RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration
SER SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Dissolved organic matter in peat and marl marshes varies with nutrient enrichment and restored hydrology

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Dissolved organic matter (DOM) drives biogeochemical processes in aquatic ecosystems. Yet, how hydrologic restoration in nutrient-enriched ecosystems changes DOM and the consequences of those changes for the carbon cycle remain unclear. To predict the consequences of hydrologic restoration on carbon cycling in restored wetlands, we need to understand how local environmental factors influence production, processing, and transport of DOM. We collected surface water samples along transects in restored peat (organic-rich, macrophyte-dominated) and marl (carbonate, periphyton-dominated) freshwater marshes in the Everglades (Florida, U.S.A.) that varied in environmental factors (water depth, phosphorus [P] concentrations [water, macrophytes, periphyton, and soil], and primary producer biomass) to understand drivers of dissolved organic carbon (DOC) concentrations and DOM composition. Higher water depths led to a "greening" of DOM, due to increasing algal contributions, with decreasing concentrations of DOC in peat wetlands, and a "browning" of DOM, due to increasing humic contributions, with increasing DOC concentrations in marl wetlands. Soil total P was positively correlated with DOC concentrations and microbial contributions to DOM in peat wetlands, and periphyton total P was positively correlated with algal contributions to DOM in marl wetlands. Despite large variations in both vegetation biomass and periphyton biovolume across transects and sites, neither were predictors of DOC concentrations or DOM composition. Hydrologic restoration differentially alters DOM in peat and marl marshes and interacts with nutrient enrichment to shift proportions of green and brown contributions to surface water chemistry, which has the potential to modify wetland food webs, as well as the processing of carbon by micro-organisms.

Key words: biogeochemistry, dissolved organic carbon, dissolved organic matter, Everglades restoration, fluorescence, freshwater, hydroperiod

Implications for Practice

- Freshwater restoration can alter dissolved organic matter (DOM), increasing dissolved organic carbon (DOC) in organic-poor, carbonate marl wetlands, and diluting high concentrations of DOC in organic-rich, peat marshes.
- Changing sources of DOM can alter the base of aquatic food webs and modify how carbon flows through oligotrophic ecosystems.
- Understanding how carbon sources and nutrient limitation impact carbon cycling is critical for managers to predict how hydrologic restoration and nutrient legacies can affect carbon storage in ecosystems.

Introduction

Dissolved organic carbon (DOC) is the most ubiquitous form of carbon in aquatic systems (Wetzel 1995). DOC controls biogeochemical processing and is an important regulator of the microbial loop (Amon & Benner 1996; Boyer et al. 1997; Qualls & Richardson 2003). The composition of DOC, which is a main portion of dissolved organic matter (DOM), is a function of organic matter production, transport, and transformation in aquatic ecosystems (Osborne et al. 2007; Fellman et al. 2010). Changing hydrology and nutrient availability drive the production and processing of DOM in aquatic ecosystems, subsequently changing its composition, quality, and bioavailability (Marschner & Kalbitz 2003; Shen et al. 2015; Graeber et al. 2021). Variation in carbon sources contribute to differences in DOM composition among ecosystems, which further influences its transport and transformation (Graeber et al. 2021).

Freshwater ecosystems play a major role in the global carbon cycle (Battin et al. 2009), but it is unclear how the composition of DOM interacts with environmental drivers (i.e., hydrology, nutrient enrichment, vegetation composition and biomass) to determine its fate (Berggren et al. 2022). The combination of environmental and compositional (chemical makeup of DOM) drivers determines how DOC is subject to biodegradation, photo-oxidation, or flocculation (Anderson et al. 2019). During

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Author contributions: KJA, JSK, AN, SH participated in the writing and editing of this manuscript; KJA, JSK, AN, SH collected data and contributed to data analyses; KJA, JSK designed the experiment.

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doi: 10.1111/rec.13905
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.13905/suppinfo

wetland ecosystem restoration, which typically involves increasing water depths, shifting ecosystems from oxic to anoxic states, and maintaining stores of carbon (Venterink et al. 2002; Evans et al. 2005; Moreno-Mateos et al. 2012; Zerbe et al. 2013; Christen et al. 2016), DOC is rarely managed for directly, largely because of a lack of consistent data on the interactions between DOC and ecosystem restoration (Stanley et al. 2012). However, recent studies have found that increases in water depth are also responsible for increases in lateral DOC fluxes which play a significant role in the net ecosystem carbon balance, potentially offsetting reductions in emissions from wetlands (Strack et al. 2011; D'Acunha et al. 2019). Although DOC fluxes are rarely managed for, a global trend of "browning" (referring to increased concentrations of DOC that increase the coloration of waters), has received attention for its potential to both increase monetary costs for drinking water purification and reducing fish production in lakes (Lavonen et al. 2013; van Dorst et al. 2019; Kritzberg et al. 2020). The potential for restoration to both mobilize DOC (reducing the carbon storage potential of wetlands) and contribute to browning of freshwater highlights the importance of understanding sources and fates of DOC in restored wetlands.

The Florida Everglades is undergoing the world's largest restoration effort to reconnect more than a century of altered hydrology and restore wetland ecosystem functions (Sklar et al. 2005). Maintaining carbon storage capacity is a major goal of Everglades restoration, and achieving that goal requires a thorough understanding of the local drivers of carbon processing and their interactions with drivers and legacies of disturbance in recovering ecosystems (Herrick et al. 2006; Meli et al. 2014). Fluxes of DOC throughout the Everglades are closely linked to hydrology, whereby water management and precipitation patterns control DOC transport (Regier et al. 2016). Increasing water depths with hydrologic restoration have the potential to change DOC production, transport, photodegradation, and biological degradation, which could also change the fate of carbon in restored areas (Chen & Jaffé 2016). As water depths increase, the microtopography of Everglades habitats is also shifting, and understanding how those shifts impact the production and transport of DOC is important for predicting how restoration will alter the fates of carbon (Choi & Harvey 2016). The fate of DOC has consequences for carbon storage potential of wetlands, as well as the potential to shift the balance of "green" and "brown" food webs within restored ecosystems (Belicka et al. 2012).

In the Everglades, restoration is primarily achieved through water management, with the goal of increasing hydroperiods (i.e., total number of days in a year with water above the soil surface) and reducing eutrophication caused by excess phosphorus loading from upstream agriculture. This is accomplished by redirecting water that was previously diverted through canals, back in wetlands of the Everglades (Juston & DeBusk 2011). However, early evidence suggests that bound phosphorus is being mobilized from legacy hotspots as a collateral effect of increased freshwater flows and hydroperiods (Sarker et al. 2020). Phosphorus enrichment is an important driver of flocculant material respiration and periphyton composition (Lu et al. 2003; Gaiser et al. 2006; Pisani et al. 2013) and has the potential to shift the relative contributions of algal and detrital basal resources of food webs (Belicka et al. 2012). Increasing water depths and the mobilization of legacy phosphorus are both contributing to increased DOC concentrations, which can also increase detrital resources to microbial consumers (Regier et al. 2016). Carbon processing within restored aquatic ecosystems is driven by autochthonous and allochthonous water and carbon sources (Anderson et al. 2019; Berggren et al. 2022). Everglades restoration moves water from upstream peatlands to downstream peat and marl wetlands, so restored wetlands are receiving increases in peat-derived DOM as more fresh water is delivered.

