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Shifting Sources and Fates of Carbon With Increasing Hydrologic Presses and Pulses in Coastal Wetlands

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Key Points:

- Dissolved organic carbon concentrations decrease with water level in peat marshes but increase with level in mangroves and marl marshes
- Detrital carbon is mobilized by both fresh and marine hydrologic pulses, but only stored during freshwater hydrologic pulses
- Freshwater restoration is increasing humic, colored dissolved organic matter entering the Everglades

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract

Coastal ecosystems are rapidly shifting due to changes in hydrologic presses (e.g., sea-level rise) and pulses (e.g., seasonal hydrology, disturbances, and restoration of degraded wetlands). Changing water levels and sources are master variables in coastal wetlands that can alter carbon concentrations, sources, processing, and export. Yet, how long-term increases in water levels from marine and freshwater sources influence dissolved organic carbon (DOC) concentrations and dissolved organic matter (DOM) composition is uncertain. We quantified how long-term changes in water levels are affecting DOC concentration (2001–2021) and DOM composition (2011–2021) differently across the Florida Everglades. DOC concentrations decreased with high water depths in peat marshes and increased with high water levels in marl marshes and across mangroves, and these relationships were reproduced in freshwater peat marshes and shrub mangroves. In the highly productive riverine mangroves, cross-wavelet analysis highlighted variable relationships between DOC and water level were largely modulated by hurricane disturbances. By comparing relationships between water level and DOC concentrations with carbon sources from DOM fluorescence indices, we found that changing water sources between the dry and wet season shift DOM from algal to detrital sources in freshwater marshes, from detrital marsh to detrital mangrove sources in the brackish water ecotone, and from detrital mangrove to algal marine sources in downstream mangroves. As climate change and anthropogenic drivers continue to alter water levels in coastal wetlands, integrating spatial and temporal measurements of DOC concentrations and DOM compositions is essential to better constrain the transformation and export of carbon across these coastal ecosystems.

Plain Language Summary

Water inputs to coastal ecosystems are changing in response to both sea-level rise and water management. Changes in the amount and source of water can have different effects on organic carbon cycling across coastal ecosystems. We analyzed 20 years of data from the Florida Everglades to understand how changing water levels control carbon cycling. Our results show that higher water levels dilute carbon concentrations, and slow the release of carbon from peat soils, while also contributing to the transport of organic carbon downstream. We additionally found evidence of seasonal shifts in the composition of organic carbon, with higher algal contributions in the dry season for freshwater sites and higher marine contributions during the dry season for sites with marine influence. Our findings highlight that inputs, of both fresh and marine water, are transporting carbon within and between coastal wetlands, but only freshwater inputs prevent the release of carbon from peat stores. This research provides valuable insights into how inputs of water from different sources control the production, release, and movement of carbon throughout coastal wetland ecosystems. These insights are needed to preserve the value of organic carbon stored in coastal ecosystems, as the water within them changes.

1. Introduction

The importance of presses and pulses as drivers of ecosystem structure and function has a long history in the field of ecology (Clements, 1916; Connell, 1978; Jentsch & White, 2019; Pulsford et al., 2016). Presses are defined as extensive and directional changes in abiotic drivers that occur over long periods of time (Ratajczak et al., 2018). Pulses are defined as abrupt changes in ecological parameters (abiotic or biotic) that alter ecosystem dynamics and vary in frequency, magnitude, and duration (Jentsch & White, 2019). The frequency, magnitude, and duration of pulses determine if they are a useable subsidy or whether, at a certain threshold, they will transition to being a stressor to the system (E. P. Odum et al., 1979). Studying the interaction between duration and magnitude of presses and pulses is important for understanding their long-term effects on ecosystems (Ratajczak et al., 2017).

Coastal waters receive hydrologic presses and pulses from both fresh and marine water, and understanding how these hydrologic changes are affecting the production, processing, and storage of carbon is needed to protect coastal waters (Harris et al., 2018). Sea-level rise and its associated subsidies and stressors (including nutrients and salinity) present a fundamental threat to coastal wetland ecosystems due to a persistent press of marine water. These subsidies and stressors, acting on ecosystems that in many cases are already degraded, have the potential to rapidly change the important role of coastal wetlands in carbon storage, with examples such as Everglades peat collapse highlighting the importance of tracking the effect of changing subsidies and stressors (Chambers et al., 2019; Mcleod et al., 2011; Pendleton et al., 2012). Fresh and marine water pulses have distinct biogeochemical signatures that allow for the use of chemical tracers to understand their relative contributions to ecosystem carbon transfer between ecosystems (Hobbs et al., 2007; Jaffé et al., 2004; E. P. Odum et al., 1979; Smith et al., 2023). Many aquatic ecosystems are highly pulse-driven but have been engineered to be less so (W. E. Odum et al., 1995), leading to recent efforts to restore aquatic ecosystems (Poff et al., 2007). Increasing hydrologic connectivity in coastal ecosystems—which occurs with sea-level rise as well as restoration—can increase and synchronize nutrients and microbial activities (Kominoski et al., 2020). The press of sea-level rise increases marine water intrusion that alters soil and water chemistries (Herbert et al., 2015; Tully et al., 2019) and influences wetland plant productivity and net ecosystem carbon storage (Ishtiaq et al., 2022; Wilson et al., 2019). Restoration of degraded ecosystems is increasing water levels and reducing light attenuation and oxygen availability to the benthos, all of which change relative contributions and production of autochthonous and allochthonous carbon (Cory et al., 2014; Howard-Parker et al., 2020).

Dissolved organic matter (DOM) connects terrestrial carbon with aquatic ecosystems and is an important component of the hydrologic and carbon cycles (Battin et al., 2009). Both externally and interally produced DOM are transported through aquatic ecosystems where they are involved in a variety of biogeochemical processes, including regulating nutrient cycling, light attenuation, and controlling the microbial loop (Amon & Benner, 1996; Qualls & Richardson, 2003). The composition of DOM is determined by a combination of its source and how it is transformed as it moves across the landscape, both of which determine its availability as a substrate for microbes (Helms et al., 2018; Medeiros et al., 2017). The composition of DOM, which varies by carbon source, can alter bacterial processing of organic matter indicated by shifts in DOM fluorescence (Jaffé et al., 2004; Osburn, Atar, et al., 2019). Pulse events can rapidly change the composition of DOM, and discrete events such as hurricanes have been shown to modify regional carbon cycling for prolonged periods (e.g., months) following pulse events, leading to large functional shifts in microbial processing of DOM in disturbed areas (Osburn, Rudolph, et al., 2019). Changing water levels, in response to both hydrologic presses and pulses, play a strong role in controlling the transport and production of DOM in coastal wetlands, but it is unclear how that relationship is responding to the combination of hydrologic changes caused by restoration and sea-level rise (Regier et al., 2020).

In slow-flowing coastal wetlands, water levels and water sources are master variables that influence organic carbon concentrations, sources, processing, and export (Kominoski et al., 2020; Regier et al., 2020). Water carries subsidies that have the potential to release both stoichiometric and redox constraints of decomposers, which can lead to abrupt changes in carbon cycling (Saha et al., 2011; Servais et al., 2019). As DOC concentration and DOM composition change in these ecosystems as a result of hydrologic presses and pulses from fresh and marine water, predicting future changes to them remains uncertain (Regier et al., 2020). To address this uncertainty, we tested two major questions: (a) How does spatiotemporal variability in water level affect DOC concentrations and DOM composition along gradients of phosphorus and salinity in peat and marl coastal wetlands? (b) How do changes in DOC concentrations and DOM composition interact with bacterioplankton productivities along phosphorus and salinity gradients in peat and marl coastal wetlands? To understand how increasing water levels from upstream restoration and downstream sea-level rise are altering production, processing, and transport of DOC, we analyzed long-term DOM fluorescence, bacterioplankton productivities, and concentrations of surface water chemistry [DOC, total nitrogen (TN), and total phosphorus (TP)] along two coastal wetland gradients in the Florida Everglades that differ in hydrology and organic carbon sources. In the Florida Everglades changes to water delivery, through the Combined Operations Plan has increased the amount of water entering the park, changing both water levels and surface water chemistry throughout the system. We used time-series analyses and evaluated fluorescent properties of DOM to test how hydrologic pulses of fresh and marine water, and their associated resource subsidies and stressors, are altering the sources, production, processing, and movement of organic carbon in the

Florida Coastal Everglades (FCE). We analyzed how long-term increases in water levels influenced DOC concentrations (2001–2021) and DOM composition (2011–2021) in fresh and brackish water marshes and mangroves in both peat- and marl-dominated drainages. We predicted that increases in water levels in freshwater marshes would increase the import of externally produced DOM from upstream wetlands and decrease internal production of DOM both through suppression of detrital breakdown, and through dilution by incoming water. We predicted that the composition of DOM would be determined by the extent of seasonal increases in as subsidies of phosphorus release nutrient limitation, and subsidies of sulfate release redox constraints in the ecotone and mangroves. Finally, we predicted that seasonal increases in marine-derived externally produced DOM would drive increases in bacterioplankton productivity with easily processed inputs of labile marine carbon.

