methanococcus voltae* (Strain A3) was used to establish standard curves for amplification of the Arch gene. Each 25 μL reaction contained 5 μL of DNA, 1.25 μL of each 0.1 uM primer (forward and reverse), 12.5 μL of SYBR green MasterMix, and 12.5 μL of PCR-grade water. Each reaction initially proceeded through steps at 50 °C and 95 °C, then 50 cycles of denaturing at 95 °C, annealing (Table 1), and extending at 72 °C.

Table 2
Significance values (*p*-values) derived from linear model for each parameter ($\alpha = 0.004$). 'NS' indicates a non-significant *p*-value, while 'NA' indicates the analysis was not performed.

Parameter	Depth
Bulk density	<0.0001
Moisture content	<0.0001
Organic matter	<0.0001
Total C	<0.0001
Total N	<0.0001
Extractable NO_3^-	<0.0001
Extractable SRP	<0.0001
Extractable NH_4^+	<0.0001
Labile Pool 1	<0.0001
Labile Pool 2	<0.0001
Refractory pool	<0.0001
$\delta^{13}C$	<0.0001
$\delta^{15}N$	<0.0001
16S	<0.0001
dsrA	<0.0001
Arch	NS

Table 3
Correlation matrix for all parameters with a distance treatment ($n = 136$, $\alpha = 0.001$, critical value = 0.279). Values in bold are positively correlated, while values in italics are negatively correlated. 'Ext.' refers to 'extractable'.

	Bulk density	Moisture content	Organic matter	Total N	Total C	Ext. NO_3^-	Ext. SRP	Ext. NH_4^+	LP1	LP2
Moisture content	*−0.962*									
Organic matter	*−0.812*	**0.809**								
Total N	*−0.719*	**0.722**	**0.933**							
Total C	*−0.768*	**0.772**	**0.971**	**0.959**						
Ext. NO_3^-	*−0.640*	**0.673**	**0.601**	**0.505**	**0.545**					
Ext. SRP	*−0.671*	**0.679**	**0.769**	**0.740**	**0.752**	**0.687**				
Ext. NH_4^+	*−0.604*	**0.631**	**0.692**	**0.656**	**0.667**	**0.633**	**0.835**			
LP1	*−0.627*	**0.625**	**0.766**	**0.710**	**0.756**	**0.367**	**0.432**	**0.405**		
LP2	*−0.524*	**0.521**	**0.597**	**0.661**	**0.638**	**0.404**	**0.568**	**0.458**	**0.353**	
Refractory	*−0.749*	**0.754**	**0.961**	**0.944**	**0.991**	**0.537**	**0.750**	**0.668**	**0.709**	**0.554**

2.7. Statistical analysis

All statistical analysis was performed in R (R Institute for Statistical Computing, Vienna, Austria) using RStudio (RStudio Inc., Boston, MA, USA). The Shapiro-Wilk test was used to verify assumptions of normality, and a logarithmic transformation was performed on all datasets. Levene's test was used to determine homogeneity of variance. A linear mixed-effect model (package 'lmer') was used to test the following predictor variables: depth, distance inland, and the interaction of depth and distance inland on the samples collected from the marsh. Transect was included as a random effect. Distance inland was found to be a non-significant predictor variable for all parameters except for extractable NH_4^+. As such, distance inland and the interaction of depth and distance was removed as a predictor variable from models except extractable NH_4^+. Isotopic determinations and quantitative PCR analysis was performed exclusively on the three replicate cores taken 1 m inland, and thus depth was the only predictor variable tested for those parameters. Following determination of significance within one of the predictor variables, the package 'lsmeans' was used for post-hoc pairwise comparisons using the Tukey method.

3. Results

3.1. Soil physicochemical properties and organic matter fractions

Bulk density, moisture content, total C, and total N all significantly differed with depth (Table 2). Bulk density ranged from 0.436 ± 0.036 g cm^{-3} at 30–40 cm to 0.177 ± 0.013 g cm^{-3} at 120–130 cm. In contrast, moisture content was lowest at 30–40 cm, averaging 60.3 ± 2.86%, and greatest at 120–130 cm, averaging 81.2 ± 0.641%. Total soil C was lowest at 50–60 cm, averaging 72.6 ± 8.18 g kg^{-1}, and highest at 130–140 cm, averaging 318 ± 6.66 g kg^{-1}. Total N concentrations exhibited a similar trend, ranging from 3.80 ± 0.438 g kg^{-1} at 50–60 cm to 18.2 ± 0.417 g kg^{-1} at 130–140 cm. The ratio of C:N was not significantly predicted by depth. Organic matter (OM) content significantly differed with depth (Table 2) and ranged from 18.0 ± 3.32% at 40–50 cm to 63.7 ± 1.13% at 120–130 cm. Bulk density was negatively correlated to all other physicochemical properties, all extractable nutrients, and organic matter fractions (Table 3). Moisture content, total C, and total N were all positively correlated to all physicochemical properties, extractable nutrients, and organic matter fractions (Table 3).