Here, our goal was to understand how restoration of water depths and variation in relative nutrient enrichment affect the concentration of DOC and the composition of DOM in oligotrophic Everglades wetlands, ranging from ridge and slough habitats in long-hydroperiod peat to short-hydroperiod marl marshes. Past studies have shown that there are significant differences in both DOC concentrations and DOM composition in peat and marl marshes (Regier et al. 2020). Compared to past studies, we added sampling along nutrient-enrichment gradients in peat and marl marshes that vary in water depth, phosphorus (P) concentrations (water, macrophytes, periphyton, and soil), and primary producer biomass to understand how these drivers affect DOC concentrations and DOM composition. We predicted that freshwater restoration would increase DOC concentrations in areas with higher P enrichment and that DOM composition would change based on periphyton and macrophyte biomass. In addition, we expected that DOC in peat marshes would be less altered by hydrologic restoration than DOC in marl marhses because of novel sallochthonous, peat-derived DOC subsidies entering marl wetland ecosystems.

Methods

Study Sites

The Greater Everglades was historically a continuous wetland flowing from north of Lake Okeechobee to Florida Bay. Prior to hydrologic alteration, the majority of water moved as sheet flow in the wet season (May–November), during which the Everglades receives 70% of its total rainfall. Hydrologic alteration began in the early 1900s with the construction of drainage canals, intended to create agricultural areas, and drainage of areas for urban development. The construction of canals for drainage has caused a compartmentalization of the system, with the creation of Water Conservation Areas (WCAs). Although a major conservation goal is the restoration of sheet flow in much of the Everglades, these compartments are still primarily linked along canal boundaries (Kominoski et al. 2019).

Sample collection for our experiment was performed at the boundary of Everglades National Park (ENP) along its two major drainages: Shark River Slough (SRS) and Taylor Slough (TS; Fig. 1). These two drainages sit at different elevations, causing a difference in hydroperiod between the two sloughs. This difference has led SRS, the longer-hydroperiod wetland,

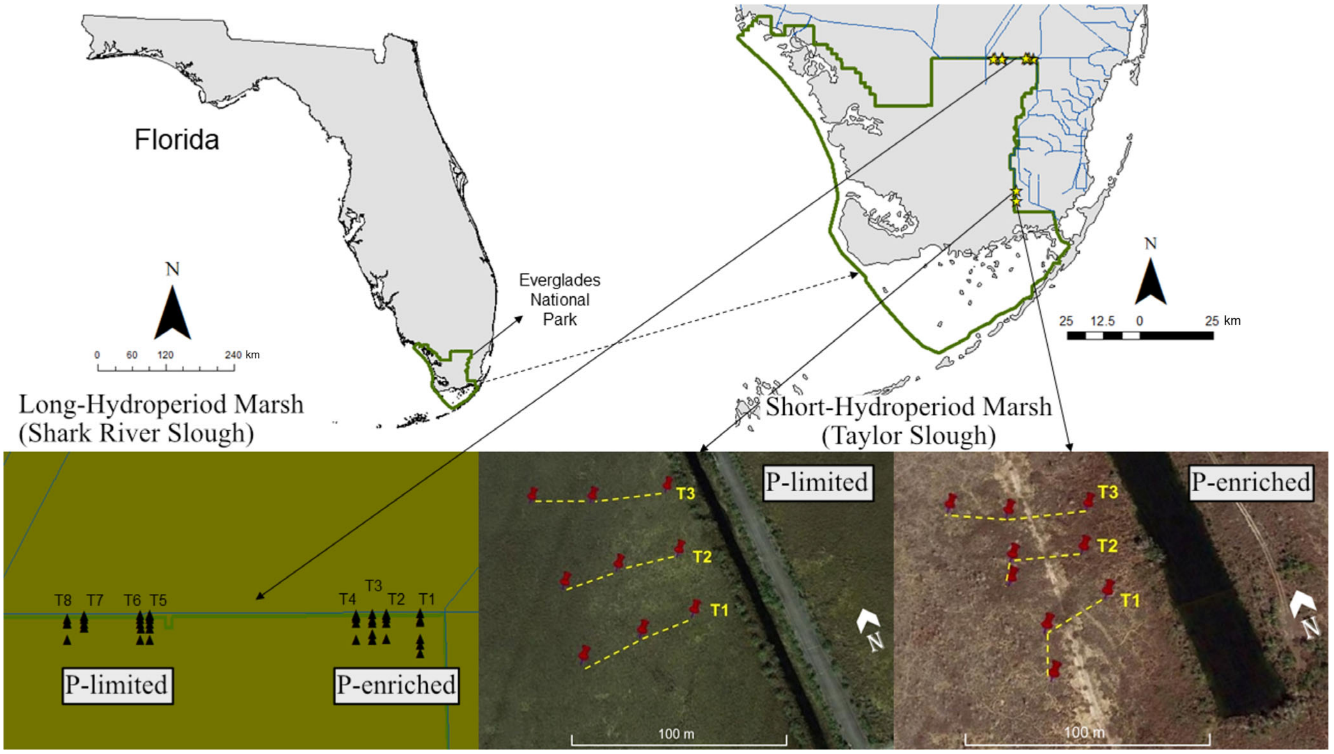

Figure 1. Location of the study sites along the boundaries of the Florida Coastal Everglades (FCE), ENP in South Florida, U.S.A. We sampled along the L29 canal in the long-hydroperiod Shark River Slough drainage and along the L-31W/Aerojet Canal in the short-hydroperiod drainage Taylor Slough.

to develop deep peat soils, whereas TS, the short-hydroperiod slough, is primarily characterized by marl soils. The boundary where upstream water enters Shark River Slough is the L-29 Canal, which runs east to west along the northern boundary of ENP and is the connection between ENP and the WCAs. The long hydroperiod of Northeast Shark River Slough (NESRS) has allowed for the formation of deep peat soils, characterized by high carbon and P concentrations (Osborne et al. 2011). Phosphorus enrichment in these soils originates in the Everglades Agricultural Area (EAA) along the border of Lake Okeechobee. Runoff from the EAA over the past 30 years led to the buildup of phosphorus along the borders of ENP (DeBusk et al. 1994, 2001). We collected surface water samples along the boundary where overland flow is increasing in response to the Modified Water Deliveries project (McLean 2015), with four transects (∼1 km in length), perpendicular to the upstream 1.6-km bridge, with a longer history of modified flow, and four transects (∼1 km in length), perpendicular to the upstream 4.2-km bridge, with a shorter history of modified flow.

In TS, our second focal area, upstream water enters a portion of the ENP boundary along the L-31W/Aerojet Canal, which runs north to south. Through the Aerojet Canal, water is delivered from upstream wetlands towards TS (Kotun & Renshaw 2014). This region has lower hydrologic connectivity with upstream Everglades wetlands and is an ecosystem largely characterized by marl soils, supporting a mix of prairie and marsh vegetation communities. Marl wetlands have relatively low organic carbon concentrations in soils made from a mix of decaying calcareous periphyton and the limestone base. This ecotype is extremely oligotrophic and highly phosphorus limited, in part because the available phosphorus is rapidly sorbed by the limestone (Osborne et al. 2011). The TS region is also characterized by the accumulation of phosphorus at canal boundaries and seasonal mobilization of phosphorus mineralized during dry conditions (Sullivan et al. 2014). We collected surface water samples along the boundaries of marl wetlands, with three transects in a marsh with a history of higher phosphorus loading as it is situated at the end of the L-31W Canal (where canal overspill increased phosphorus loading during high flow) and three transects further North in a marsh with a history of lower phosphorus loading, away from the overspill zone (see Nocentini et al. 2022).