2. Materials and Methods

2.1. Site Description and Experimental Design

We analyzed long-term data from the FCE, an International Biosphere Reserve, World Heritage Site, and Ramsar Wetland of International Importance. The Everglades ranges from Lake Okeechobee in central Florida to Florida Bay at the southern tip of the state. It consists of a series of highly oligotrophic, diverse, and heterogeneous wetlands, with variation in hydrology, productivity, and relative nutrient limitation (Castañeda-Moya et al., 2013; Noe et al., 2001). The hydrology of the Everglades was radically altered starting in the early 1900s with the construction of drainage canals which created agricultural and inundated areas. Current restoration is focused on restoring sheet flow across the Everglades during the wet season (May–October), when the area receives over 70% of its total rainfall. As part of restoration efforts, phosphorus from upstream farming has been removed from water coming into Everglades National Park (ENP) by a series of water management areas. However, freshwater restoration appears to be mobilizing stores of legacy phosphorus from hotspots in degraded wetlands, leading to increasing phosphorus concentrations where restorative freshwater is entering the system (Sarker et al., 2020). Phosphorus also enters the system from marine water; phosphorus in Florida Bay and the Gulf of Mexico are low in concentration (0.25–0.65 μmol/L; Fourqurean & Zieman, 2002), but they still have slightly higher concentrations than the extremely oligotrophic coastal mangroves and inland freshwater wetlands. This dynamic means that pulses of both fresh and marine water can lead to increasing phosphorus delivery to interior ecosystems of the Everglades, making it an ideal location to study how those pulses can change biogeochemical cycling.

We analyzed data from the FCE-LTER sampling sites within the two major drainages of the Everglades: Shark River Slough (SRS) and Taylor Slough (TS/Ph). We focused our analysis on six paired focal sites, from each drainage (with the best data coverage for each type): two freshwater marsh (SRS-2, TS/Ph-2), two ecotone (SRS-4, TS/Ph-3), and two mangrove (SRS-6, TS/Ph-7; Figure 1). We defined our ecotones, as areas at the transition between freshwater marsh and mangrove wetlands. We also included data from the full range of inland FCE-LTER sites (SRS 1–6, TS/Ph 1–7). SRS is a wide, deep, and higher-productivity drainage of long-hydroperiod wetlands (inundated for >9 months of the year), which transition from sawgrass-dominated, ridge and slough peat marshes to tidal riverine mangrove forests connecting to the Gulf of Mexico (Castañeda-Moya et al., 2013; Childers et al., 2006). TS is a smaller, shallower, and lower-productivity drainage of short-hydroperiod wetlands (inundated for <9 months of the year), which transition from sawgrass- and periphyton-dominated marl marsh prairies to microtidal shrub mangrove forests draining into the shallow Florida Bay seagrass estuary. Productivity in TS is highest in the ecotone, where marine groundwater upwelling brings subsidies of phosphorus inland (Ewe et al., 2006). When moving from freshwater to marine ecosystems in SRS, DOC decreases in concentration and becomes less influenced by decaying organic matter (humic) and more microbially derived (Regier et al., 2020). TS has very low concentrations of DOC in the freshwater and derives most of its DOM from the mangroves, becoming more humic as mangrove densities increase (Kominoski et al., 2020; Regier et al., 2020).

2.2. History of Disturbance and Restoration

The Everglades has experienced a series of important disturbances and restoration efforts over the past 20 years while the FCE-LTER has monitored the Everglades. Both Everglades drainages have been impacted by major hurricanes (2005, 2017), cold snaps (2010, 2011), fire (2008), drought (2010, 2015, 2021), and flooding (2015). The Comprehensive Everglades Restoration Plan was authorized by the U.S. Congress in 2000 as a multi-agency plan and is one of the biggest restoration efforts in the world. A series of joint plans, including the Combined Operational Plan and the Modified Water Deliveries plan, have been working to create new canals, reservoirs, and

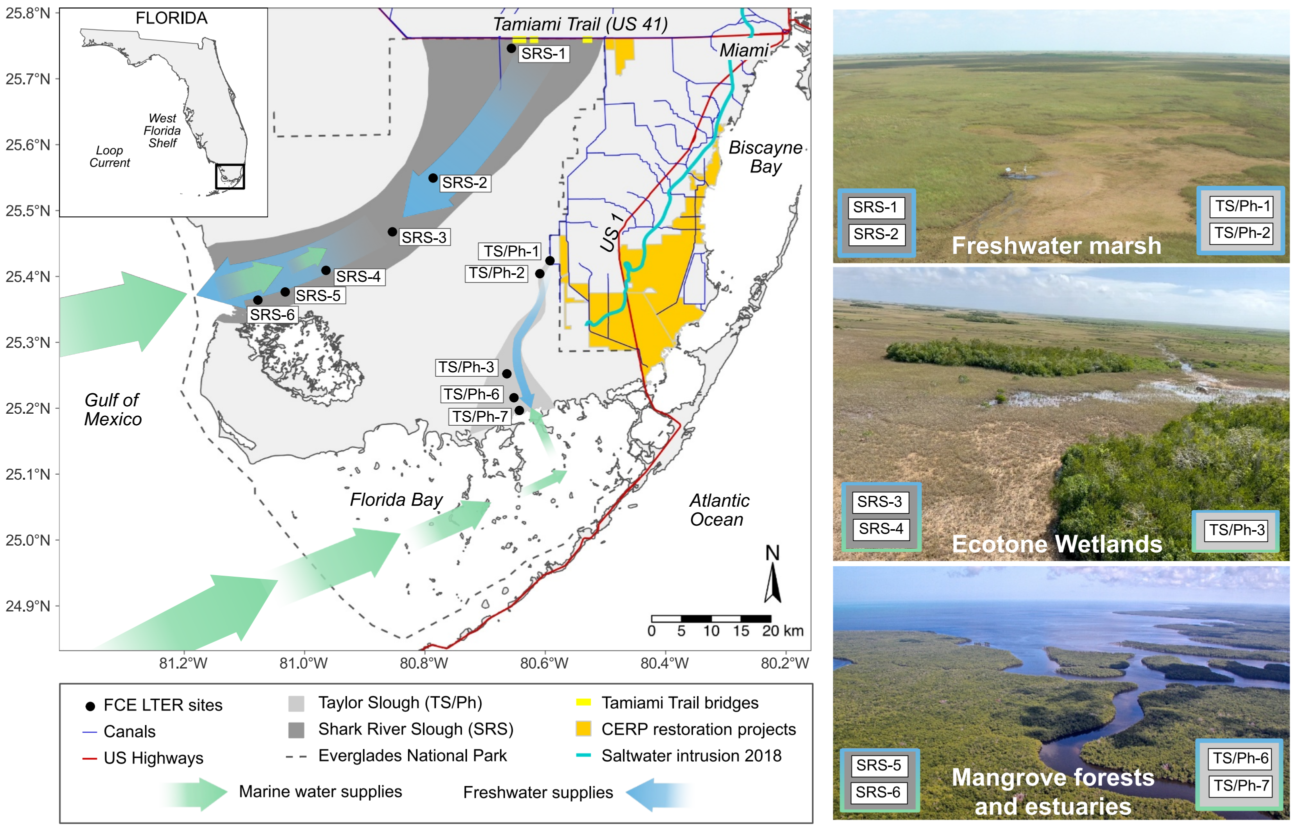

Figure 1. Location of the study sites in the Florida Coastal Everglades (FCE), Everglades National Park in South Florida, USA. We sampled at a marsh, ecotone and mangrove site along the long-hydroperiod peat drainage of Shark River Slough (SRS-2, -4, -6), and the short hydroperiod marl drainage of Taylor Slough (TS/Ph-2, -3, -7). All sites are part of the FCE Long Term Ecological Research (FCE-LTER) program.

culverts to move water into and through ENP. In 2012, a series of canals and pumping stations, including the C-111 and Aerojet canals, were constructed to transport more water into TS. A year later in 2013, a 1.6-km bridge was constructed along Tamiami Trail to allow more water to enter SRS. In 2015 and 2017, flow was increased (under the Combined Operational Plan) to transport water from outside of the park to both Shark River and TS. In 2019, another 3.7-km bridge was completed along Tamiami Trail, and the combination of the two bridges increased the total water entering ENP by nearly 80% (McLean, 2015).