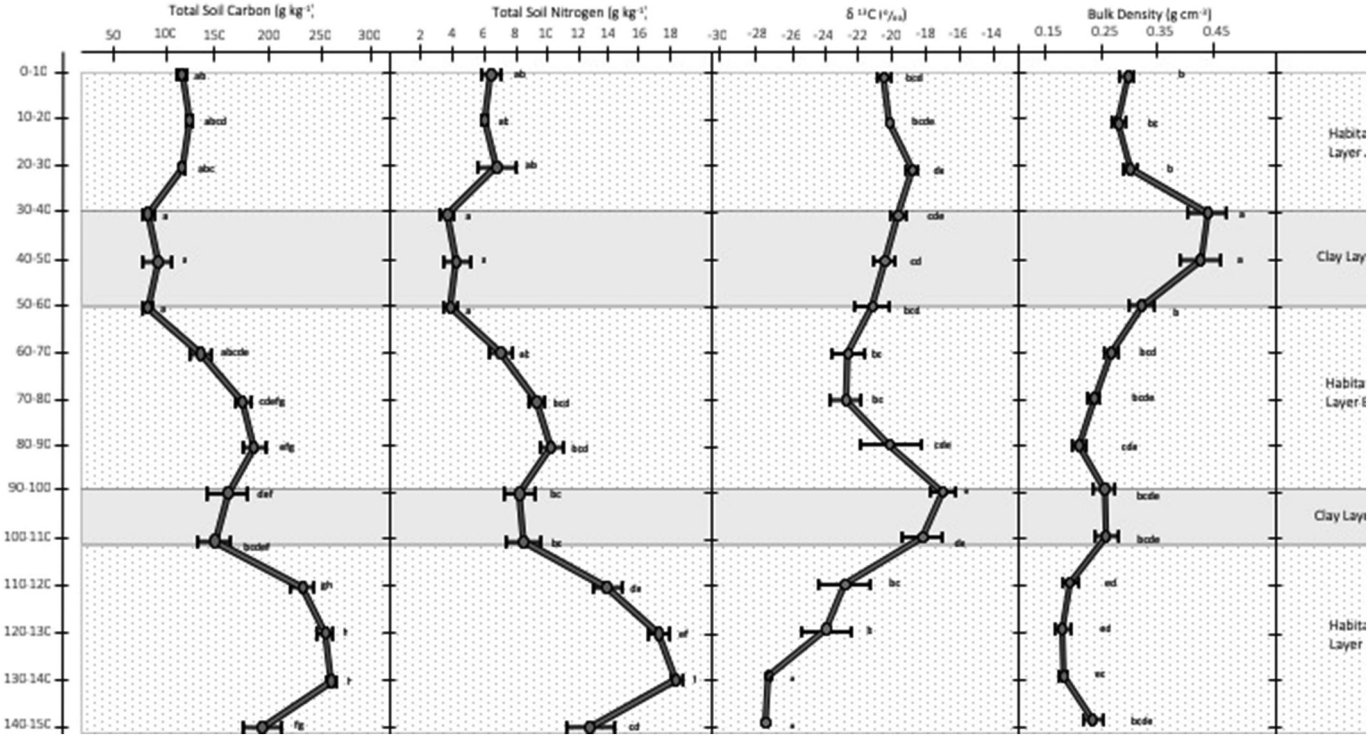

Fig. 3. Total soil carbon content (A), total soil nitrogen content (B), soil $\delta^{13}C$ (‰), bulk density (D), and organic matter content (E), as well as multiple habitat types and clay layers. Values are mean ± standard error, $n = 9$. Lowercase letters denote significance ($\alpha = 0.05$).

Organic matter content was negatively correlated to bulk density and positively correlated to all other physicochemical parameters (Table 3).

Labile pool 1 (LP1) significantly differed with depth (Table 2), ranging from 96.3 ± 15.3 mg g C^{-1} at 130–140 cm to 189 ± 12.9 mg g C^{-1} at 30–40 (Fig. 4). Depth was not a significant predictor variable for labile pool 2 (LP2). The refractory C pool was also significantly predicted by depth (Table 2), and ranged from 702 ± 20.9 mg g C^{-1} at 0–10 cm to 823 ± 12.6 mg g^{-1} at 140–150 cm. When combined, the ratios of LP1 + LP2: refractory (henceforth referred to as labile: refractory ratio) was significantly different with depth ($p < 0.001$). Labile: refractory ratios remained relatively consistent between 0 and 60 cm, averaging 0.363 ± 0.018, then decreased to an average of 0.256 ± 0.009 between 60 and 150 cm. All three organic matter pools were significantly positively correlated to each other, as well as total N, total C, moisture content, and all extractable nutrients (Table 3). All pools were negatively correlated to bulk density (Table 3).

3.2. Extractable nutrients

Extractable NO_3^- concentrations increased with depth (Table 2), ranging from 1.44 ± 0.130 mg NO_3-N kg^{-1} at 30–40 cm to 3.47 ± 0.527 mg NO_3-N kg^{-1} at 120–130 cm. Both extractable SRP and NH_4^+ concentrations generally increased with depth (Table 2, Fig. 5), though concentrations decreased precipitously between 130–140 cm and 140–150 cm. Extractable SRP concentrations ranged from 0.908 ± 0.126 mg kg^{-1} at 30–40 cm to 12.0 ± 0.973 mg kg^{-1} at 130–140 cm. The lowest extractable NH_4^+ concentrations were at 20–30 cm, averaging 9.64 ± 4.27 mg kg^{-1}, while the greatest concentrations were at 130–140 cm, averaging 206 ± 33.3 mg kg^{-1}. All extractable nutrients were positively correlated to each other and total nutrients (Table 3).