Water Physicochemistry

In September (wet season) of 2020 and March (dry season) of 2021, along each sampling transect, we collected two surface water samples at each site, one filtered and one unfiltered. Samples were filtered in the field using cellulosic 0.45-μm filters (GVS MicronSep, Zola Predosa, Bologna, Italy) and stored in 60-mL acid-washed amber high-density polyethylene (HDPE) bottles. Unfiltered grab water samples were collected in 250-mL acid-washed amber HDPE bottles. All samples were transported to the laboratory on ice and then stored at 4°C until analyzed. Filtered samples were analyzed for DOC on a Shimadzu TOC-V total organic carbon analyzer, after acidification to remove inorganic carbon. Unfiltered samples were analyzed for total organic carbon (TOC), total nitrogen (TN), and total phosphorus (TP). TOC was analyzed using a Shimadzu TOC Analyzer (Shimadzu Corporation, Columbia, MD, U.S.A.), TN was measured with an Antek TN analyzer (Antek Instruments, Houston, TX, U.S.A.), and TP was analyzed following Solórzano and Sharp (1980).

Fluorescence spectroscopy was performed on all filtered samples to determine the chemical composition of the DOM of each sample. Fluorescence excitation-emission matrices (EEMs) were measured on a Horiba Aqualog (Jobin Yvon Horiba, France). Samples were measured at room temperature at 3 nm wavelengths, over excitation wavelength intervals between 240 and 455 nm and an emission wavelength range of $\lambda_{ex} + 10$ to $\lambda_{ex} + 250$ nm in a 1-cm quartz cuvette. EEMs were corrected, Raman normalized, and blank subtracted using MATLAB R2019a (Mathworks, Natick, MA, U.S.A.).

We measured water depth as an average of three measurements within three replicate 1 × 1 m quadrats during each sampling. We calculated the average depth between the three quadrats at each site for each time point.

Macrophytes, Periphyton, Flocculant Organic Matter, and Soils

Along each sampling transect, we collected vegetation, organic matter, and periphyton in 1 × 1 m quadrats, and we collected three replicate quadrats at each site. We recorded percent cover of vegetation, canopy height, and the total number of plant stems in each quadrat. From the number of stems and the canopy height, we calculated species-specific mass corrections to estimate the total live macrophyte biomass in each quadrat (Childers et al. 2006; Nocentini et al. 2022). We measured floc depth and periphyton biovolume from each quadrat. We collected grab samples of soil, periphyton, sawgrass leaves, and floc for nutrient analysis. All grab samples were oven-dried at 40°C for 72 hours, and ground using an 8000D ball mill (SPEX SamplePrep, Metuchen, NJ, U.S.A.). Then, ground samples were analyzed for TC and TN by high-temperature dry combustion using a Carlo-Erba NA-1500 CNS Analyzer (Nelson & Sommers 2018), and TP was measured by oxidation (dry combustion) and hydrolysis of the P-containing compounds in the sample to soluble forms using $MgSO_4/H_2SO_4$ and HCl (Solórzano & Sharp 1980).

Data Analyses

We processed absorbance and fluorescence data using the DrEEM 3.0 toolbox in MATLAB R2019a and calculated five common metrics of DOM fluorescence: fluorescence index (FI) as an indicator of microbial versus terrestrial sources of DOM (McKnight et al. 2001), humification index (HIX) as an indicator of higher molecular weight and refractory DOM (Zsolnay et al. 1999), biological index (BIX) as an indicator of new autochthonous inputs to DOM (Huguet et al. 2009), aromatic index as an indicator of aromaticity of DOM (specific UV absorbance at 254 nm wavelength [$SUVA_{254}$]; Weishaar et al. 2003), and slope ratio (SR) as an indicator of molecular weight of DOM (Helms et al. 2008).

To test how legacies of hydrologic and phosphorus enrichment alter the composition and concentrations of dissolved organic matter in peat and marl wetlands, we grouped sites by soil type (peat, marl) and phosphorus legacy impact (P-enriched, P-limited). In peat wetlands of NESRS, the P-enriched sites were located downstream of the bridge constructed in 2012, and the P-limited sites were located downstream of the bridge constructed in 2018. In marl wetlands along the Aerojet Canal, the P-enriched sites were located at the end of the canal, whereas the P-limited sites were located along the middle section and perpendicular to the canal. We used one-way analysis of variance (ANOVA) to test for significant ($\alpha \le 0.05$) effects of soil type, season, and nutrient legacy impact on fluorescence metrics, emergent macrophyte biomass, periphyton biovolume, and water and particulate biogeochemistry. Although not in the objectives of the study, we analyzed these variables as they mediated the combined effects of hydrologic restoration and relative P-limitation on DOC concentrations and DOM composition.

To better understand the drivers of carbon fluorescence, we used Pearson's bivariate correlation (r) and linear regression analysis (R^2) to test significant relationships between fluorescence metrics, emergent macrophyte biomass, periphyton biovolume, and water and particulate biogeochemistry. To investigate how hydrology, emergent macrophyte biomass, periphyton biovolume, and phosphorus enrichment differentially drive DOC concentration and DOM composition in marl and peat wetlands, we used a series of covariates corresponding to each potential driver, created a series of linear models, and performed model selection (see information below). We used water depth as a covariate corresponding to hydrology, macrophyte biomass and periphyton biovolume as covariates corresponding to primary producers, and TN:TP ratios for sawgrass, soil, and water as measures of relative phosphorus enrichment. We constructed a series of linear models including all combinations of the three covariate groups (Table S1). We removed sawgrass TN:TP ratios from the peat models a priori, in order to fit all models to the same number of observations after finding that sawgrass TN:TP ratios did not have a significant relationship with DOC concentration or DOM composition (Fig. S1).

We calculated Akaike's information criterion (AIC_c) for small sample size scores for each model and selected the best-fitting model as the one with the highest adjusted R^2 score that had a ΔAIC less than or equal to 2 (Burnham & Anderson 2004). We calculated coefficient estimates for each explanatory variable in the best-fitting models and tested for significant relationships between coefficients and response variable for each model. All analyses were performed using R version 4.2.0 (R Core Team 2022). All plots were constructed with the "ggplot2" package (Wickham 2009).

Results

Water Physicochemistry

Peat wetlands had deeper water depths than shorter hydroperiod marl wetlands (ANOVA, $F_{[3,109]} = 115.3$, $p < 0.001$; Fig. 2A).