2.3. Surface Water Physicochemistry

Average monthly measurements of surface water levels were collected from 2001 to 2021 at water level stations for marsh (Kominoski et al., 2022; Troxler and Childers, 2022) and mangrove sites (Castañeda-Moya & Rivera-Monroy, 2021). Water levels in riverine mangroves were collected within the mangroves (not in the channel of the river), and positive values indicate a water level above the soil surface, while negative values indicate water level is below the soil surface. Any data gaps were filled by auxiliary data gathered by the U.S. Geological Survey Everglades Depth Estimation Network at the closest station to the focal site collected (SRS [NP201, P36, MO-215, TE, Gunboat Island, SH3]; TS/Panhandle [NTS1, TSB, E146, UTR, TRM]). We created linear models between water level and EDEN water level and used those models to predict water level where there were data gaps (Haider et al., 2020). The linear model fit and the percentage of data gaps filled by this method for each site was as follows: SRS-2 (R^2 = 0.89, 11%), SRS-4 (R^2 = 0.52, 24%), SRS-6 (R^2 = 0.47, 15%), TS/Ph-2 (R^2 = 0.76, 1%), TS/Ph-3 (R^2 = 0.59, 3%), TS/Ph-7 (R^2 = 0.73, 54%).

Monthly surface water grab samples were collected from 2001 to 2021 at all sites for DOC, TN, TP, and salinity concentrations (Gaiser et al., 2023; Kominoski et al., 2022; Troxler, 2023). TP was measured following the method of Solórzano and Sharp (1980). TN was measured using an Antek TN analyzer (Antek Instruments, Houston, Texas, USA). Dissolved organic carbon concentrations were measured using filtered water samples (0.7-μm GF/F filters; Whatman, Maidstone, UK) with a Shimadzu TOC Analyzer (Shimadzu Corporation, Columbia, Maryland, USA). All water chemistry analyses were conducted by the CREST CAChE Nutrient Core Facility, which is NELAC Certified for non-potable water-General Chemistry under State Lab ID E76930.

2.4. Bacterioplankton Productivity

Bacterioplankton productivity was measured from monthly surface water grab samples at each site (Briceño, 2023). Samples were collected, placed on ice, and filtered with 0.2-μm mesh nitrocellulose filters at the laboratory within 24 hr. Bacterioplankton productivity was quantified as uptake of tritiated thymidine during 1-hr incubations in the laboratory at 22°C. Each duplicate sampling per site was incubated with three replicates and one blank for each sample, and carbon uptake was calculated using linear growth rate constants (Bell, 1993).

2.5. Fluorescent Optical Properties of DOM

Fluorescence spectroscopy was performed on filtered samples from 2011 to 2021 at our six focal sites (SRS-2, SRS-4, SRS-6, TS/Ph-2, TS/Ph-3, TS/Ph-7) and from 2019 to 2021 at the remaining sites (SRS-1, SRS-4, SRS-5, TS/Ph-1, T/Ph-6) to determine the chemical composition of the DOM of each sample (Kominoski & Smith, 2023). Fluorescence excitation-emission matrices (EEMs) from before 2011 are available (Regier et al., 2020) but were not included in this study because they were measured using a decommissioned Fluoromax-3 fluorometer that is not comparable to the Aqualog. Here, fluorescence EEMs were measured on a Horiba Aqualog (Jobin Yvon Horiba, France) with 150 W continuous output xenon lamp. Samples were measured at room temperature at 3 nm wavelengths over excitation wavelength (λex) intervals between 240 and 455 nm and an emission wavelength (λem) range of 250–705 nm in a 1 cm quartz cuvette. EEMs were corrected for inner filtering effect, Raman normalized, and blank subtracted using in-house processing codes written in MATLAB R2019a (Mathworks, Natick, MA, USA).

2.6. Data Analyses

DOM fluorescence was processed using the drEEM 3.0 toolbox in MATLAB R2019a to calculate five common metrics of DOM fluorescence: Fluorescence Index (FI; McKnight et al., 2001), Humification Index (HIX; Zsolnay et al., 1999), Biological Index (BIX; Huguet et al., 2009), Specific UltraViolet Absorbance at 254 nm ($SUVA_{254}$; Weishaar et al., 2003), Slope ratio (S_R; Helms et al., 2008). FI is calculated as the emission at 470 nm divided by emission at 520 nm for excitation at 370 nm and indicates a balance between microbial and terrestrial sources of DOM, and typically ranges between 1.2 and 1.9. HIX is calculated as the area under the emission curve between 435 and 480 nm divided by the area under the emission curve between 300 and 345 nm for excitation at 254 nm, indicates humification of DOM and typically ranges between 2 and 16. BIX is calculated as emission at 380 nm divided by emission at 430 nm for excitation at 310 nm, indicates contributions of local production to DOM, and typically ranges from 0.6 to 1. $SUVA_{254}$ is calculated as the decadal absorption of light at 254 nm divided by DOC concentration, is an indicator of aromaticity, and typically ranges from 0.5 to 5.3. S_R is calculated as the best fit slope of the natural log of absorbance from 275 to 295 nm divided by the slope of the natural log absorbance between 350 and 400 nm, is an indicator of molecular weight, molecular composition, and photobleaching, and typically ranges from 0.7 to 10. Across the listed fluorescence metrics there is some degree of overlap, and no single metric tells the full story of DOM composition, so care should be taken in interpretation of fluorescence results. Our goal with fluorescence metrics was to support our understanding of the relationship between water levels and DOC concentrations, and to use fluorescence to better understand temporal changes in sources of organic carbon. To that end, we elected to use fluorescence indices as opposed to parallel factor analysis (PARAFAC). The aforementioned fluorescence indices are the most parsimonious data available to answer our questions of interest about the sources of organic carbon present at each site. A full investigation of individual PARAFAC components may provide valuable information about carbon cycling in the Everglades but was beyond the scope of this study. We are focused instead on understanding how water level works as a master variable to control carbon processing across the Everglades landscape, and the fluorescence indices facilitate that understanding.

To understand how bacterioplankton productivity responds to the composition of DOM, we performed a Principal Component Analysis for each site in R, using the base R function "prcomp." We created principal components of

DOM using concentrations of DOC, TN, and TP, as well as fluorescence measures FI, HIX, BIX, $SUVA_{254}$, and S_R. TN and TP are both measures of total unfiltered nutrients, but we grouped them with fluorescence measures; Everglades phosphorus is so rapidly taken up that concentrations of soluble reactive phosphorus are frequently undetectable. TN and TP give a more reliable measure of nutrients available in the water column. All variables were centered and standardized to the same scale before the creation of principal components using the scale function in R, for each site.

To understand both seasonal and pulse dynamics of DOC, water level, and bacterioplankton productivity, we computed both single and cross-wavelet power spectra by applying the Morlet wavelet, using the package WaveletComp in R (Roesch & Schmidbauer, 2022). We employed cross-wavelet power spectra analysis to better understand both how correlation between DOC and water level change over time, as well as the phase differences and time-lags between variables at endmember sites for each slough. We performed these analyses at freshwater and mangrove endmember ecosystems for Shark River and TS (SRS-2: peat freshwater, SRS-6: peat riverine mangrove, TS/Ph-2: marl freshwater, TS/Ph-7: marl shrub mangrove). We chose to focus on the endmember sites as the sites that are furthest up and downstream, which are the most influenced by incoming pulses of fresh or marine water, respectively, and which also had the best data coverage available. Wavelet analysis requires continuous data, so we gap-filled any missing values for DOC and bacterioplankton productivity with the median value for the site to provide the most conservative estimate for a specific date. We elected to gap fill with the median value as both DOC and bacterioplankton productivity concentrations can be highly variable. The percent data gap filled for DOC at each site is as follows: SRS-2 (6%), SRS-6 (1%), TS/Ph-2 (25%), TS/Ph-7 (3%). The percent data gap filled for bacterioplankton productivity at each site is as follows: SRS-2 (12%), SRS-6 (8%), TS/Ph-2 (32%), TS/Ph-7 (17%). We used cross-wavelet power spectra to analyze the coherence and time-lags between DOC and water level over time, and we used single wavelet power spectra to understand how temporal bacterioplankton productivity has shifted over the past 20 years. We estimated the significance level of wavelet coherence using the Monte Carlo permutation test. For a more in-depth description of the use of wavelet analysis in ecological research, see Cazelles et al. (2008).

