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Dissolved organic matter variations in coastal plain wetland watersheds: The integrated role of hydrological connectivity, land use, and seasonality

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Abstract

Dissolved organic matter (DOM) is integral to fluvial biogeochemical functions, and wetlands are broadly recognized as substantial sources of aromatic DOM to fluvial networks. Yet how land use change alters biogeochemical connectivity of upland wetlands to streams remains unclear. We studied depressional geographically isolated wetlands on the Delmarva Peninsula (USA) that are seasonally connected to downstream perennial waters via temporary channels. Composition and quantity of DOM from 4 forested, 4 agricultural, and 4 restored wetlands were assessed. Twenty perennial streams with watersheds containing wetlands were also sampled for DOM during times when surface connections were present versus absent. Perennial watersheds had varying amounts of forested wetland (0.4–82%) and agricultural (1–89%) cover. DOM was analysed with ultraviolet–visible spectroscopy, fluorescence spectroscopy, dissolved organic carbon (DOC) concentration, and bioassays. Forested wetlands exported more DOM that was more aromatic-rich compared with agricultural and restored wetlands. DOM from the latter two could not be distinguished suggesting limited recovery of restored wetlands; DOM from both was more protein-like than forested wetland DOM. Perennial streams with the highest wetland watershed cover had the highest DOC levels during all seasons; however, in fall and winter when temporary streams connect forested wetlands to perennial channels, perennial DOC concentrations peaked, and composition was linked to forested wetlands. In summer, when temporary stream connections were dry, perennial DOC concentrations were the lowest and protein-like DOM levels the highest. Overall, DOC levels in perennial streams were linked to total wetland land cover, but the timing of peak fluxes of DOM was driven by wetland connectivity to perennial streams. Bioassays showed that DOM linked to wetlands was less available for microbial use than protein-like DOM linked to agricultural land use. Together, this evidence indicates that geographically isolated wetlands have a significant impact on downstream water quality and ecosystem function mediated by temporary stream surface connections.

KEYWORDS
dissolved organic matter, geographically isolated wetland, microbial bioavailability, PARAFAC, restoration, temporary streams

1 | INTRODUCTION

Freshwater wetlands are well known to play disproportionate ecological roles relative to the area they occupy. They support numerous species for all or part of their life cycles, absorb water in flood-prone areas, regulate local air temperature, and can act as sinks for excess phosphorus and nitrogen (Cheng & Basu, 2017; Wetzel, 2001). They also are critical to global carbon (C) budgets because they store up to 30% of the world's soil C and can be important sources of greenhouse gases (Nahlik & Fennessy, 2016). Wetlands supply organic matter to downstream waters such that there is a significant relationship between the proportion of wetlands contributing and the concentration and flux of DOM in receiving waters (Creed, Sanford, Beall, Molot, & Dillon, 2003; Mattsson et al., 2009) and that DOM is typically characterized by high apparent molecular weight aromatics (Graeber, Gelbrecht, Pusch, Anlanger, & von Schiller, 2012). This DOM provides energy and nutrients for stream heterotrophic microbes and associated food webs (Kaplan & Cory, 2016), and the amount available for microbial uptake is dependent not only on the quantity but also on the molecular composition of the organic matter (Fellman, D'Amore, Hood, & Boone, 2008; Hosen, McDonough, Febria, & Palmer, 2014; McDowell et al., 2006). Thus, changes to DOM composition due to upstream wetland land cover can alter food webs in downstream reaches (Hall & Meyer, 1998).

Water level and hydroperiod are known to influence all biogeochemical processes in wetlands (Miao et al., 2017), and researchers have argued that wetland hydrological connectivity should significantly influence downstream biogeochemical functions (Leibowitz, 2003; Marton et al., 2015; Rains et al., 2016). Although modelling studies have supported this argument (e.g., Ameli & Creed, 2017; Evenson et al., 2018), the relationship between surface hydrological connectivity of wetlands to adjacent waters and the amount and composition of DOM exported by these systems has received little empirical investigation. An important exception is work by Yu et al. (2015) showing that although surrounding land use was the largest driver of wetland DOM, seasonal connectivity to surface waters can also play a role.