3.3. $\delta^{13}C$ and $\delta^{15}N$ values

Both $\delta^{13}C$ and $\delta^{15}N$ values significantly different with depth (Table 2). $\delta^{13}C$ was most depleted at 130–140 cm, averaging −27.3 ± 0.131, and most enriched at 90–100 cm, where values averaged −16.9 ± 0.729 (Fig. 3). Generally, $\delta^{15}N$ values decreased with depth, ranging from 1.90 ± 0.110 at the surface to −0.65 ± 0.124 at 110–120 cm (Fig. 6). $\delta^{13}C$ was negatively correlated to total C and N content, as well as extractable SRP, extractable NH_4^+, and the refractory OM component (Table 4). $\delta^{15}N$ positively correlated to bulk density, and was negatively correlated to moisture content, total C and N, all extractable nutrients, and the refractory OM component (Table 4).

3.4. Quantitative PCR

Gene abundance of 16S and dsrA both different with depth (Table 2, Fig. 7). Gene abundance of 16S was greatest at 0–10 cm, averaging $5.92 \times 10^9 \pm 6.98 \times 10^8$ gene copies, while dsrA gene abundance was greatest at 10–20 cm, and averaged $9.58 \times 10^9 \pm 1.39 \times 10^9$. The lowest abundance of both genes was recorded at 50–60 cm, where 16S averaged $1.59 \times 10^9 \pm 8.02 \times 10^8$ gene copies, while dsrA averaged $2.95 \times 10^9 \pm 7.66 \times 10^8$ gene copies. Gene abundance of the Archaea gene (Arch) was not significantly predicted by depth (Table 2, Fig. 7). Both 16S and dsrA gene abundance were positively correlated to each other (Table 4).

4. Discussion

4.1. Site history

Previous studies within Barataria Bay, LA have documented nonlinear changes in soil C content with depth (Dodla et al., 2012a, 2012b; Steinmuller et al., 2019), as was observed here. Total C content increased dramatically, though not linearly, from the surface to 150 cm (Fig. 3). Combining C content with $\delta^{13}C$ values and knowledge of the dynamic nature of the Mississippi River delta, we can hypothesize the presence of multiple habitat types or depositional periods over the chronological timescale the soil core represents. The majority of brackish marsh vegetation is C4 plants, which have more depleted $\delta^{13}C$ values compared to the C3 plants that inhabit freshwater marshes (Smith and Epstein, 1971). The C3 plant signature of less depleted $\delta^{13}C$ values is evident within the first 30 cm of the soil (Fig. 1, Habitat Layer A), under which there is a distinct clay layer (Clay Layer A), likely a relic of hydrologic change in the area (Delaune, 1986). Under the clay layer, the $\delta^{13}C$ values indicate a more depleted environment (−21.7), which we hypothesize to be a freshwater marsh (Fig. 1, Habitat Layer B). Delaune (1986) identified a similar trend in Barataria Bay, where isotopic signatures of a freshwater marsh underlaid those of a brackish marsh, separated by a clay later. Deeper in the soil profile, between 90 and 110 cm, the soil again shifted to more clay dominated (Clay Layer B), possibly indicating another hydrologic event, under which $\delta^{13}C$ values again became more depleted (Habitat Layer C). Both total soil C and N content are different within each of these layers, and are greatest within Habitat Layer C. The unique history and habitat switching at this site allows for the storage of considerably more C than would be assumed if only surface (e.g., 0–30 cm) cores were collected, as is common in wetland studies (Reddy et al., 2013). This study indicates the importance of

Table 4
Correlation matrix for parameters that did not include a distance treatment ($n = 46$, $\alpha = 0.001$, critical value = 0.469). Values in bold are positively correlated, while values in italics are negatively correlated. Non-significant r values are denoted with a dash. Ext. refers to 'extractable'.

	Bulk density	Moisture content	Organic matter	Total N	Total C	Ext. NO_3^-	Ext. SRP	Ext. NH_4^+	LP1	LP2	Refractory	16S	dsrA	Arch	δ15N
Moisture content	*−0.957*														
Organic matter	*−0.858*	**0.861**													
Total N	*−0.748*	**0.756**	**0.933**												
Total C	*−0.789*	**0.791**	**0.946**	**0.979**											
Ext. NO_3^-	*−0.753*	**0.767**	**0.729**	**0.633**	**0.669**										
Ext. SRP	*−0.688*	**0.649**	**0.817**	**0.845**	**0.815**	**0.581**									
Ext. NH_4^+	*−0.592*	**0.612**	**0.708**	**0.696**	**0.659**	**0.611**	**0.700**								
LP1	*−0.623*	**0.663**	**0.709**	**0.623**	**0.646**	–	**0.475**	**0.477**							
LP2	*−0.475*	–	**0.561**	**0.649**	**0.616**	–	**0.621**	–	–						
Refractory	*−0.767*	**0.778**	**0.927**	**0.960**	**0.989**	**0.668**	**0.789**	**0.651**	**0.614**	**0.521**					
16S	–	–	–	–	–	–	–	–	–	–	–				
dsrA	–	–	–	–	–	–	–	–	–	–	–	**0.622**			
Arch	–	–	–	–	–	–	–	–	–	–	–	–	–		
$\delta^{15}N$	**0.663**	*−0.651*	*−0.762*	*−0.710*	*−0.719*	*−0.601*	*−0.736*	*−0.541*	–	–	*−0.714*	–	–	–	
$\delta^{13}C$	–	–	**0.508**	*−0.654*	*−0.560*	–	*−0.510*	*−0.534*	–	–	*−0.554*	–	–	–	–

collecting deep soil cores (1+ m) in establishing coastal wetland C budgets, particularly in this systems where ~1–2 m of peat could be lost to the bay during erosion (DeLaune and White, 2012).