We constructed linear models to track the relationships between biogeochemical covariates, both for use independently and in comparison, and the wavelet analysis methods. All analyses were performed using R version 4.2.0, and all plots were constructed using the ggplot2 package (Wickham, 2009; R Core Team, 2022).

3. Results

3.1. Surface Water Physicochemistry

TP increased across the spatial gradient from freshwater to marine, with freshwater sites ranging from 0.26 μmol/L in TS marl marshes to 0.37 μmol/L in SRS peat marshes and mangrove sites ranging from 0.40 μmol/L in TS shrub mangroves to 0.71 μmol/L in SRS riverine mangroves (Table S1 in Supporting Information S1). TN varied by drainage, with freshwater sites ranging from 34.50 μmol/L in TS marl marshes to 70.34 μmol/L in SRS peat marshes and mangrove sites ranging from 51.15 μmol/L in TS shrub mangroves to 34.40 μmol/L in SRS riverine mangroves (Table S1 in Supporting Information S1). Dissolved organic carbon followed opposite patterns in SRS and TS; peat marshes had high concentrations (19 mg/L) that decreased by nearly half (9.8 mg/L) closer to the coast. Dissolved organic carbon concentrations in TS were lower in the marsh (7.3 mg/L) and increased at the coast (12.3 mg/L; Table S1 in Supporting Information S1).

3.2. Long-Term Patterns of Changing Hydrology and DOM

Over the past 20 years, water level increased at all sites except for TS/Ph-2 (Figure 2). TP increased at all sites except for TS/Ph-7, and over the past 10 years microbially processed DOM (FI) decreased at all sites (Table 1; Figure S1 in Supporting Information S1). In riverine mangroves, S_R increased suggesting that the molecular weight of DOM decreased (Chen et al., 2010). In SRS freshwater peat marshes, humic contributions to DOM (HIX, $SUVA_{254}$) increased, while algal contributions (BIX) decreased (Table 1). In contrast, detrital contributions to DOM (HIX) in TS freshwater marl marshes decreased (Table 1). In the marl ecotone marsh (TS/Ph-3), algal contributions to DOM (BIX) decreased, while the aromaticity of DOM increased ($SUVA_{254}$; Table 1).

Water level was negatively correlated with DOC concentration in all freshwater sites except TS/Ph-1 (Figure 3). There was no correlation between water level and DOC concentration in SRS mangrove sites; however, in TS/Ph-

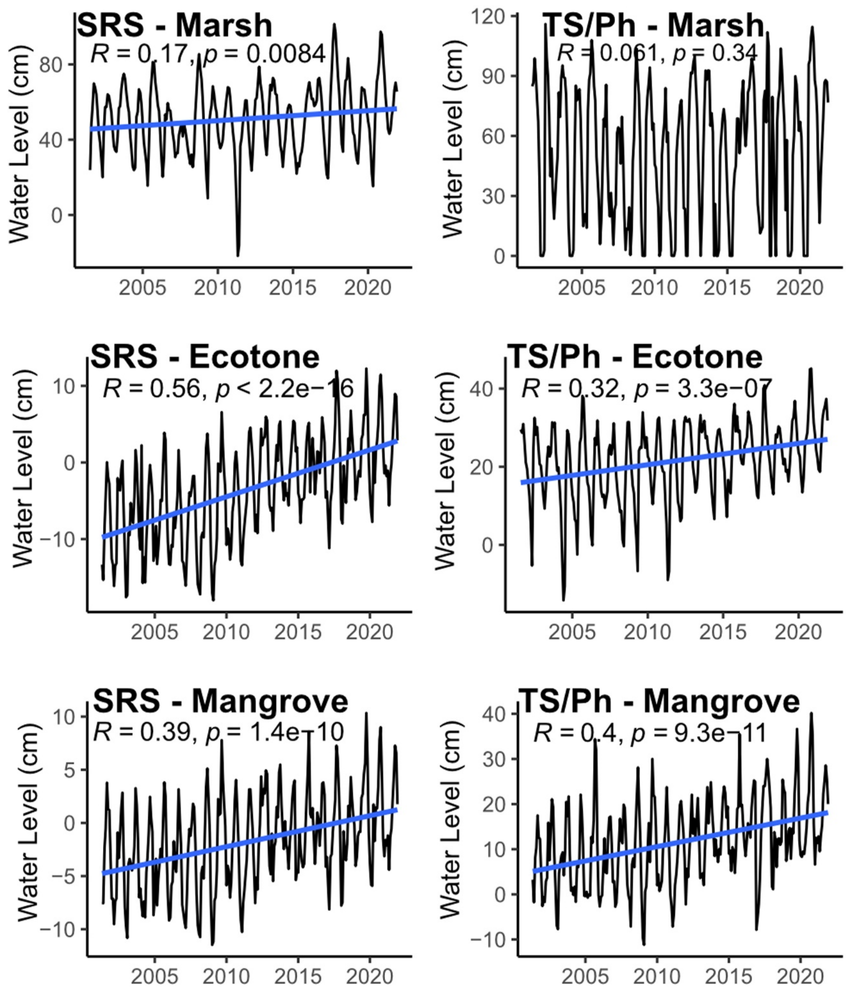

Figure 2. Changing water level over time in marsh, ecotone, and mangrove sites along the long-hydroperiod peat marshes of Shark River Slough (SRS-2, -4, -6), and the short-hydroperiod marl marshes of Taylor Slough (TS/Ph-2, -3, -7).

Table 1
Linear Models of Nine Metrics of Dissolved Organic Matter, Over Time

	SRS 2		SRS 4		SRS 6		TS/Ph 2		TS/Ph 3		TS/Ph 7	
Variable	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*
Level (cm)	2.066	0.041	3.035	<0.001	2.012	0.047	1.133	0.259	3.072	0.003	2.860	0.005
DOC (μmol/L)	0.718	0.474	1.300	0.196	1.321	0.189	−1.029	0.305	−2.004	0.047	1.216	0.226
TP (μmol/L)	5.393	<0.001	4.194	<0.001	2.078	0.040	3.082	0.003	3.211	0.002	−0.348	0.728
TN (μmol/L)	−0.121	0.904	1.923	0.057	4.544	<0.001	2.954	0.004	−0.037	0.970	3.850	<0.001
FI	−4.216	<0.001	−3.573	<0.001	−3.777	<0.001	−2.288	0.024	−2.376	0.020	−3.447	<0.001
BIX	−4.574	<0.001	−0.476	0.635	0.832	0.407	−0.129	0.897	−2.867	0.005	−0.596	0.553
HIX	5.788	<0.001	0.212	0.833	−0.294	0.77	−2.929	0.004	−0.652	0.515	−1.661	0.099
$SUVA_{254}$ (L/mg C-m)	2.114	0.0367	0.782	0.436	−0.433	0.666	−0.261	0.795	2.803	0.006	−0.754	0.452
S_R	−1.219	0.225	2.731	0.0073	5.217	<0.001	1.704	0.091	0.843	0.401	−0.588	0.557

Note. Linear models were constructed for the change in total nitrogen (TN, μmol/L), total phosphorus (TP, μmol/L), dissolved organic carbon (DOC, μmol/L) over the past 20 years and five fluorescence metrics over the past 10 years. The fluorescence metrics included are: Fluorescence Index (FI), Humification index (HIX), Biological Index (BIX), Specific absorbance at 254 ($SUVA_{254}$), Slope ratio (S_R).