Interest in understanding the importance of hydrological connectivity has increased given emerging evidence from remote sensing and field studies that many so-called geographically isolated wetlands (GIWs) surrounded by uplands actually connect to larger water bodies periodically (Lang, McDonough, McCarty, Oesterling, & Wilen, 2012; Leibowitz, 2015; McDonough et al., 2015; Mushet et al., 2015). Such GIWs (Tiner, 2003) can be found worldwide and constitute most of the wetlands in many North American landscapes (Cohen et al., 2016). Hydrological connectivity has also emerged as a policy-relevant issue in the United States given regulatory decisions questioning the value of wetlands unless they have a direct impact (significant nexus) on perennial waters (Alexander, 2015; Creed et al., 2017; Golden et al., 2017).

Loss of freshwater wetlands globally has been pronounced (Davidson, 2014), and upland wetlands including GIWs are especially prone to loss or modification by anthropogenic activity because of their small size and upland position (Cohen et al., 2016; Creed et al., 2017). Formation of these wetlands is often the product of topographic depressions, where water residence times are high and downstream surface hydrological connectivity is limited (Creed et al., 2003). Alteration of wetland hydrology by ditching has been extremely common (Boland-Brien, Basu, & Schilling, 2014) and results in reduced wetland inundation as water moves efficiently down-gradient (McDonough et al., 2015). Ditching has, in effect, increased hydrological connectivity between wetlands and downstream waters (Epting et al., 2018; Lang et al., 2012).

Many efforts to restore wetlands have focused on recovering natural hydrology by blocking ditches (i.e., decreasing connectivity to downstream waters). The goals of such efforts are typically to recover biodiversity and promote functions, for example, water storage and groundwater recharge (Jones et al., 2018), enhanced sediment and nutrient retention (Cheesman, Dunne, Turner, & Reddy, 2010), and high water residence time and redox conditions that drive production of large stocks of aromatic-rich dissolved organic matter (DOM) in many GIWs (Cohen et al., 2016). Researchers have suggested that the degree of hydrological isolation of a wetland may play an important role in wetland recovery following restoration (Ballantine & Schneider, 2009) as does land use within the watershed (Yu, Huang, Sun, & Sun, 2017), but this work has focused largely on soil carbon or wetland plants. What is less clear is how hydrological connections mediate the transport of organic matter and other compounds from GIWs to perennial stream networks. Attempts to restore peatland bogs by blocking ditches have been associated with changes in DOM yield and composition (Strack, Zuback, McCarter, & Price, 2015; Wilson et al., 2011), but for other types of wetlands, little research has focused on the relationship between hydrological restoration and DOM.

Whether restored or natural, understanding the relationship between hydrological connectivity and DOM export from wetlands requires much more work (Bortolotti, Vinebrooke, & St. Louis, 2016; Stanley, Powers, Lottig, Buffam, & Crawford, 2012). Wetland hydroperiod is a major control over carbon dynamics (Nahlik & Fennessy, 2016), and one would expect surface water connections to downstream waters that act to reduce water residence in a wetland should also exert control. These connections certainly vary significantly in duration and magnitude (Ameli & Creed, 2017; Vanderhoof, Alexander, & Todd, 2016), and even intermittent connectivity could influence DOM in receiving waters (Laudon et al., 2011). Subsurface connectivity (groundwater flow paths) may also influence downstream DOM because some researchers that found that wetland presence in a watershed can be associated with increased levels of wetland DOM downstream even when surface water connections are absent (Gergel, Turner, & Kratz, 1999; Richardson, Mitchell, Branfireun, & Kolka, 2010). Overall, the relative importance of surface and subsurface contributions to downstream DOM and how restoration might influence this are open questions.

Given this, we organized empirical research to explore the relationship between wetland DOM, restoration, and hydrological connectivity using U.S. Coastal Plain catchments with high GIW cover as test beds. In the mid-Atlantic region, numerous depressional GIWs called Delmarva Bays punctuate forested and agricultural landscapes, and several of these have been subjected to restoration actions that changed their connectivity to perennial receiving streams (Epting et al., 2018; McDonough et al., 2015; McFarland et al., 2016). We asked: (1) Does DOM exported from forested, agricultural, and restored wetlands differ significantly in quantity or composition? (2) Is there evidence that DOM concentration and composition in perennial streams are influenced by the timing of hydrological connectivity to wetlands? and (3) Are seasonal changes in stream DOM composition linked to the microbial bioavailability of that organic matter?