4.2. Carbon quality and degree of decomposition

Though the quantity of organic C sequestered within this site is greatest at deeper depths, the quality of that organic matter is also critical to consider when evaluating potential degradability. By parsing-out relative contributions of labile and recalcitrant organic matter within the soil at multiple depths, we can infer the relative mineralization potential of these C stocks via microbial respiration (Dodla et al., 2012a, 2012b). Use of the selective preservation model would suggest that at deeper depths, where decomposition processes have been greatest, SOM should consist of generally refractory C that is resistant to decomposition (Sollins et al., 1996). Within this study, the ratio of labile: refractory C did decrease with depth (0.42 at 0–10 cm to 0.22 at 140–150 cm; Fig. 4), implying decomposition has taken place, though labile fractions still comprise a range of 17–30% of the total C pool between 100 and 150 cm below the soil surface. Placing this number in context is difficult; to our knowledge, this analysis method has not previously been performed on wetland soils, and thus it is challenging to determine whether this number represents either extensive or minor decomposition of labile components. Using a different method, Dodla et al. (2012a, 2012b) assessed acid-hydrolyzable C content (assumed to be somewhat similar to our labile fractions) to be 17% of total organic C at depth (150–175 cm) and 23% at the surface (0–50 cm) within brackish marsh soils in Barataria Bay (though non-linear with depth). This is slightly lower than the 24–32% of labile soil organic C reported within forested wetlands (0–20 cm) (Silveira et al., 2010). In a study comparing the acid hydrolyzable C content within three upland soils, Xu et al. (1997) documented a range of 29–34% hydrolyzable soil organic C fractions in surface soils (0–15 cm), which would likely be indicative of relatively labile, undecomposed material.

The degree of decomposition of the SOM at depth can also be ascertained by examining $\delta^{15}N$ isotope values, which can provide insight by indicating whether these soils have undergone substantial fractionation, and therefore decomposition. Within our study, $\delta^{15}N$ decreased with depth (Fig. 6). Within the continuum of decomposition, fractionation of N isotopes occurs as soil microbial biomass processes organic material (Craine et al., 2015). Initially during the process of decomposition, $\delta^{15}N$ within the soil becomes more depleted (Melillo et al., 1989) as a result of net immobilization of N and microbial anabolism. However, as mineralization progresses, microbial consortia no longer require significant N constituents for anabolism, and mineralization processes begin to prevail over immobilization, with $\delta^{15}N$ values becoming more enriched over the long term. As a result, soil $\delta^{15}N$ values have been shown to become more enriched with depth within upland systems (Hobbie and Ouimette, 2009). In wetlands, where soils are generally water-logged and decomposition proceeds much slower, our $\delta^{15}N$ profile may suggest, a) SOM only advances through the initial stage of decomposition before being inhibited by low redox conditions (i.e., a lack of available terminal electron acceptors), or b) habitat switching/major disturbances within this system resulted in multiple depositional