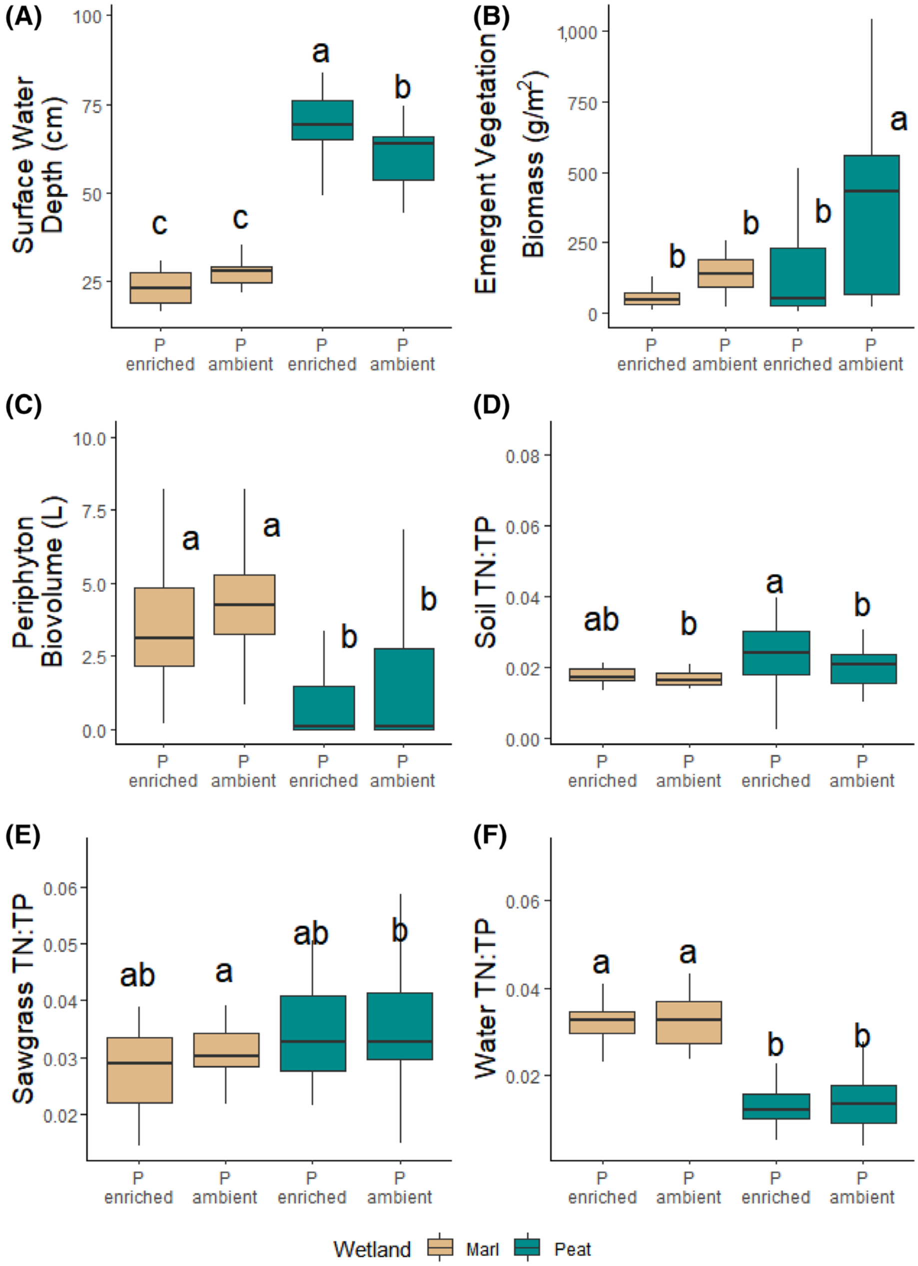

Figure 2. Comparison of hydrology, primary producers, and nutrient availability between marl and peat wetlands, across P-enriched and P-ambient sites in the Everglades (Florida, U.S.A.). Boxplots represent the interquartile range for each variable, and the solid line is the median. Error bars represent the 95% confidence intervals. Letters above boxplots indicate significant ($\alpha \leq 0.05$) differences among groups using one-way ANOVA.

In peat wetlands, the P-enriched transects had higher water depths (Fig. 2A), and there was no change in water depth between seasons, as freshwater restoration and water management maintained similar water levels year round (ANOVA, $F_{[1,109]} = 0.115$, $p = 0.74$). In contrast, marl wetlands were deeper in the wet season than in the dry season (ANOVA, $F_{[1,109]} = 50.60$, $p < 0.001$).

Water chemistry varied across sites and seasons. Surface water TP concentrations were similar between peat and marl wetlands during the dry season, but during the wet season surface water TP in peat wetlands decreased while marls wetlands did not (ANOVA, $F_{[1,109]} = 5.993$, $p = 0.02$). TN was higher in peat than in marl wetlands regardless of season (ANOVA, $F_{[3,109]} = 11.93$, $p < 0.001$), and TN increased during the dry season across all wetlands (ANOVA, $F_{[1,109]} = 11.22$, $p < 0.001$).

Primary Producer Biomass and Soil Chemistry

Phosphorus-enriched wetlands had less macrophyte biomass compared to P-limited wetlands, and macrophyte biomass was higher in peat than marl wetlands (ANOVA, $F_{[3,109]} = 10.678$, $p < 0.001$; Fig. 2B). Biomass of emergent macrophytes and periphyton biovolume were characterized by high spatial variability in peat wetlands, and by low spatial variability in marl wetlands. High biovolumes of periphyton were ubiquitous in marl wetlands. In contrast, periphyton was highly variable, ranging from absent to complete coverage, in peat wetlands. Overall, marl wetlands had higher biovolume of periphyton than peat wetlands (ANOVA, $F_{[3,109]} = 26.04$, $p < 0.001$; Fig. 2C), and while not statistically significant there was a trend of periphyton biovolumes increasing in the wet season for both wetland types (ANOVA, $F_{[3,109]} = 3.66$, $p = 0.058$).

Soil TC concentrations were higher in peat than marl wetlands (ANOVA, $F_{[3,109]} = 62.197$, $p < 0.001$), and did not vary between dry and wet season in either wetland type. Soil TN concentrations, on the other hand, were lower in marl wetlands during the dry season compared to the wet season, and wet season soil TN was similar to both wet and dry season values for the peat wetlands (ANOVA, $F_{[1,33]} = 12.898$, $p = 0.001$). Soil TP concentrations were higher in all peat wetland sites than marl wetland sites (ANOVA, $F_{[3,109]} = 3.083$, $p = 0.03$) and were marginally lower during the dry than wet season across all sites (ANOVA, $F_{[3,109]} = 3.249$, $p = 0.074$).

Trends in DOC Concentrations and DOM Fluorescence

Mean DOC concentrations in peat wetlands ranged between 13.6 mg C/L in P-enriched wetlands and 20.4 mg C/L in P-limited wetlands and were higher in the dry than in the wet season (ANOVA, $F_{[3,109]} = 109.6$, $p < 0.001$; Table 1). Mean DOC concentrations in marl wetlands were lower than those of peat wetlands and more variable between seasons, with mean concentrations of 9.5–9.6 mg C/L in the marl and 10–12 mg C/L in the peat, for the dry and wet seasons, respectively (Table 1). Mean HIX values in peat wetlands ranged from 12.7 in P-enriched to 14.0 in P-limited wetlands, indicating highly humic DOM, whereas marl wetlands mean HIX values were significantly lower (ANOVA, $F_{[3,109]} = 241.4$, $p < 0.001$) and ranged from 6.9 at P-enriched sites to 9.4 at P-limited sites. HIX values varied seasonally at both sites, but in opposite directions; in marl wetlands HIX increased in the wet season (ANOVA, $F_{[1,40]} = 19.75$, $p < 0.001$), while in peat wetlands HIX decreased in the wet season (ANOVA, $F_{[1,75]} = 10.20$, $p < 0.001$).