Wetlands in general are known as sources of DOM in watersheds and depressional wetlands, such as the Delmarva Bays have intermittent hydrological connectivity and vary in their water residence times (Jones et al., 2018), which likely influences the amount and composition of DOM (Yu et al., 2015). Residence time is the shortest in agricultural wetlands, and the hydrology of these restored wetlands has not yet fully returned to reference conditions (McDonough et al., 2015). Thus, we hypothesized that forested wetlands would have greater quantities of DOM that is more aromatic in nature than either agricultural or restored wetlands. Hydrological studies suggest that water from upland wetlands reaches perennial stream networks via both surface (McDonough et al., 2015) and ground water (McLaughlin, Kaplan, & Cohen, 2014); thus, we further hypothesized that DOC concentration and aromatic content in perennial streams draining forested wetlands (vs. agricultural or restored) would be the greatest, whether or not temporary connections to those forested wetlands were active. However, because surface water fluxes from our study wetlands can be substantial during wet periods (McDonough et al., 2015), we predicted that perennial stream DOM concentrations would be the highest and the most similar to forested DOM on sampling dates when upstream forested wetlands were connected. On the basis of evidence that aromatic DOM common to many types of freshwater wetland is less available to microbial use (Fellman et al., 2008), we further hypothesized that DOM availability for microbial use would depend on upstream connectivity and DOM composition. Specifically, we predicted that microbial use of DOM would be the lowest when perennial streams had high levels of aromatic DOM from forested wetlands.

2 | METHODS

2.1 | Study sites and research design

Study sites are in the Tuckahoe Creek watershed (Figure 1) where depressional wetlands range in size and are the most common wetland type (most with surface area between 0.5 and 5.7 ha). Wetland relief ranges between approximately 0.5 and 2.0 m with seasonal drying occurring in smaller wetlands when evapotranspiration is high (Fenstermacher, Rabenhorst, Lang, McCarty, & Needelman, 2014). During our study period (2010–2012), wetland export (Figure 2a) into temporary channels (Figure 2b–d) connected wetlands to perennial stream networks during late fall, winter, and spring when evapotranspiration is low (Epting et al., 2018; McDonough et al., 2015). Precipitation in the watershed is seasonal with a 30-year mean (1983–2012) at Goldsboro, Maryland of 1,165 ± 187 mm (PRISM Climate Group, Oregon State University, 2018). Mean precipitation was near average in 2010 (1,246 mm) and 2012 (1,074 mm) but was substantially higher in 2011 (1,470 mm) due to rain from Hurricane Irene and the remnants of Tropical Storm Lee. Restored wetlands had been ditched, and the wetlands were converted to agricultural use. These sites were restored in 2002 and 2003, wetland ditches were plugged and manipulated to enhance hydrological storage, that is, decrease connectivity. Hummocks were also added at some sites to restore topology. To increase sediment stability, grasses were planted at all sites, and trees were planted at two of the four restoration sites; however, vegetation at restored sites remains predominately herbaceous in contrast to forested natural wetland sites (Yepsen et al., 2014). Additional site details including climate and vegetation types are in (McDonough et al., 2015; McFarland et al., 2016; Yepsen et al., 2014).

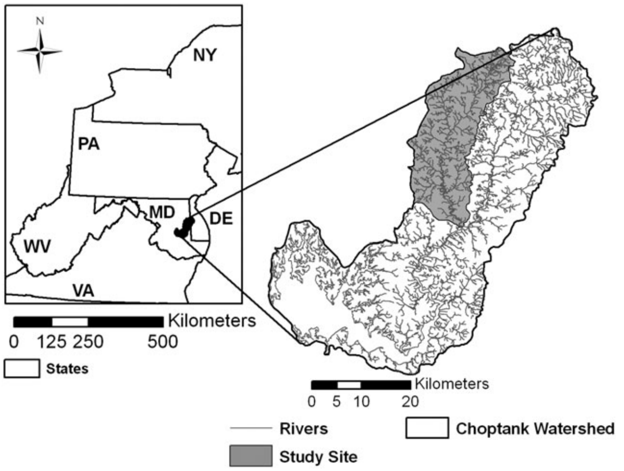

FIGURE 1 The Tuckahoe Creek watershed and stream network, a subbasin of the Choptank River watershed in Maryland, USA

For Question 1, we studied 12 wetlands (four forested, four agricultural, and four restored; Table 1), also sampling the water being exported monthly via temporary streams from October 2009 to September 2011 to compare dissolved organic carbon (DOC) concentration and DOM composition among the three wetland types. There was generally no water export during dry seasons (June–October) except for 2 days in mid-July 2010 from the agricultural and restored wetlands following rain events (see figure 5 in McDonough et al., 2015). Hydrology differed between the three site types: In 2010, temporary streams in forested wetlands had surface water for 165 days on average, restored wetlands were connected for 74 days on average, whereas agricultural wetlands were only connected an average of only 15 days (McDonough et al., 2015). When temporary streams were connected, discharge was measured, and samples were collected to estimate DOC flux.