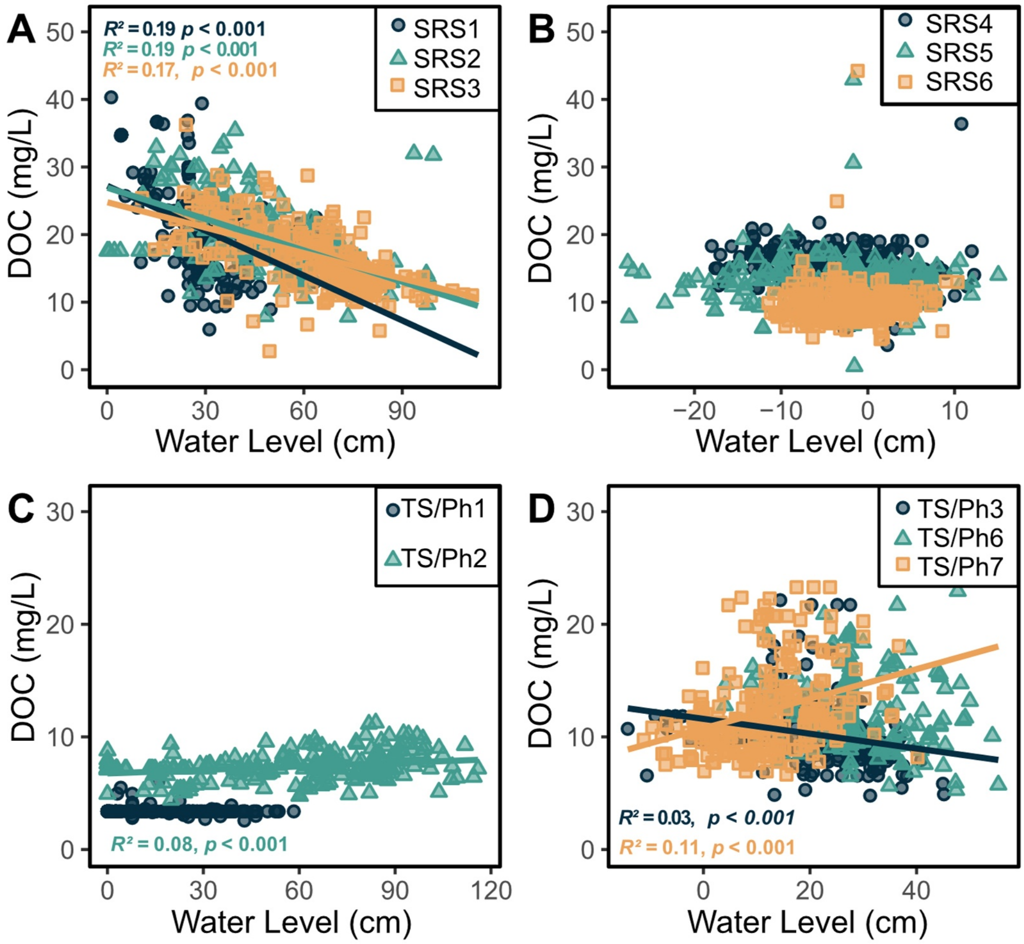

Figure 3. Linear relationships between dissolved organic carbon and water level for all sites in the long-hydroperiod Shark River Slough (SRS-1:6) and short-hydroperiod Taylor Slough (TS/Ph-1:7).

7, there was a significant positive correlation between DOC concentration and water level (Figure 3). There was a significant negative correlation between water level and BIX across freshwater peat marshes and both riverine and shrub mangroves, as well as a positive correlation between water level and HIX at freshwater peat marsh and TS mangroves (Figure 4).

Both DOC and water level rapidly change, and time series measurements of both variables are highly auto correlated, requiring time series analysis to better understand the relationship between variables. We utilized wavelet analysis, which allowed us to pick out inconsistent patterns across a time series, and to better understand the relationship between variables. Wavelet power is calculated as the comparison of our time series at a specific time point (as seen on the x axis) to a series of hypothetical wave functions of varying periods (as seen on the y axis). Higher wavelet power then means that our time series is acting similar to the wavelet of a certain period at a certain time. Our plots show cross-wavelet analysis, and cross-wavelet power means that both of our variables are matching with the hypothetical wave at a certain timepoint. The arrows in the plot indicate whether the waves of our two variables are in phase (moving in the same direction), or out of phase (moving in opposite directions; Figure 4).

Linear models of the relationship between water level and DOC concentration grouped by ecosystem type (marsh vs. mangrove) showed similar results to the stronger wavelet patterns, but wavelet analysis accounted for inconsistent, or changing patterns that standard regression is unable to account for. Cross-wavelet power spectra showed significant wavelet power at the 12-month period (indicating that both DOC and water level are going through an annual cycle at the given point in time where the 12-month period is significant) for all sites, but only SRS freshwater marsh and TS shrub mangroves had significant wavelet power across the entire time series of

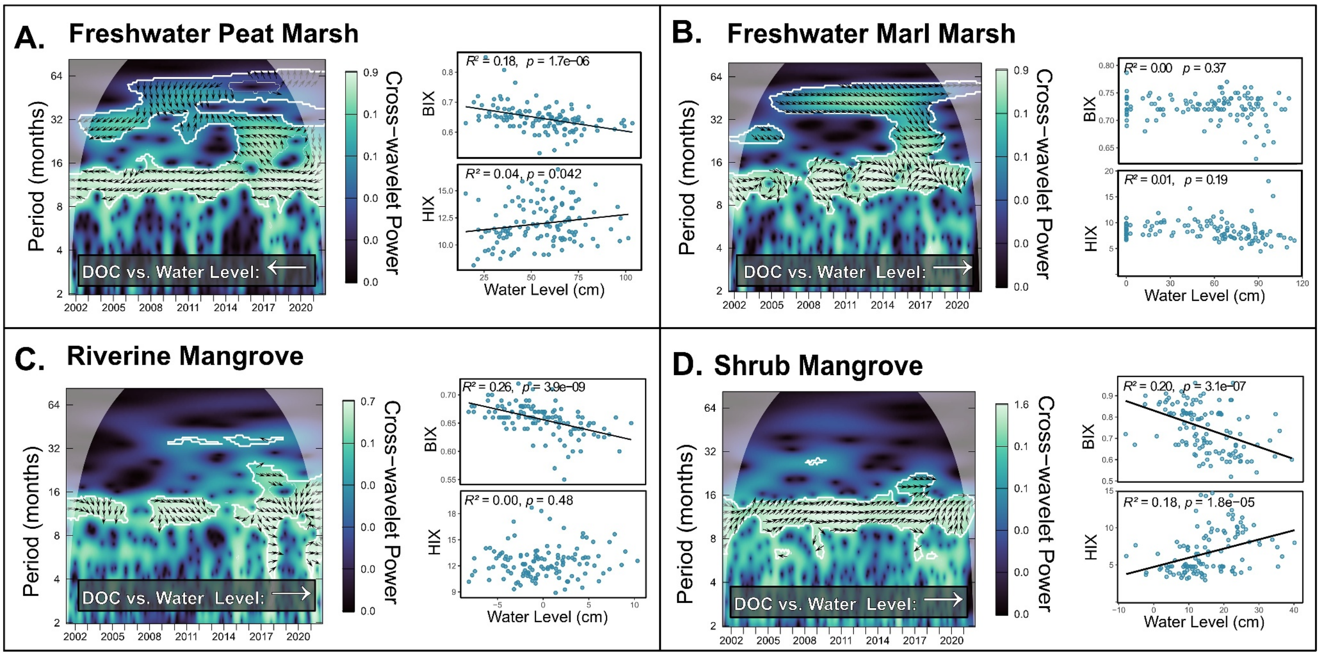

Figure 4. Trends in dissolved organic carbon (DOC) concentrations and dissolved organic matter quality in Everglades freshwater peat marsh (a), marl (b) marsh, riverine (c), and shrub (d) mangrove habitats. White contour lines in wavelet plots indicate statistically significant cross-wavelet power between DOC concentrations (μmol/L) and water level (cm). Arrows are plotted where wavelet power is significant, and the direction of arrows at each time point describes the relationship between the two variables. Right-facing arrows indicate the two variables are in phase, while left-facing ones indicate the variables are out of phase. Arrows facing up indicate that changes in level lag after changes in DOC, while arrows facing down indicate that changes in DOC lag after changes in level. Below each plot we have included the most consistent trend in the relationship between DOC and water level over the full time period. The scatterplots use two fluorescence metrics: Biological Index (BIX) and Humification Index (HIX). Increasing BIX indicates increasing algal influence on DOC, while increasing HIX indicates increasing humic influence on DOC.

20 years (Figure 4). At mangrove sites, DOC concentration and water level were largely in phase; at SRS freshwater sites, DOC and water level were consistently out of phase (Figure 4). The TS freshwater marl marsh time series had no consistent phase relationship between DOC concentration and water level (Figure 4b). In SRS mangroves, we detected disturbance and pulse events had the most significant impacts on the relationship between DOC and water level during the multiple periods in which Hurricane Irma (2017) increased wavelet power (Figure 4c). Notably, there were long periods of significant correlation between water level and DOC (the majority of the time series) in the Shark River mangroves despite a lack of overall relationship between DOC and water level found with regression analysis. This highlights the importance of our observing the relationship between DOC and water over time in these data sets because we show that it is not stable across the whole landscape.