Mean FI values ranged from 1.49 to 1.55 across wetland type, nutrient enrichment, and season and indicated a moderate level of microbial influence on DOM for both marl and peat wetlands (Table 1). FI values were higher in marl than peat wetlands. They were highest at P-enriched sites of marl wetlands during the dry season (ANOVA, $F_{[1,109]} = 8.404$, $p = 0.004$), and were lower at P-enriched sites in both wetland types (ANOVA, $F_{[3,109]} = 14.55$, $p < 0.001$).

Mean BIX values range from 0.71 in marl to 0.64 in peat wetlands. BIX values indicated low autochthonous productivity in both peat and marl wetlands, but were significantly higher in marl than in peat wetlands, and were higher in P-enriched sites of both wetland types (Table 1; ANOVA, $F_{[3,109]} = 294.3$, $p < 0.001$). BIX values were generally higher in the dry season, except at the P-limited sites of marl wetlands, where they did not vary seasonally (ANOVA, $F_{[1,49]} = 2.69$, $p = 0.107$).

Table 1. Average ± SD of DOC concentrations and fluorescence indices of DOM composition across ecosystem compartments and seasons. Indices calculated are FI, BIX, HIX, $SUVA_{254}$, and SR.

		Marl				Peat			
		P-Enriched		*P-Limited*		*P-Enriched*		*P-Limited*	
Covariate	*Range/Units*	*Dry Season*	*Wet Season*	*Dry Season*	*Wet Season*	*Dry Season*	*Wet Season*	*Dry Season*	*Wet Season*
DOC	mg/L	9.50 (±0.64)	10.40 (±0.37)	9.59 (±0.86)	12.37 (±2.78)	16.20 (±3.00)	13.65 (±2.99)	20.42 (±0.86)	19.92 (±1.53)
FI	1.2 (terrestrial) – 1.9 (microbial)	1.55 (±0.02)	1.50 (±0.02)	1.52 (±0.01)	1.52 (±0.02)	1.51 (±0.01)	1.51 (±0.02)	1.50 (±0.01)	1.49 (±0.01)
BIX	0.6 (low productivity) – >1 (high autochthonous productivity)	0.71 (±0.01)	0.70 (±0.01)	0.70 (±0.01)	0.70 (±0.01)	0.66 (±0.00)	0.65 (±0.01)	0.66 (±0.01)	0.64 (±0.01)
HIX	2 (mineral soils) – 16 (fulvic acids)	6.94 (±0.37)	7.79 (±0.43)	8.12 (±0.33)	9.42 (±0.77)	13.48 (±1.31)	12.67 (±0.95)	13.99 (±1.06)	13.27 (±0.58)
$SUVA_{254}$	0.5 (fulvic acid) – 5.3 (humic acid)	2.21 (±0.14)	2.60 (±0.25)	2.11 (±0.20)	2.13 (±0.46)	3.04 (±0.12)	3.26 (±0.78)	3.07 (±0.09)	3.14 (±0.22)
SR	0.7 (blackwater) – 10 (open ocean)	1.00 (±0.05)	1.21 (±0.38)	1.06 (±0.05)	1.07 (±0.04)	1.01 (±0.03)	1.00 (±0.03)	0.99 (±0.01)	1.00 (±0.03)

$SUVA_{254}$ values ranged from 2.1 in marl to 3.2 in peat wetlands. $SUVA_{254}$ values indicated low carbon complexity in the DOM of both peat and marl wetlands, although they were significantly higher in peat compared to marl wetlands (Table 1; ANOVA, $F_{[3,109]} = 41.49$, $p < 0.001$). $SUVA_{254}$ values did not vary seasonally except at the P-enriched marl wetland sites (ANOVA, $F_{[1,109]} = 5.282$, $p < 0.02$).

Mean SR values ranged from 0.99 in peat to 1.21 in marl wetlands, indicating high molecular weight DOM in both wetland types. They were significantly higher in the P-enriched marl than peat wetland sites (ANOVA, $F_{[3,109]} = 3.076$, $p = 0.01$). Mean SR values did not differ between seasons (ANOVA, $F_{[1,109]} = 1.268$, $p = 0.28$).

In summary, our analyses of the optical properties of fluorescence showed that DOM in peat wetlands was highly concentrated, humic, minimally influenced by autochthonous productivity, and more aromatic than the DOM of marl wetlands. In marl wetlands, DOM was more influenced by autochthonous productivity (composed of less humic and less aromatic compounds), especially in P-enriched marl wetlands, where we detected more autochthonous components in DOM (Fig. 3).

Drivers of DOC Concentration and DOM Composition

DOC concentrations were best explained by the combined effects of hydrology and phosphorus enrichment in peat wetlands (Table S1), where both increasing depth and soil TN:TP ratio correlated with decreasing concentrations of DOC (Table 2; Fig. 4). Surface water TN:TP did not have a significant effect on the model. In marl wetlands, hydrology, emergent macrophyte biomass, and periphyton biovolume best explained DOC concentrations (Table S1). Although water depth was the only covariate that showed a significant, positive correlation with DOC concentrations (Table 2; Fig. 4), the inclusion of macrophyte biomass (negative relationship with DOC) and periphyton biovolume (positive relationship with DOC) improved the overall model fit (Table S1).

In both peat and marl wetlands, FI was best explained by the combined effects of hydrology and phosphorus enrichment (Table S1), but the relationships between hydrology and FI trended in opposite directions in the two wetland types (Table 2; Fig. 4). In peat wetlands, FI increased with increasing water depth and increasing soil TN:TP ratios. In marl wetlands,