For Questions 2 and 3, seasonal samples (March 2, 2011, June 29, 2011, October 11, 2011, and February 14, 2012) were collected from 20 perennial headwater streams (non-nested) and the downstream Tuckahoe River that drained catchments with varying amounts of forested wetlands—composed primarily of depressional wetlands—and cropland cover (Table 2). We collected water samples seasonally to compare perennial stream water quality when upstream depressional wetlands were and were not connected by temporary streams. The

FIGURE 2 (a) A flowing temporary stream delivers aromatic-rich dissolved organic matter from a depressional wetland to a perennial stream draining an agricultural watershed. Examples of temporary streams connecting (b) forested, (c) restored, and (d) agricultural wetlands to adjacent perennial streams within the Tuckahoe Creek watershed

TABLE 1 Wetland classifications, physical attributes, and baseflow discharge via temporary streams from wetlands sites used to address the Question 1

Wetland site ID	Wetland type (year restored)	Wetland area (m^2)	Watershed area (m^2)	Mean discharge (L/s)
F1	Forested	335,052	567,304	46.9
F2	Forested	25,166	36,291	3.8
F3	Forested	17,208	43,400	3.3
F4	Forested	127,853	324,890	12
R1	Restored (2002)	9,334	42,080	[a]
R2	Restored (2002)	67,145	245,387	5.9
R3	Restored (2003)	1,433	13,317	0.3
R4	Restored (2003)	1,970	146,729	2.4
A1	Agricultural	8,060	18,652	0.3
A2	Agricultural	2,571	14,620	0.3
A3	Agricultural	3,955	11,348	0.2
A4	Agricultural	10,276	18,101	0.1

[a] Discharge could not be measured.

TABLE 2 Characteristics of the watersheds used in this study to address Questions 2 and 3 vary according to size and landcover

Perennial site ID	Drainage area (km^2)	Mean watershed TWI	Forested wetland cover (% watershed)	Cropland cover (% watershed)	Mean discharge (L/s)
1	1.04	11.12	0.41	88.66	3.0
2	10.4	11.55	3.21	75.59	204.2
3	0.74	11.53	5.77	79.95	13.7
4	3.88	11.54	5.89	53.58	48.4
5	1.73	11.28	6.76	52.82	27.5
6	6.54	11.49	7.58	60.10	127.1
7	2.49	11.47	11.26	63.16	45.2
8	3.51	11.35	12.24	44.95	47.6
9	9.51	11.44	12.63	58.24	171.8
10	4.13	11.42	14.75	39.16	78.3
11	12.6	11.66	19.61	36.48	317.7
12	4.41	11.11	19.69	45.79	90.9
13	3.73	11.82	19.75	45.00	56.6
14	5.52	11.51	20.91	50.29	76.4
15	1.47	11.56	30.65	28.93	38
16	2.80	11.82	31.92	22.00	24.3
17	1.87	11.57	39.34	11.83	12.1
18	1.00	12.53	45.86	1.02	0.5
19	1.13	12.59	57.85	6.12	26.6
20	0.53	11.44	81.52	2.34	7.4
Tuck. Mainstem	2,256	11.40	15.62	57.24	3,501

Note. TWI = topographic wetness index.

goal was to test for a statistically significant difference in perennial stream DOM composition and DOC quantity when wetlands were connected versus not while also taking into account catchment attributes including wetland influence (% wetland cover; topographic wetness index [TWI]) and land use (wetland, forested, and cropland). TWI is a landscape metric that predicts saturation potential and water residence time using the equation $\ln(\alpha/\tan\beta)$ where α is upslope contributing area and $\tan\beta$ is local slope (Beven & Kirkby, 1979). Thus, TWI captures landscape depressions associated with wetland production of DOM (Seibert, Stendahl, & Sørensen, 2007), providing an ideal metric to assess the influence of small upland wetlands as sources of DOM in the landscape.