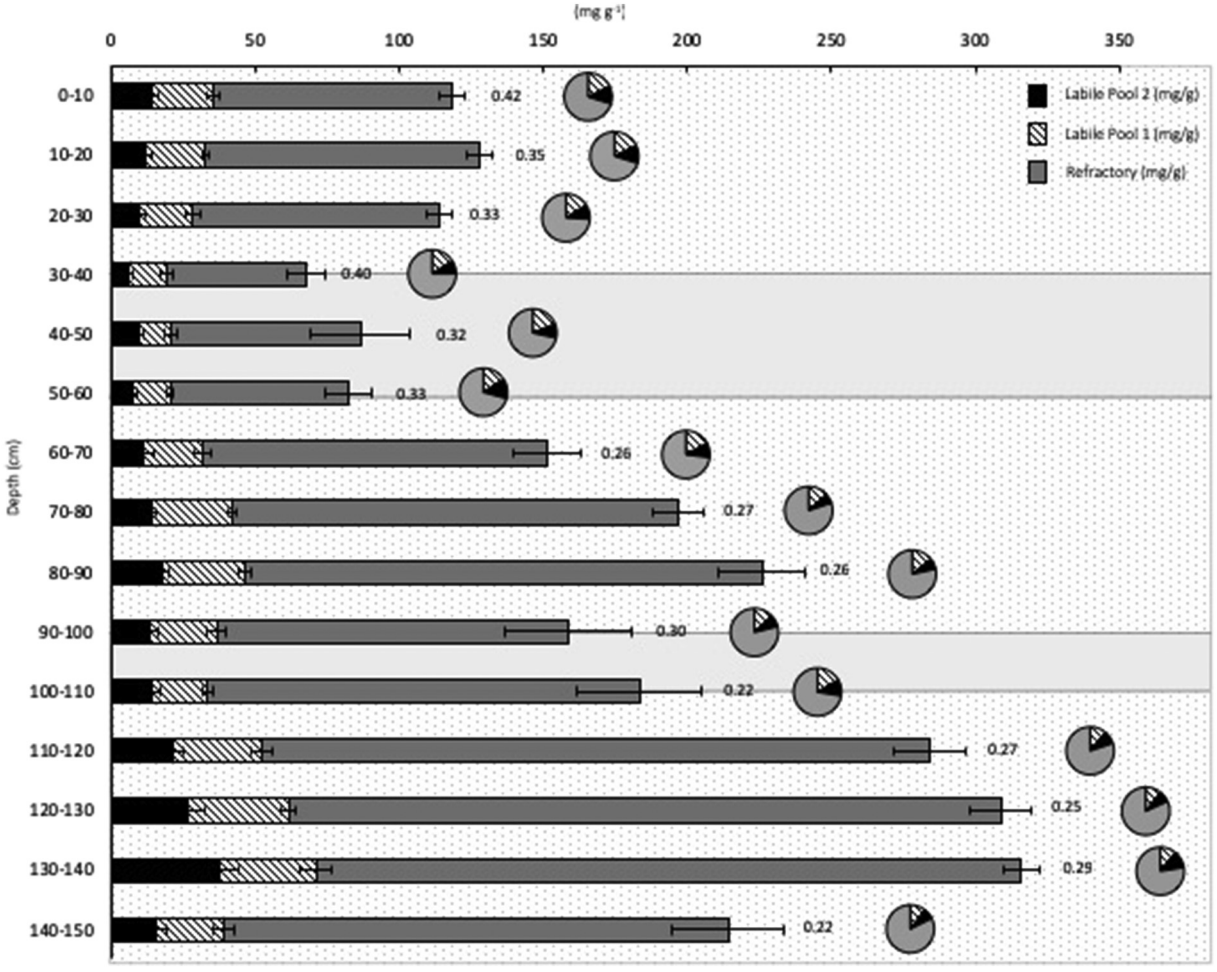

Fig. 4. Fractionation of organic C into two labile pools and a refractory pool. Values are mean ± standard error. Numbers adjacent to bars indicate labile: refractory ratio for that soil depth. Pie charts represent the percentage of total C that each pool represents for the associated depth. Shading indicates layers established in Fig. 3.

periods and rapid burial of organic soils. Overall, the $\delta^{15}N$ profile, taken in concert with the trends observed for labile: refractory ratios and the lack of changes in elemental C:N with depth, suggests that only limited SOM decomposition has occurred at depth, though additional studies of deep wetland soil profiles are needed to corroborate this idea. The potential implication of the existence of relatively labile C deep within the soil profile is an increased likelihood of rapid mineralization if the abiotic conditions are altered, such as due to coastal erosion.

4.3. Microbial gene abundance at depth

Microbial abundance and function are regulated by a variety of both biological and physicochemical factors within wetland systems. The prevailing anaerobic conditions within wetlands regulate which microbial communities are functioning, a result of the availability of terminal electron acceptors (Reddy and DeLaune, 2008). Within surface soils in brackish and saltwater wetlands, sulfate reduction is the dominant respiration pathway for microbial consortia and is replaced by methanogenesis in deeper soils where either sulfate concentrations have been depleted, or do not penetrate (DeLaune et al., 1983). While this study did not quantify gene copies of mcrA, the gene for methanogenesis, abundance of dsrA, the gene for sulfate reduction, was highest at surface depths, indicating that the microbial communities at the surface are likely respiring via sulfate reduction. The number of copies of the 16S gene, an indicator of abundance of all bacteria, was lower than the number of gene copies of dsrA between 0 and 40 cm, likely a product of decreased efficiency of primers for the 16S gene, relatively to the efficiency of primers amplifying dsrA. Interestingly, the