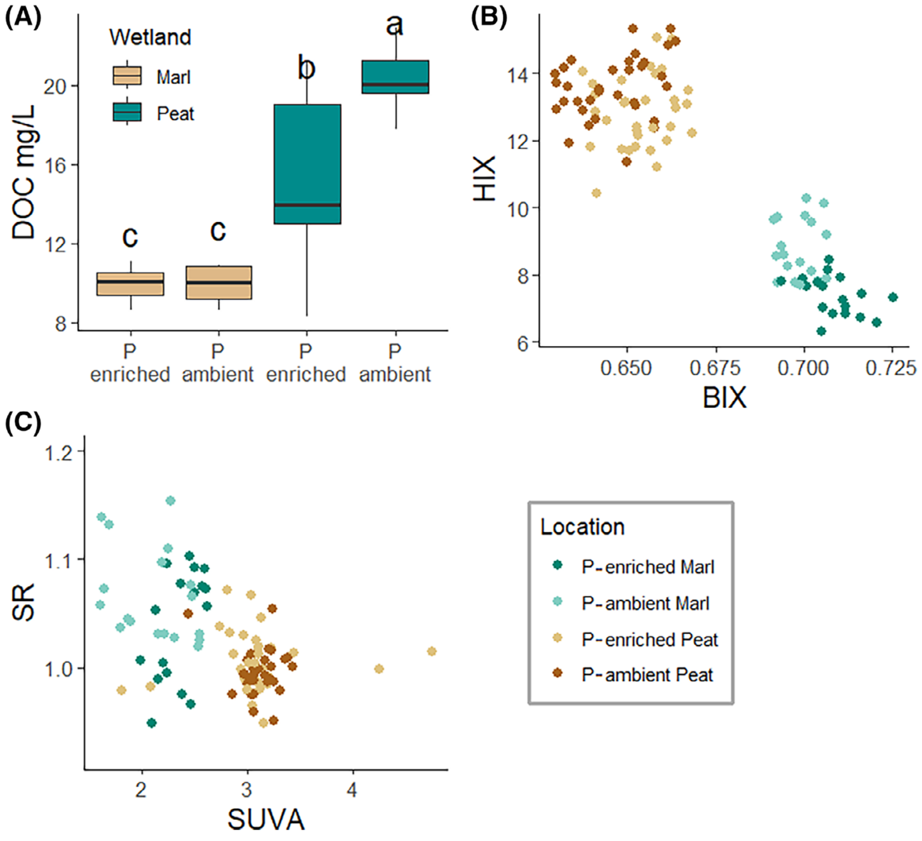

Figure 3. DOC concentrations and dissolved organic matter (DOM) composition across habitats in peat and marl wetlands. (A) HIX and BIX across ecosystem compartments. Increasing HIX indicates increasing humic influence to DOM, whereas increasing BIX indicates increasing autochthonous influence to DOM. (B) Concentrations of DOC across ecosystem compartments. Boxplots represent the interquartile range for each variable; the solid line represents the median. Error bars represent 95% CI. Letters above boxplots indicate significant ($\alpha \leq 0.05$) differences among groups using one-way ANOVA. (C) SR and aromaticity (SUVA) across ecosystem compartments. Increasing SR indicates decreasing molecular weight, while increasing SUVA indicates increasing aromaticity. [Correction added on 14 April 2023, after first online publication: In Figure 3(A), one of the labels on the x-axis was incorrect. It referred to Canal and P enriched, and it should instead refer to P enriched and P ambient.]

Table 2. Estimate effect sizes for best fitting models for dissolved organic matter (DOM) metrics [dissolved organic carbon (DOC) concentration; FI; BIX; HIX; $SUVA_{254}$ (Specific UV absorbance at 254 nm wavelength); and SR (Slope Ratio)] from A. peat, and B. marl wetlands. Covariates not included in the best model are marked as NA.

A. Peat

	DOC		*FI*		*BIX*		*HIX*		*$SUVA_{254}$*		*SR*	
Covariate	t	p	t	p	t	p	t	p	t	p	t	p
Water depth	−4.20	<0.001	2.665	0.010	3.50	<0.001	−1.50	0.14	1.03	0.31	NA	NA
Periphyton biovolume	NA	NA	NA	NA	−1.86	0.07	−1.64	0.11	NA	NA	1.68	0.10
Macrophyte biomass	NA	NA	NA	NA	−0.59	0.56	−0.17	0.86	NA	NA	0.11	0.92
Soil TN:TP	−2.73	0.009	2.83	0.01	−0.73	0.47	NA	NA	NA	NA	1.09	0.28
Water TN:TP	0.307	0.760	1.24	0.22	3.96	<0.001	NA	NA	NA	NA	1.06	0.30

B. Marl

	DOC		*FI*		*BIX*		*HIX*		*$SUVA_{254}$*		*SR*	
Covariate	t	p	t	p	t	p	t	p	t	p	t	p
Water depth	2.97	0.01	−1.889	0.068	−2.84	0.01	3.40	0.00	−0.99	0.33	NA	NA
Periphyton biovolume	0.71	0.48	NA	NA	NA	NA	1.58	0.12	NA	NA	NA	NA
Macrophyte biomass	−1.59	0.12	NA	NA	NA	NA	−0.09	0.93	NA	NA	NA	NA
Soil TN:TP	NA	NA	0.25	0.81	0.497	0.62	NA	NA	−0.18	0.86	1.27	0.21
Water TN:TP	NA	NA	1.25	0.22	2.92	0.01	NA	NA	0.39	0.70	0.07	0.95
Sawgrass TN:TP	NA	NA	−1.10	0.28	−0.06	0.96	NA	NA	1.92	0.06	2.58	0.01

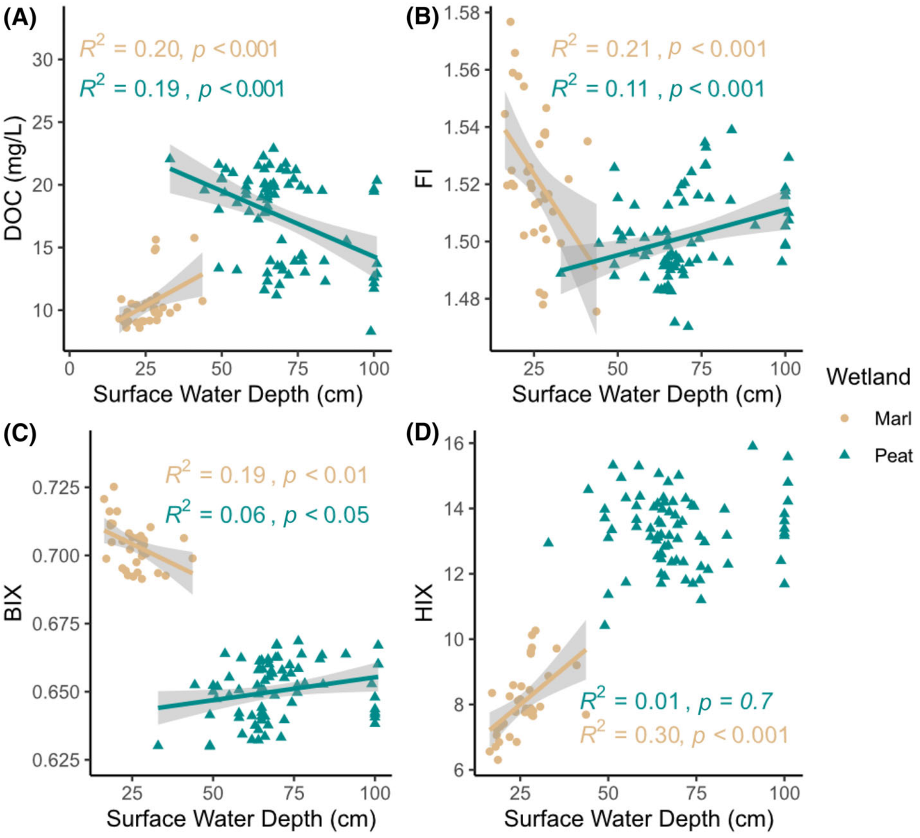

Figure 4. Linear regressions comparing effects of surface water depths on DOC concentrations (A), and fluorescence indices of DOM composition (B–D) between peat and marl wetlands. (B) Increasing FI indicates increasing microbial processing of DOM. (C) Increasing BIX indicates increasing autochthonous influence on DOM. (D) Increasing HIX indicates increasing humic influence to DOM. The shaded area indicates 95% CI. Data were collected along a series of transects and for each wetlands includes data from areas with both high and low historic impact of restoration water.