To test whether changes to DOM composition (e.g., aromatic content) altered microbial activity and use of DOM (Question 3), bioassays were conducted on water from wetlands and downstream perennial channels (McDowell et al., 2006).

2.2 | Sample collection

At Delmarva wetland sites, samples were collected from the wetland as well as the associated temporary outlet if water was present. Samples were collected in amber high-density polyethylene bottles and stored on ice for transport to the laboratory. Samples were filtered with 0.7-μm GF/F filters (GE Healthcare, Chicago, IL, USA) within 24 hr and stored at 4 °C until analysis, which occurred within 72 hr of sample collection. Discharge of temporary streams was measured volumetrically when possible and otherwise using the cross-sectional area method (McDonough et al., 2015).

2.3 | Chemical analysis

To estimate DOM composition, we applied ultraviolet–visible (UV–Vis) absorbance and excitation–emission matrices coupled with parallel factor analysis (PARAFAC). Total dissolved nitrogen (TDN) and DOC concentrations were measured using a Shimadzu TOC-Vcph.

2.3.1 | DOM spectroscopy

UV–Vis absorbance spectra were measured on filtered samples from 200 to 800 nm using a spectrophotometer with a 1-cm path-length quartz cuvette. UV–Vis spectra were baseline-corrected by subtracting the mean absorbance at 600–650 nm from each absorbance measurement. Specific UV absorbance at 254 nm ($SUVA_{254}$), which has been shown to correlate positively with DOM aromatic content (Weishaar et al., 2003) and age (Butman, Raymond, Butler, & Aiken, 2012), was calculated by standardizing UV absorbance at 254 nm by DOC concentration. The spectral slope ratio (S_R) was calculated from UV–Vis spectra by taking the ratio of log-transformed absorbance slopes at 275–295 and 350–400 nm. This metric decreases with increasing DOM average molecular weight (Wünsch, Stedmon, Tranvik, & Guillemette, 2017) and is positively correlated with DOM photodegradation (Helms et al., 2008). UV–Vis absorbance metrics can be sensitive to iron and nitrate interference. We determined iron (Hach Ferrover) and nitrate (Dionex ICS-1000) on a subset of samples and determined that at no site did iron or nitrate contribute to more than 5% of absorbance at 254 nm.

Fluorescence excitation–emission matrices (EEMs) were collected using a Horiba Instruments Fluoromax-4 spectrofluorometer. EEMs were measured across excitation wavelengths 250–450 nm at 5-nm increments and emission wavelengths 300–550 nm at 2-nm increments and corrected for inner filter effects, instrument bias, and Raman scatter (Cory, Miller, McKnight, Guerard, & Miller, 2010).

To identify the likely molecular character of DOM, PARAFAC was conducted on 333 EEMs representing samples collected from Delmarva wetlands and temporary and perennial streams; MATLAB v.R2016b (MathWorks, Inc., Natick, MA) and the drEEM v.0.2.0 package were used (Murphy, Stedmon, Graeber, & Bro, 2013). Analysis with PARAFAC decomposes DOM fluorescence EEMs into distinct components that can be traced back to different groups of organic matter compounds (Coble, 1996; Stedmon & Markager, 2005). These relationships are built by referencing fluorescence peaks present in each PARAFAC component to studies that related these peaks to particular chemical fractions extracted by column (Coble, 1996), obtained from source material of known composition (Riu & Bro, 2003) or from a particular environmental setting (Hosen et al., 2014; Stedmon & Markager, 2005). These components include different types of humic and fulvic acids, including terrestrial humic substances that are of high apparent molecular weight and derived from degraded plant matter, and humics of microbial origin that are newer, smaller, and generally more available to microbial degradation (Hosen et al., 2014; Stedmon & Markager, 2005; Thurman, 1985). Protein-like fluorescence of tryptophan and tyrosine, likely of recent microbial origin, can also be differentiated with PARAFAC analysis (Coble, 1996). For this study, four fluorescent PARAFAC components were validated (Table 3 and Figure S1). To identify the nature of the DOM represented by each fluorescent component, the excitation and emission loadings for the four components were matched with PARAFAC components from previously reported studies on the basis of component excitation and emission maxima (Table 3).