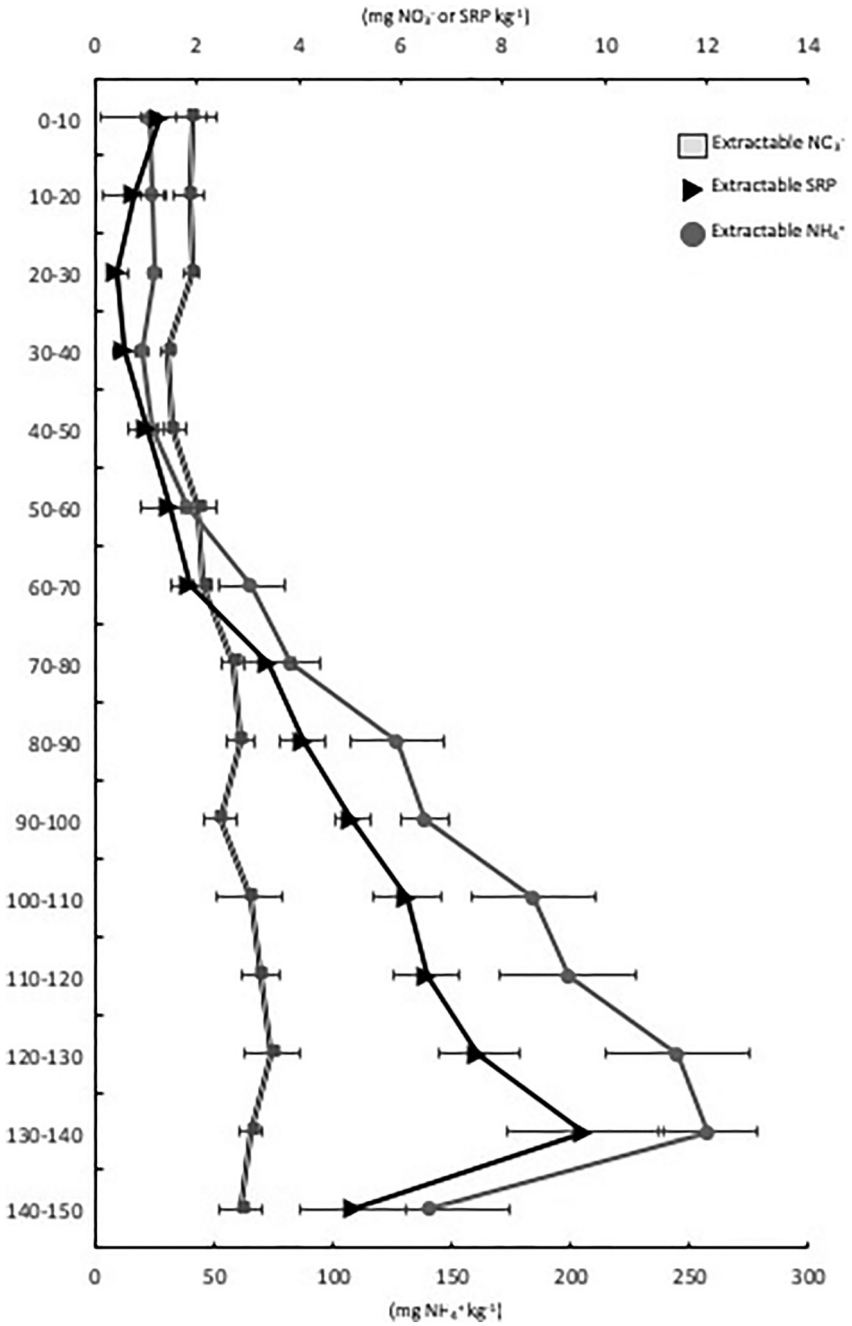

Fig. 5. Extractable nutrient concentrations at each soil depth. Values are mean ± standard error.

abundance of the Arch gene was greater than the Bac gene deeper than 20 cm, which is likely an indication of methanogenesis, a process controlled by *Archaea* rather than *Bacteria* being the dominant microbial respiration pathway at depth (Reddy and DeLaune, 2008).

Carbon quality and quantity have been documented to strongly regulate microbial abundance and function within wetland systems (Reddy and DeLaune, 2008). However, within this study, neither C density, total C content, nor C quality correlated well with abundance of any microbial gene quantified (Table 4). This indicates that there is potentially another regulator of microbial abundance within this system, such as redox conditions or environmental factors. Alternatively, the microbial community composition itself may shift with C indices, but the overall abundance of genes remains unchanged (due to a variety of groups that possess the same gene), or the community composition shift is occurring outside of the sulfate reducer group. Further research is required to determine the importance of organic matter quality and quantity as regulators of microbial functional abundance within wetland systems.

Similarly, determining whether those microbial communities present at depth are active and alive is critical in further determining the fate of sequestered organic material at depth. Based on the data collected here, we can determine that microbial communities are present in significant proportions at depth but cannot determine whether those communities are metabolically dormant. However, the presence of these microbial communities at depth, coupled with the high potential degradability of these C stocks demonstrated in Steinmuller et al. (2019), indicates these microbial communities can become active when conditions change, such as soil disarticulation and oxygenation following submergence into coastal waters.

4.4. Fate of stored carbon, nitrogen, and phosphorus

Both extractable NH_4^+ and SRP increased an order of magnitude below the root zone (~30 cm) within these soils (Fig. 5). Within the active root zone, these bioavailable nutrients are assimilated by plants to sustain growth and primary productivity (Brannon, 1973). Below the root zone, availability of these nutrients is mediated by microbiota (i.e. mineralization versus immobilization) or physicochemical properties (i.e. binding to the cation exchange complex). Within these deep soils, nutrients are not being utilized by biological processes, and thus persist at depth. The 11× and 7× increase in SRP and NH_4^+ concentrations between 0–10 cm and 130–140 cm, coupled with the significant C stocks within this wetland, represent bioavailable nutrients and relatively labile C that is vulnerable to export into the coastal zone through physical and chemical processes associated with both sea level rise and erosion. Bioavailable N and P exported from coastal marshes can contribute the formation of a hypoxia zone that develops annually within the northern Gulf of Mexico (Bianchi et al., 2008; Dagg et al., 2007). Similarly, export of C from coastal marshes is estimated to account for 3–34% of the organic C within the inner Louisiana shelf (Bianchi et al., 2011) and