3.3. Dissolved Organic Matter Composition

DOM was highly humic in SRS, with HIX ranging from an average of 12.12 in the marsh to 12.41 in the riverine mangroves. In TS, DOM was only moderately humic with averages ranging from 8.35 in the marsh to 6.73 in the shrub mangroves. Algal contributions to DOM (BIX) were very low in SRS, with averages from 0.64 to 0.65, and only somewhat higher in TS, with averages from 0.72 to 0.74. Aromaticity ($SUVA_{254}$) was higher in SRS and increased from marsh to mangroves, with an average of 2.85 in the marsh to 3.37 in the riverine mangroves. TS was lower in aromaticity and did not vary across the slough, with averages from 2.58 in the marsh and 2.59 in the shrub mangroves. The SR of DOM (S_R) was higher in SRS, ranging from an average of 0.97 in the marsh to 1.09 in the riverine mangroves, while in TS S_R ranged from an average of 1.07 in the marsh to 1.23 in the shrub mangroves. These S_R values indicate a lower molecular weight in marine sites and could also indicate higher photobleaching further downstream (Helms et al., 2008). Microbial contributions to DOM (FI) were even across SRS, ranging from 1.50 in the marsh to 1.52 in the mangroves, and were higher in TS, where they decreased from 1.58 in the marsh to 1.53 in the mangroves.

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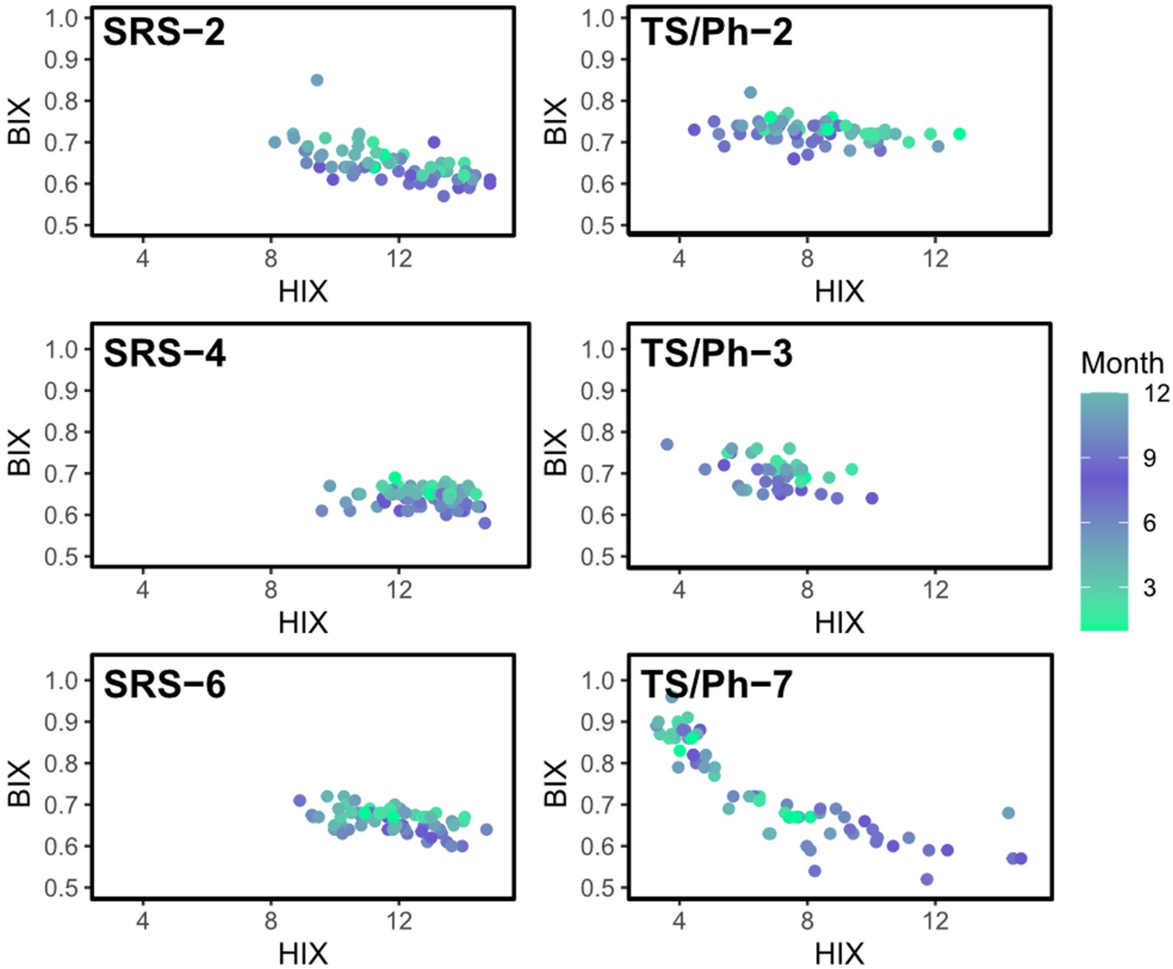

Figure 5. Seasonal changes in Humification Index (HIX) and Biological Index (BIX) in marsh, ecotone, and mangrove sites along the long-hydroperiod peat marshes of Shark River Slough (SRS-2, -4, -6), and the short-hydroperiod marl marshes of Taylor Slough (TS/Ph-2, -3, -7). Increasing BIX (Biological Index) indicates more prevalent local influence on dissolved organic matter (DOM). Increasing HIX indicates more prevalent humic influence on DOM. Blue colors signify the wet season (May–October) while green colors signify the dry season.

We found seasonal shifts in DOM composition which appear to be driven by changing water sources. In SRS peat marshes, wet-season DOC became lower in concentration, while in the dry season microbial and algal influence becomes more common and DOC concentrations increased (BIX, FI; Figure 5). In TS marl wetlands, freshwater upstream inputs increased concentrations of DOC and nutrient loading in the wet season but increased in microbial processing (FI) in the dry season. At both SRS peat (R^2 = 0.16, $P < 0.001$) and TS marl (R^2 = 0.57, $P < 0.001$) ecotone sites, HIX significantly increased with salinity, but there was no relationship at downstream mangroves. To better understand carbon movements in the mangroves we used the full complement all 5 FCE-LTER mangrove sites and found that salinity had a significant relationship with BIX at the most downstream mangroves in both SRS peat ($R^2 = 0.21$, $P < 0.001$) and TS marl ($R^2 = 0.38$, $P < 0.001$) sites and at the upstream ecotone in the peat ($R^2 = 0.06$, $P < 0.05$), but not in the middle mangroves (SRS-5; Figure 6).

3.4. Bacterioplankton Productivity

To investigate whether bacterioplankton productivity played a role in altering DOM composition, we created principal components of DOM using concentrations of DOC, TN, and TP, as well as fluorescence measures FI, HIX, BIX, $SUVA_{254}$, and S_R. We found no correlation between either of the first two constructed principal components of DOM and bacterioplankton productivity at any site except for SRS-2 ($R^2 = 0.09$, $P < 0.001$), and TS/Ph-7 ($R^2 = 0.03$, $P = 0.03$). Wavelet power spectra showed that bacterioplankton productivity does not have a