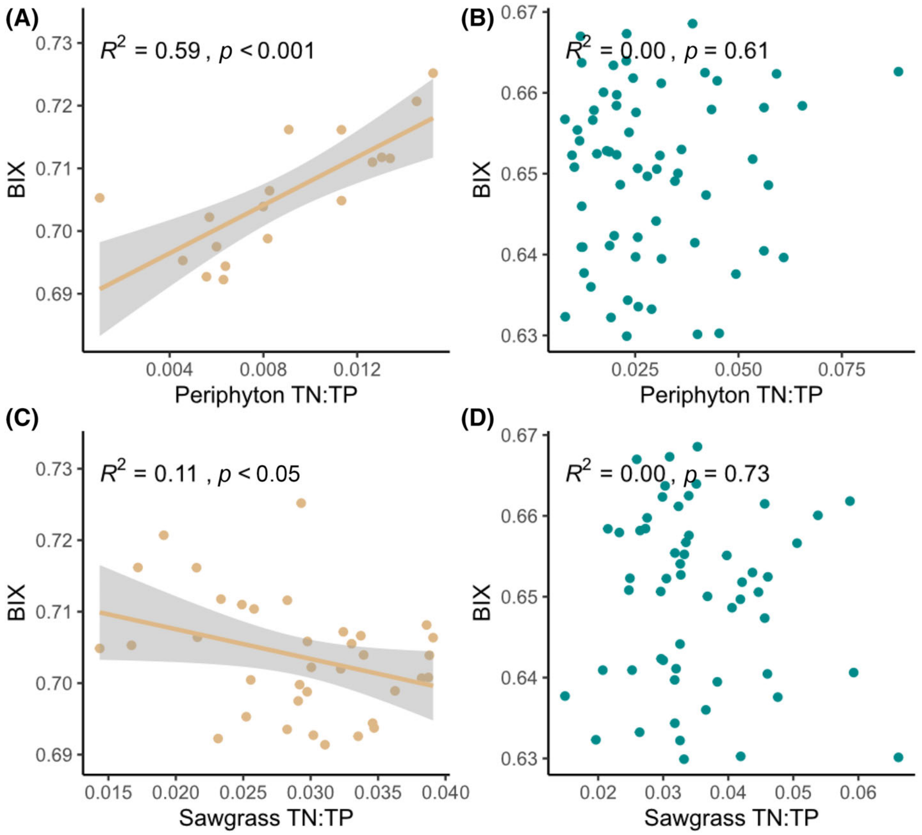

Figure 5. Linear regressions comparing the relationship between BIX and dominant primary producer nutrient stoichiometric ratios (indicating relative nutrient limitation) of the major primary producers between marl (A,C) and peat (B,D) wetlands. Increasing BIX indicates increasing autochthonous influence to dissolved organic matter. The shaded area indicates 95% CI.

FI decreased with water depth, although it was only a marginally significant predictor ($p = 0.06$). Marl wetlands soil nutrient stoichiometric ratios did not correlate significantly with FI, but their inclusion improved the overall model fit.

The full model best explained BIX in peat wetlands (Table S1), whereby increasing water depth and surface water TN:TP ratios corresponded to an increase in BIX (Table 2; Fig. 4). Increasing periphyton biovolume ($p = 0.07$), macrophyte biomass ($p = 0.56$), and soil TN:TP ratio ($p = 0.47$), all corresponded to decreasing BIX, but none showed a significant correlation. In marl wetlands, BIX was best explained by the combined effects of hydrology and phosphorus enrichment (Table S1). BIX decreased as water depth increased, but it increased as surface water TN:TP ratios increased (Table 2; Fig. 4). There was no significant response of BIX to soil or sawgrass TN:TP ratios in peat wetlands, but there was a significant relationship in marl wetlands between BIX and sawgrass TN:TP ratios ($R^2 = 0.11, p = 0.046$; Fig. 5C). Periphyton stoichiometric ratios were excluded from models, as they were collected only in the dry season from marl wetlands. However, there was a strong, positive correlation between BIX collected in marl wetlands and periphyton TN:TP ratio ($R^2 = 0.59$, $p < 0.001$; Fig. 5A). Conversely, BIX in peat wetlands did not correlate with periphyton TN:TP ratio (Fig. 5B).

HIX in peat wetlands was not well explained by the model; the best model included the effects of hydrology, emergent macrophyte biomass and periphyton biovolume, but had an R^2 of only 0.10 (Table S1). The best-fitting model in marl wetlands included the effects of hydrology, emergent macrophyte biomass, and periphyton biovolume (Table S1). Periphyton nutrient concentrations were excluded from models because they were collected only in the dry season for marl sites; however, in marl wetlands HIX decreased with increasing periphyton TN:TP ratio ($R^2 = 0.32$, $p = 0.01$). Conversely, HIX in peat wetlands did not correlate with periphyton TN:TP ratio (Fig. 5B).

Models did not explain $SUVA_{254}$ or SR well in either peat ($R^2 = 0.02$, $p = 0.001$) or marl ($R^2 = 0.001$, $p = 0.19$) wetlands (Table S1). There was no significant correlation between $SUVA_{254}$ or SR and the covariates in either of the best fitting models (Table 2).

Discussion

The results presented here support our prediction that freshwater restoration would have different effects on DOM based on its interactions with local drivers. We found that hydrology and phosphorus are the major drivers of changes to DOM in both peat and marl wetlands. However, our data also showed that the source of a carbon in water used to restore an ecosystem can determine the direction of its interactions with local environmental conditions, such as water depth and nutrient enrichment. We found that increasing water depths caused a “greening” of DOM in peat wetlands (increasing BIX and FI, decreasing concentration of DOC), but a “browning” of DOM in marl wetlands (decreasing BIX and FI, increasing HIX). We found that soil phosphorus enrichment in peat wetlands enhanced microbial production of peat DOM, while in marl wetlands, we found that phosphorus shifted DOM from “brown” to “green” sources based on BIX and FI, suggesting an increase in algal and periphyton contributions. BIX and FI correspond to algal and microbial contributions to DOM, respectively, and their increases of both indicate a growing influence of periphyton as a conglomeration of algal and microbial organisms contributing to both metrics. Despite high variation within and between wetland types, macrophyte biomass, and periphyton biovolume were not significant predictors of DOC concentrations, or DOM composition. Our data highlight the importance of water depth and phosphorus as the major drivers of DOM in oligotrophic Everglades wetlands, where the direction of change depends on their interactions with different types of carbon.

Hydrologic Controls on Wetland DOM

We found that DOM in peat and marl wetlands had an opposite relationship with water depth, which is a master variable in wetland ecosystems, especially the Everglades (Jackson et al. 2014; Regier et al. 2016). Increasing water depths caused a “greening” of DOM in peat (decreasing concentrations, and increasing BIX which indicates algal influence), but a “browning” of DOM in marl wetlands (increasing concentrations and increasing HIX which indicates humic influence). A fundamental difference in hydroperiod between peat and marl wetlands likely explains this difference. Peat wetlands are characterized by longer hydroperiods that maintain anoxic conditions and allow for the buildup of organic matter to create peat soils (Fenner & Freeman 2011; Ritson et al. 2017). In contrast, marl wetlands are characterized by ephemeral organic matter pools, where carbon stored as floc is rapidly mobilized following the annual dry down (Pisani et al. 2013). This difference in carbon sources explains why increasing water depths dilute peat-derived DOM, but mobilize ephemeral marl wetland carbon and import upstream humic DOM.