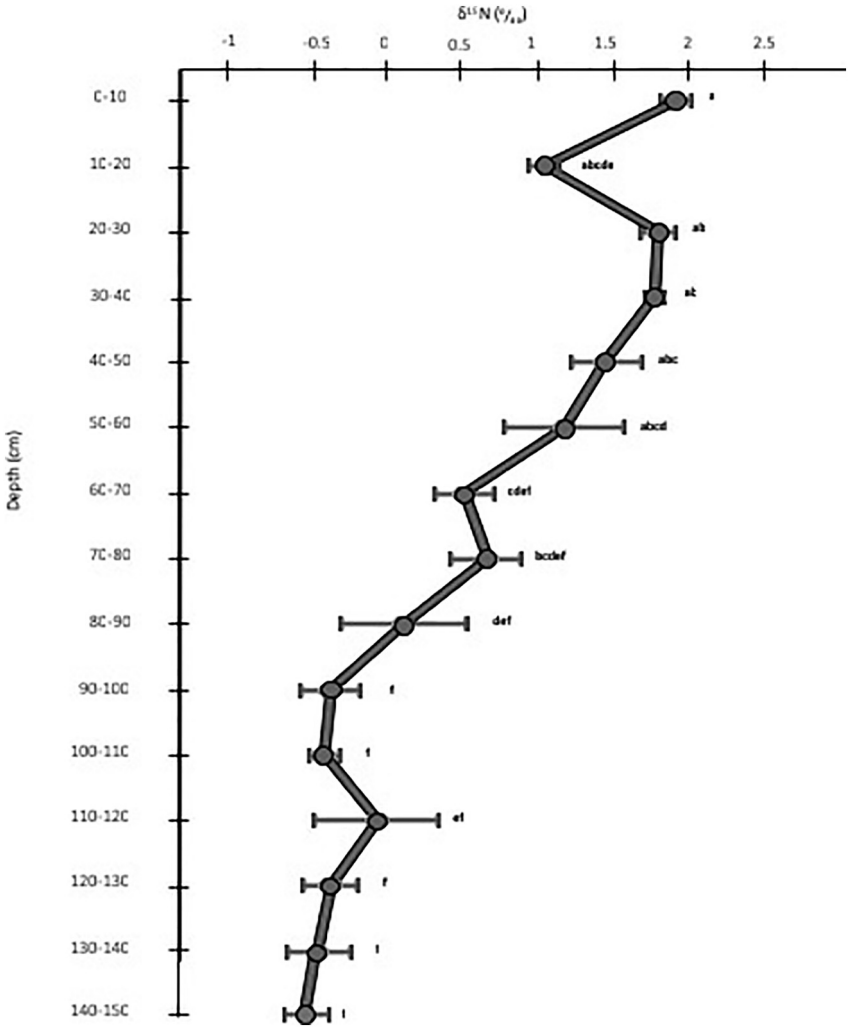

Fig. 6. Values of $\delta^{15}N$ within each soil depth. Plotted values are mean ± standard error. Letters indicate significance (alpha = 0.05).