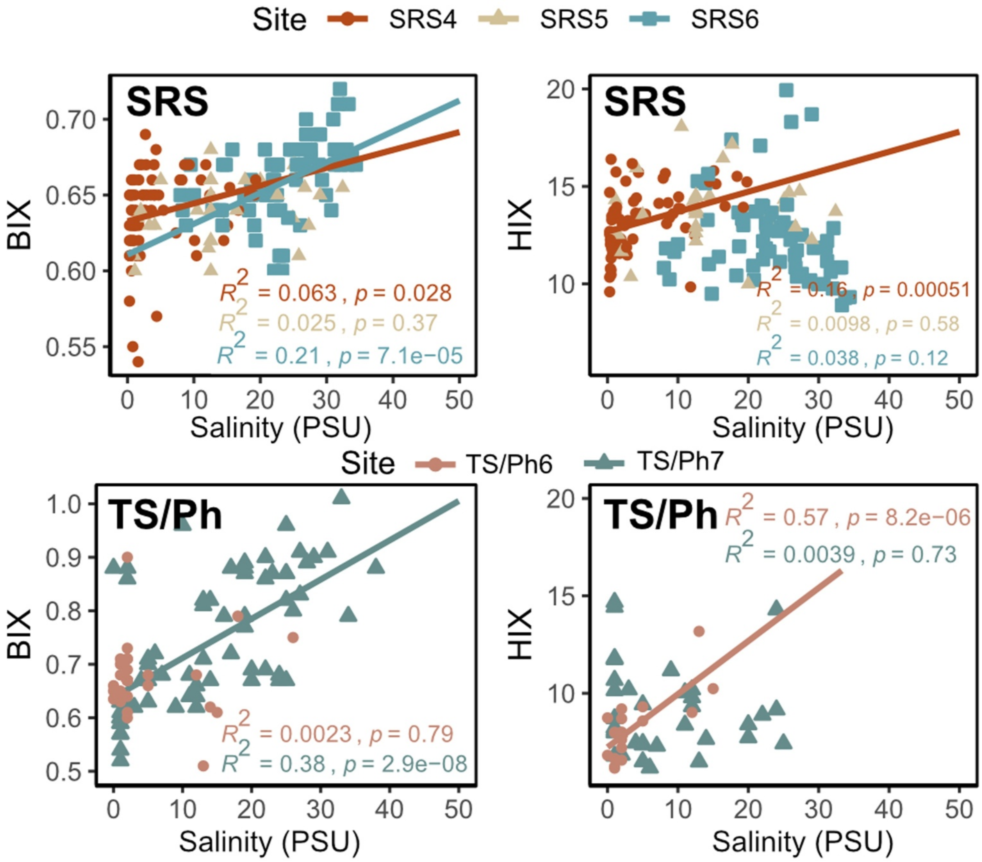

Figure 6. Salinity as a driver of Biological Index (BIX) and Humification Index (HIX) at mangrove sites in the riverine mangroves of the peat-based Shark River Slough (SRS-4, -5, -6) and the shrub mangroves of the marl-based Taylor Slough (TS/Ph-6, -7). Data on fluorescent dissolved organic matter (DOM) ranges from 2011 to 2021 at SRS-4, -6, and TS/PH-7 and ranges from 2019 to 2021 at SRS-5, and TS/Ph-6. Increasing BIX indicates increasing local influence on DOM. Increasing HIX indicates increasing humic influence on DOM.

consistent annual pattern; it instead is associated with changing water level only during disturbance pulse events (Figure S2 in Supporting Information S1).

4. Discussion

Restoration of the Florida Everglades is occurring at the same time as sea-level rise and increasingly frequent disturbance events (Hobbs et al., 2007; Tully et al., 2019). As such, coastal nutrient subsidies come from both freshwater and marine sources, as restoration mobilizes legacy phosphorus from freshwater sources (Sarker et al., 2020), and marine water has higher phosphorus concentrations than the highly oligotrophic Everglades freshwater marshes (Kominoski et al., 2020). At the same time, increasing salinity from marine water is a stressor to coastal ecosystems, leading to large shifts in ecosystem function and structure. These include the collapse of carbon-rich peat stores (Chambers et al., 2019) and increasing subsidies of marine DOM to coastal ecosystems (Zeller et al., 2020). Predicting the fate of restored systems relies on an understanding of the interactions between multiple drivers of ecosystem trajectories (Kominoski et al., 2018).

Water levels and water sources are master variables in aquatic ecosystems that are linked to fluxes of carbon across aquatic ecosystems (Strack et al., 2011; Wen et al., 2020). Our wavelet analysis showed a consistent relationship between water level and DOC concentrations where DOC concentrations are the highest at lowest water levels, agreeing with previous work showing that freshwater peat marshes and shrub mangroves are the major sources of DOM production in the Everglades (Regier et al., 2016). A shift from more labile (FI, BIX) to more recalcitrant (HIX, $SUVA_{254}$) DOM in the Everglades peat marsh over the study period suggests that the mobilization of legacy phosphorus (Sarker et al., 2020) is leading to higher production of recalcitrant DOC both in the peat marsh and in upstream marshes of the greater Everglades (Yamashita et al., 2010). This is often seen in peatlands where increasing water flow flushes more recalcitrant DOM out of the system (Austnes et al., 2010).

Seasonal shifts in the composition of DOM and concentration of DOC can further clarify how water levels are changing the makeup of Everglades carbon. In peat marshes, high water levels correspond with lower DOC concentrations and BIX (i.e., algal derived DOM), but higher HIX (i.e., detrital DOM). This pattern suggests that high water levels in the wet season flush high concentrations of locally produced DOC to downstream ecosystems, reducing the algal influence on DOM, while low-concentration inputs of highly humic DOM from upstream peat marshes increase the detrital signal (HIX). The reduction in algal DOM may be a response to reduced light attenuation caused by higher concentrations of humic DOM (Karlsson et al., 2009). Like other systems, seasonal variation in water level seems to shift the role of freshwater peat marshes from producing and storing organic carbon to exporting it (Wen et al., 2020). Dilution likely plays a role in reducing organic carbon concentrations, but our wavelet analysis supports the importance of local organic carbon production with a strong and very consistent relationship between water level and DOC concentrations. If dilution were the primary factor driving changing DOC concentrations, we would likely see a relationship that is more variable, similar to the relationship in the marl marsh, where organic carbon is largely imported into the system. Similar relationships where DOC concentrations decrease with water level have been found across Everglades peat marshes, further supporting variable organic carbon production as an important driver of DOC concentration in peat marshes (Anderson et al., 2023).

In freshwater marl wetlands, changing water level does not shift the contribution of either detrital (HIX) or algal (BIX) DOM, indicating that the dominant source of organic carbon does not change seasonally in the marl wetland. Water enters TS through a series of canals and pumping stations, and the lack of a relationship between water level and DOM composition in the last 10 years, alongside inconsistent phase relationships between DOC and water level, suggests that marl wetland DOC concentrations are dominated by the contributions of externally produced DOM imported from upstream wetlands through the canals (Janssen et al., 2022). The opposite was found on the border of TS in 1999, where marl marshes produced a significant amount of internally produced DOM (Lu et al., 2003). This contrast could be explained either by restoration efforts within the past 20 years drastically increasing the amount of water and organic carbon entering TS or could be indicative of variation in DOM production across the landscape that our data does not capture, including factors such as changing redox conditions (Janssen et al., 2022).

Mangrove ecosystems play a significant role in the production and export of DOM into marine ecosystems, and understanding the roles of restoration and sea-level rise in that dynamic is important for tracing the relationship of the Everglades to its surrounding waters (Dittmar et al., 2006; Sippo et al., 2017). Our optical indices suggest that mangrove ecosystems seasonally shift between marine (higher BIX/FI values) and detrital mangrove (higher HIX/$SUVA_{254}$ values) sources of carbon, where higher water levels typically correspond to lower influence of marine carbon. Using cross-wavelet analyses, we showed strong seasonal shifts in the extent of marine water intrusion in shrub mangroves. We did not find this seasonal marine influence in riverine mangroves of SRS, which are strongly tidal with diurnal changes in water levels where the relationship between water level likely occurs on a smaller temporal scale than we measured in this study (Regier & Jaffé, 2016). Our findings highlight the power and utility of using time-series analyses to capture dynamic spatiotemporal patterns in long-term hydrology and water chemistry. Additionally, we found that BIX has a strong relationship with salinity in the most coastal mangroves, but they do not have the same relationship further inland, indicating that BIX at the most coastal sites is dominated by marine carbon imports. Instead, salinity is positively correlated with HIX at further inland mangrove sites indicating that seasonal marine pulses are pushing detrital carbon further inland from exterior mangroves, or that marine subsidies are accelerating the production of detrital DOM. Marine subsidies of sulfate could accelerate the release of detrital carbon by releasing redox constraints for decomposers, as has been shown to happen in freshwater Everglades systems that receive sulfate subsidies (Poulin et al., 2017; Weston et al., 2011). The extent of tidal variation is a strong driver of the amount of DOM being transported from and between mangroves in coastal wetlands and a more in-depth study of that relationship is needed to better understand riverine mangrove carbon export (Bergamaschi et al., 2012).