The production and release of DOM from humic wetland ecosystems (e.g., “browning”) is increasing globally in response to changes in climate and precipitation (Freeman et al. 2001; Worrall et al. 2004). Our data show a similar pattern where increasing water flows from peat-rich upstream wetlands increased humic DOM (both in terms of HIX and concentration), overwhelming the limited local production of DOM in marl wetlands (Duan et al. 2017). Droughts commonly stimulate microbial activity in peat, increasing breakdown and leading to a feedback loop where breakdown-derived increases in pH enhance anaerobic breakdown (Fenner & Freeman 2011; Ritson et al. 2017). In contrast, high water depths can shift conditions from aerobic to anaerobic breakdown of peat as benthic oxygen decreases, leading to slower breakdown and lower concentrations of humic DOM. As water levels increase and potentially suppress peat production of DOM, DOM can become diluted and transported downstream, decreasing its concentrations (Hornberger et al. 1994; Wen et al. 2020).

Phosphorus Enrichment as a Driver of DOM

Phosphorus enrichment (included in every best fitting model) contributed to both the composition and concentration of DOM produced in peat and marl wetlands. Nutrient enrichment is a critical factor affecting many ecological processes, including the storage, processing, and release of carbon (Deegan et al. 2012; Rosemond et al. 2015; Kominoski et al. 2018). Our finding that DOC concentration decreases in response to increasing soil TP and FI (which indicates microbial processing) increases in response to soil TP increases, may reflect a characteristic pattern to the Everglades: primary producer biomass decreases with P enrichment and wetlands become open water sloughs with more labile vegetation. Low phosphorus in these wetlands typically corresponds to more dense and recalcitrant vegetation (such as *Cladium jamaicense*), which likely explains the negative correlation between DOC concentration and soil TP. As restoration mobilizes legacy phosphorus through the Everglades (Sarker et al. 2020), it is essential to continue monitoring how carbon storage and processing interact with nutrient cycling during long-term hydrologic restoration efforts. Given that local variation in P-availability and hydroperiods shape the ridge and slough landscapes (Watts et al. 2014), understanding interactions among hydrology, legacy nutrients, and carbon processing will improve predictions of structure and function of primary producers in restored Everglades marshes.

Dominant carbon sources and relative labilities interact with nutrient enrichment to drive patterns of DOC concentrations and DOM composition. Nutrient enrichment often has higher magnitude effects on the breakdown of recalcitrant organic matter (Manning et al. 2015; Rosemond et al. 2015), which may explain how P enrichment increased DOC concentrations in peat wetlands. In marl wetlands, instead of controlling the concentration of DOC, elevated periphyton TP shifted the sources of DOM to higher autochthonous algal contributions. In oligotrophic wetlands like the Everglades, periphyton has a unique response to eutrophication and nutrient loading, where increasing nutrients lead to losses of biomass (Gaiser et al. 2006). Our finding of increasing algal-derived DOM (BIX) with increasing periphyton phosphorus concentrations suggests that losses in periphyton biomass due to P-enrichment may be detected in DOM. In many areas of the Everglades, periphyton is the dominant primary producer, and understanding how nutrients will shift its production and contribution to DOM is necessary to predict how restoration will impact periphyton assemblages and the DOM derived from them (Childers et al. 2003).

Wetland Type Determines Carbon Sources of DOM

We did not find evidence that primary producer biomass influenced DOM, but restoration in the Everglades, that alters the structure and composition of vegetation communities across the landscape (Sah et al. 2020), is also both mobilizing and creating stores of carbon (Sarker et al. 2020). Much of the data currently available on DOM have focused on long-term data from just a few locations, which misses out on the spatial heterogeneity and microtopographic variations that have been highlighted as key variables to the success of restoration of Everglades wetlands (Harvey et al. 2017). Our findings highlight the variability of carbon production across water depths which drive the variation between ridge and slough habitats across the Everglades. As water depths increase, our findings showing a "greening" of "browner" peatlands, and a "browning" of "greener" marl wetlands suggests that DOM will become more similar between wetlands, with marl wetlands receiving increasing inputs of peat DOM, and peat wetlands producing more algal DOM. Our data suggest that peat significantly contributes to DOC concentrations, more than leaf litter being produced by macrophytes, similar to other peat wetlands (Ritson et al. 2017). In agreement with previous findings (Chen et al. 2013), higher BIX in DOM of marl wetlands, as compared to peat, is best explained by increased periphyton contributions to DOM. Autochthonous marl DOM is likely entering the water column through floc, which, in Everglades marl wetlands, is primarily formed by periphyton and submerged aquatic vegetation (Pisani et al. 2013). Seasonal dry down of marl sites explains increases of BIX in the wet season, as autochthonously derived floc is mobilized to the water column with rewetting of the ecosystem (Pisani et al. 2013).

As increasing water depths increase hydrologic connectivity throughout Everglades wetlands and both become dominated by more humic DOM, carbon and nutrient cycling in the water column of peat and marl wetlands are changing (Dessu et al. 2018; Kominoski et al. 2020). Humic DOM (i.e., higher HIX) reduces photo-degradation of DOM, is more recalcitrant than microbial DOM sources, less bioavailable to microbes, and commonly reduces ecosystem productivity (Moran & Hodson 1990; Qualls & Richardson 2003). A shift from more labile to more recalcitrant carbon could reduce microbial activity, and lead to higher export of DOC from freshwater wetlands into Everglades estuaries (Tranvik 1992; Raymond et al. 2016). This export caused by increases in carbon recalcitrance can lead to undetected fluxes of carbon between ecosystems (Strack et al. 2011; D'Acunha et al. 2019).

The "greening" or "browning" of carbon sources has the potential to alter the path of ecosystem food webs based on the interactions between consumers and carbon (Cole et al. 2006). Understanding food web pathways is a major concern in Everglades restoration and we show that measurements of DOM provide a window into potential changes in the base of the food web in response to restoration activities. Further study is needed to understand how those changes in detrital and algal carbon sources may affect energy flow to the base of the food web (Moore et al. 2004; Sobczak et al. 2005). This is especially relevant in Everglades food webs that are closely tied to periphyton mats that are ubiquitous throughout the Everglades; our results suggest that increasing water depths could homogenize food webs across the landscape, increasing detrital resources in marl marsh food webs, and increasing algal resources in peat marsh food webs (Rader 1999; Sargeant et al. 2010; Sanchez & Trexler 2018).

Acknowledgments

Funding for this project was provided by the Everglades National Park, Task Agreement Numbers P16AC01704, P18AC01041, and P21AC10854. This research was also enhanced by collaborations with the Florida Coastal Everglades Long-Term Ecological Research Program (funded by the National Science Foundation, DEB-2025954 and DEB-1832229). The authors are grateful to the Everglades National Park staff and pilots based out of Homestead Executive Jet Center who made sampling for this project possible. The authors thank colleagues at Florida International University for laboratory and field assistance, especially Christopher Rizzie, Ryan Bremen, Matt Smith, Yan Ding, and Mark Kershaw. The authors thank Robin Miller and Evelyn Gaiser for editing and comments on this manuscript. This is contribution #1546 of the Institute of Environment at Florida International University.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Peat wetland linear relationships between fluorescence indices, and periphyton and sawgrass TN:TP.

Figure S2. Relationships between marl wetland fluorescence indices and periphyton TN:TP.

Table S1. Model selection on factors explaining DOM metrics: DOC concentration, FI, BIX, HIX, SUVA, and SR.

Coordinating Editor: Sara Ashpole

Received: 4 November, 2022; First decision: 3 December, 2022; Revised: 13 March, 2023; Accepted: 20 March, 2023