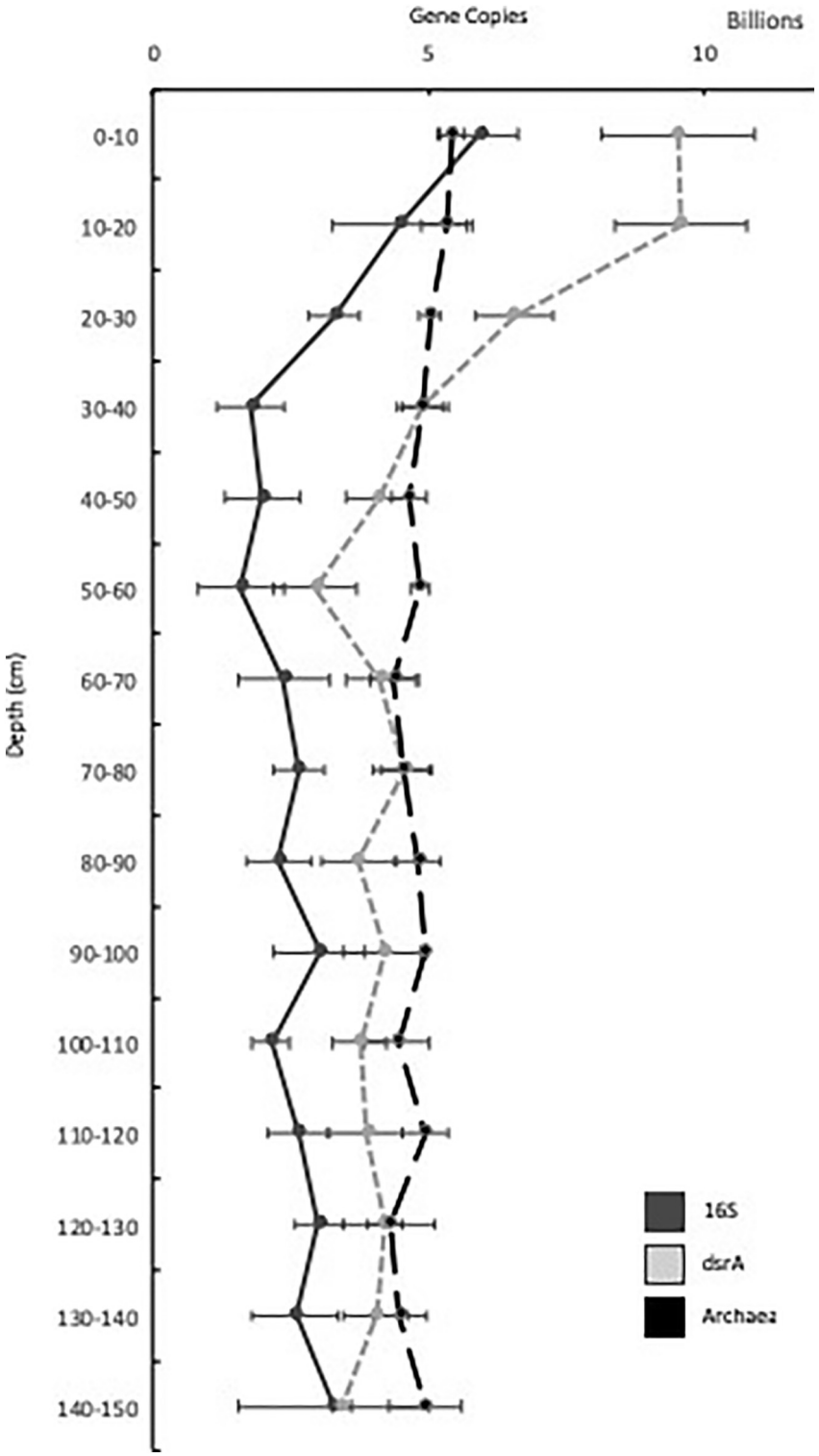

Fig. 7. Number of gene copies for each functional gene (dsrA, Bac, Arch) in billions for each soil depth. Values are mean ± standard error.

could increase with wetland submergence. In addition to export, these stores of minimally decomposed organic material and high concentrations of bioavailable nutrients, when combined with oxygenated seawater and/or available sulfate, represent optimal conditions for mineralization and loss of C into the atmosphere as a climate change feedback. Specifically, Steinmuller et al. (2019) documented a 66% increase in mineralization following exposure of soils from this site to aerobic seawater.

4.5. Understanding SOM stabilization in wetlands

Recently, multiple conceptual models have emerged within the upland literature to explain SOM formation and stabilization, most of which indicate SOM persistence is more closely linked to environmental factors, the degree of microbial processing, and protection via association with minerals and aggregation, rather than the inherent molecular properties of the SOM that are highlighted by the selective preservation

theory (Castellano et al., 2015; Cotrufo et al., 2013; Lehmann and Kleber, 2015; Schmidt et al., 2011). Although application of these conceptual models has yet to be tested in wetlands, evidence from the current study suggests selective preservation may not be the dominant regulator of SOM formation in coastal wetlands. Rather, our results indicate the percent of refractory material only increased by 7% over the entire 150 cm depth interval, while labile material decreased roughly 10%. This, taken together with the lack of change in C:N with depth and a depletion of $\delta^{15}N$ values, suggests this SOM remains relatively degradable (i.e., has high C quality) to a depth of 150 cm. While we cannot yet theorize which conceptual models most accurately depict SOM stabilization within peat-forming wetlands, our data suggest it is more complex than selective preservation and may be linked to microbial access and efficiency (Lehmann and Kleber, 2015; Cotrufo et al., 2013) or the unique conditions found in wetlands, such as the dominance of anaerobic environments or rapid rates of soil accretion.

5. Conclusion

Currently, much of the coastal wetland soils research focuses on C quantity, such as documenting blue C pools, with less attention given to the properties of the SOM itself (e.g., molecular complexity, nutrient availability, microbial community). Since few studies on SOM structure and stabilization have been performed in wetlands, it is often assumed wetland soils follow the traditional concepts for SOM decomposition and preservation developed in terrestrial soils, such as the decay continuum and the theory of selective preservation (Melillo et al., 1989; Reddy and DeLaune, 2008). Under these conceptual models, soil quality is anticipated to decrease significantly with depth in wetlands, making only the more surficial soils easily degradable and at risk of rapid mineralization if conditions were altered, such as a shift in redox status. Understanding SOM quality, how it changes with depth, and how it influences the biogeochemical response of soils to shifting environmental conditions is particularly important in Barataria Bay, LA (USA), where coastal wetlands are rapidly submerging into oxygenated coastal waters due to the combined effects of high rates of relative sea level rise and edge erosion.

This study assessed key SOM properties that commonly regulate the rate of decomposition, and thus the properties of buried SOM: molecular complexity (through acid hydrolysis), C and nutrient availability (total and extractable pools), and the abundance of key microbial taxa and functional genes. Soil stratigraphy inferred from changes in physicochemical properties with depth revealed a highly dynamic environment with multiple depositional phases and presumed shifts between vegetation communities (from C3-dominated (more common of freshwater marsh species) to C4-dominanted communities (more indicative of brackish marsh species)). These dynamics, along with persistent anaerobic conditions, promoted the preservation and burial of large stores of SOM that appear to have only undergone minimal processing and decomposition, based on the existence of only small changes in the ratio of labile:recalcitrant material with depth, no change in soil C:N, and a profile of diminishing $\delta^{15}N$ values with depth. In addition to these indices suggesting the presence of high quality SOM at depth, our data also indicates total C content and extractable nutrient (NH_4^+ and SRP) availability peaks at depth (between ~110 and 140 cm) without any significant declines in the abundance of bacteria or archaea below the root zone. Taken together, these results demonstrate a high potential for rapid mineralization of this SOM when redox constraints are released during mixing with oxygenated coastal waters, and the release of C and nutrients into coastal waters following wetland erosion and submergence. This work also highlights the need for additional analysis on wetland SOM properties with depth and development of a conceptual framework for SOM formation and preservation in wetland soils that may be unique from those developed for terrestrial soils.

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