In the riverine mangroves of SRS, $SUVA_{254}$ increases when mangrove influence outweighs marsh influence (Cawley et al., 2014; Regier et al., 2020). Our data showed increases in $SUVA_{254}$ during the wet season in the ecotone of SRS, but not in the downstream mangrove forests. This suggests that, during the dry season, upstream marsh DOM dominates the SRS ecotone as the mangrove forests dry down, while in the wet season, increasing water levels mobilize mangrove-derived DOM (Adame & Lovelock, 2011). At the same time, dry-season DOM appears to be more influenced by marine sources, as indicated by higher BIX and FI values associated with increasing salinity. At SRS mangroves, increases in freshwater flow appear to decrease the contributions of marine carbon. Our data showed that seasonal changes in riverine mangroves lead to a shift between BIX and HIX, where ecotone riverine mangroves seasonally shift between marsh and mangrove influence. During these seasonal shifts, salinity associated increases in HIX indicate further mangrove influence in the dry season. HIX does not vary seasonally in downstream riverine mangroves; instead, BIX varies, indicating seasonal shifts in the presence of marine carbon and consistent production of humic mangrove carbon. Mangrove-produced DOM has significant implications for the future health of Everglades wetlands and likely originates in declining soils before being flushed into Florida Bay (Arnaud et al., 2020; Charles et al., 2019).

The Everglades relies on the storage of carbon in soils to keep pace with sea-level rise, and one of the goals of restoration has been to maintain Everglades soils (Chambers et al., 2019). Tracking DOM sources allows for low impact measurements of indicators of both processing and sources of carbon within changing wetlands. Our long-term DOM data suggests that increasing water levels may be changing the microbial processing of organic carbon (decreasing FI) from Everglades soils. Regier et al. (2020) showed that FI increased across the same six sites from 2002 to 2014, whereas our data from 2012 to 2021 show that the trajectory of FI has flipped and is now decreasing. Production of DOM in wetland soils is often controlled by water level, where changing anaerobic conditions can reduce microbial activity on soil carbon and change the concentration and makeup of carbon being released from soils (Strack et al., 2008). However, at the same time changing subsidies (including phosphorus and sulfates) to microbial communities that co-occur with higher water levels can increase microbial breakdown (Chambers et al., 2014). The decrease in FI over the past 10 years may reflect a decrease in soil microbial activity in response to a reduction in aerobic conditions to Everglades soils. However, the decrease we see in FI is relatively small and is not accompanied by changing HIX or BIX, which would be expected from large shifts in carbon sources. Additionally, Everglades aquatic productivity is highly variable and decoupled from overall ecosystem productivity (Malone et al., 2022). While this trend in FI is not conclusive, it is highly consistent across habitats and opposite the trend of the previous 10 years, highlighting the importance for continued monitoring of DOM as an indicator of changes to organic matter storage in coastal wetlands. Because DOM carries a signal of productivity both in the soil and the water column, long-term DOM data are valuable for detecting changes to ecosystem trajectories in response to the interaction of restoration and sea-level rise across multiple compartments (Kominoski et al., 2018; Sarker et al., 2020).

Based on previous work showing hydrology as a strong driver of larger spatial scale patterns in carbon and nutrients (Kominoski et al., 2020; Regier et al., 2020), we predicted that the interaction between water levels and dominant carbon sources (i.e., peat, marl, mangrove) would explain pulsed changes in DOC concentrations and composition. We additionally predicted that the interaction between water levels and dominant organic carbon sources would explain changing bacterioplankton productivity at smaller spatial scales. Instead, we found that water level is a strong and consistent driver of DOC only at locations where carbon is being produced (freshwater marsh of SRS, and shrub mangroves of TS) and that increases in bacterioplankton productivity are not associated with any specific driver (including DOC concentration, composition, nutrient availability, water level) but are associated with disturbance events (see also Kominoski et al., 2020). Together these results suggest that lateral fluxes of carbon outweigh any effects that bacterioplankton activity has in shaping the composition or concentration of DOM throughout the Everglades.

An in-depth understanding of carbon processing in coastal wetlands is needed to better inform carbon storage restoration strategies. Peat marshes are created by high water levels that create anoxic conditions and allow for the buildup of humic organic matter, and our data suggests that increased water levels from restoration are creating conditions that are more conducive to the buildup of peat (Fenner & Freeman, 2011; Ritson et al., 2017). In marl wetlands, where floc is seasonally mineralized by microbes when oxygen becomes available, organic matter pools are largely ephemeral (Pisani et al., 2013), and our data suggest that restoration may be increasing their potential to store carbon; however, the decrease in microbial signals may also originate in upstream peat marshes that dominate the DOM pool of short-hydroperiod freshwater wetlands. Rewetting of wetland soils typically increases their biomass by reducing microbial activity (Zerbe et al., 2013), but the microbial response depends on subsidies or stressors (such as salinity and phosphorus) delivered along with the water (Saha et al., 2011; Servais

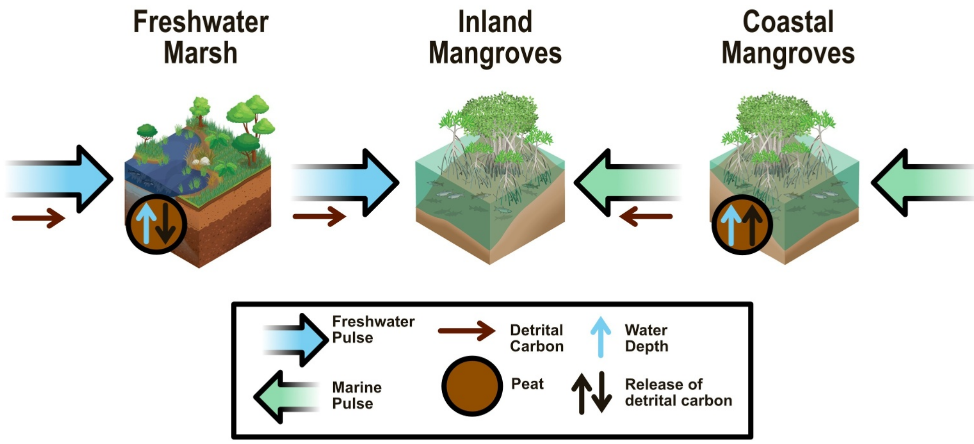

Figure 7. Detrital carbon is seasonally mobilized by both fresh and marine hydrologic pulses. Freshwater pulses that increase water depths also lead to decreasing concentrations of dissolved organic carbon, as they dilute and suppress the release of carbon from peat sediments. Marine pulses transport carbon from mangrove soils further inland.

et al., 2019). Marine water intrusion typically reduces carbon storage capacity and increases the leaching of DOM and the microbial breakdown of soils (Servais et al., 2019; Weston et al., 2011). Continued monitoring is needed to track how accelerating sea-level rise will change the production, processing, and movement of carbon throughout the Everglades, especially where legacies of salinity and phosphorus from marine water persist in affected soils (Lee et al., 2021).

5. Conclusions

Parsing how increasing hydrologic presses and pulses will change ecosystems relies on an understanding of how sources of organic carbon are being shifted through ecosystems. We show that restoration is mobilizing detrital carbon, reducing microbial processing of organic carbon, increasing the connectivity between carbon sources, while biogeochemical cycling across the Everglades is becoming synchronized (Kominoski et al., 2020). Our study highlights the mechanisms through which presses and pulses fresh water (from restoration) and marine water (from sea-level rise) are driving lateral movements of organic matter between ecosystems, and the importance of time series analysis for elucidating those relationships. Specifically, we found that both freshwater and marine presses and pulses are mobilizing detrital carbon, while at the same time the restoration of water to freshwater peat marshes is suppressing the local release of detrital carbon, while also importing carbon from upstream wetlands (Figure 7). Understanding the specific drivers and dynamics of lateral movements of nutrients and organic matter allows for improved predictions and more effective management of aquatic ecosystems that are being exposed to rapidly changing hydrologic presses and pulses. Tracing these dynamics of resources and organic matter is critical to understanding changes in carbon storage and long-term trajectories of ecosystems (Kominoski et al., 2018; E. P. Odum, 1969).

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Data Availability Statement

All data used in this study is archived as part of the environmental data initiative and is available on the FCE-LTER data catalog (https://fce-lter.fiu.edu/data/core/). Specific datasets used in this manuscript are cited within the text. The datasets used include knb-lter-fce.1256.3 (Kominoski & Smith, 2023), knb-lter-fce.1072.17 (Gaiser et al., 2023), knb-lter-fce.1074.17 (Troxler, 2023), knb-lter-fce.1056.12 (Briceño, 2023), knb-lter-fce.1094.18 (Kominoski et al., 2022), knb-lter-fce.1098.13 (Troxler & Childers, 2022), and knb-lter-fce.1168.13 (Castañeda-Moya & Rivera-Monroy, 2021).

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