Of the four PARAFAC components, two have been identified as most likely to represent DOM of relatively recent, microbial origin (C1 and C4). The other two components represent aged, terrestrial humic substances (C2 and C3). Component C1 was identified as a humic substance that is likely of microbial origin in either terrestrial or aquatic environments. Both Components C2 and C3 appear to be fluorescent signatures of terrestrial humic substances that are likely aged and of high molecular weight. Finally, Component C4 matches fluorescence produced by the amino acid tryptophan and is likely an indicator of recent primary production.

To reduce the influence of DOC concentration on model scores, the per cent relative contribution of each of the validated components within a water sample was calculated by dividing the fluorescence maximum ($F_{\max}$ in Raman units) of each individual component by the summed fluorescence maxima of all components (Hosen et al., 2014).

2.3.2 | DOM bioassays

A DOM bioavailability assay was conducted on all perennial samples and a subset of temporary stream samples. Water samples were collected in the field, stored on ice, and filtered to 0.2 μm within 24 hr. Aliquots (125 ml) of samples were inoculated with 1 ml of a filtered (1 μm) sediment slurry (bacterial inoculate) collected from Tuckahoe Creek—a downstream reach common to all sample locations. Assays for samples collected on a given date were run within 48 hr of sample collection. The inoculum used for each round of assays was collected

TABLE 3 Characteristics of the fluorescent components identified by the PARAFAC model in this study

Component	Excitation maxima (nm)	Emission maxima (nm)	Comparable components (identified by reference and original component name)	Component description
C1	<250 (310)	424	Guéguen, Granskog, McCullough, and Barber (2011)—Component 2 Stedmon and Markager (2005)—Component A Yamashita, Kloeppel, Knoepp, Zausen, and Jaffé (2011)—Component 1 Williams, Frost, and Xenopoulos (2013)—Component 2 Stubbins et al. (2014)—Component 5 Cook, Birdwell, Lattao, and Lowry (2009)—Component 2	UVC humic, likely new, and of microbial origin. Terrestrial or autochthonous origin—related to agricultural land cover and bacterial production. Fluorescence signature of TPIA fraction of DOM.
C2	255 (390)	502	Cawley et al. (2012)—Component 2 Guéguen et al. (2011)—Component 1 Coble (1996)—Peak C Ohno and Bro (2006)—Component 1 Yamashita et al. (2011)—Component 3 Murphy et al. (2013)—Component 2 Wünsch et al. (2017)—Component 3 Fellman et al. (2008)—Component 2	Terrestrial, humic-like substance associated with high apparent molecular weight, aromatic DOM. One of Top 2 components in forested wetland DOM (Fellman et al., 2008).
C3	<250 (360)	450	Yamashita, Boyer, and Jaffé (2013)—Component 2 Ohno and Bro (2006)—Component 1 Fellman et al. (2008)—Component 1	Humic-like and of terrestrial origin
C4	<250	350	Coble (1996)—Peak T Stedmon and Markager (2005)—Component 7 Cawley et al. (2012)—Component 5 Yamashita, Jaffé, Male, and Tanoue (2008)—Component 7	Tryptophan-like DOM

Note. Wavelength values in parentheses indicate local maxima. DOM = dissolved organic matter; PARAFAC = parallel factor analysis; TPIA = transphilic organic acid; UVC = ultraviolet C.

on the same day as the water samples analysed. Samples were incubated in Erlenmeyer flasks, which were loosely covered with parafilm to allow ventilation. Paired *t* tests of sample DOC levels before and after inoculation found no significant increase in concentration following addition of the filtered slurry. To ensure nonlimiting nutrient conditions, nitrate $\left(NO_3^-\right)$ and phosphate $\left(PO_4^{3-}\right)$ were added to all flasks to raise ambient NO_3^--N and PO_4^{3-}-P concentrations by 100 and 20 μg/L, respectively (McDowell et al., 2006). Immediately following inoculation and nutrient addition, an initial 20 ml sample from each flask was filtered (0.2 μm), and DOC concentration was determined as described above. Flasks were stored in the dark at 20 °C for 28 days and shaken weekly. Following the incubation period, a final 20-ml sample was filtered (0.2 μm), and DOC concentration was measured. Per cent bioavailable DOC was calculated as the per cent decrease in initial DOC concentration during the 28-day incubation. To account for potential microbial production of DOC, triplicate control vials containing Nanopure water in place of streamwater and amended with nitrate and phosphate as above, were also incubated with the bacterial inoculate. Paired *t* tests comparing DOC concentrations of 0- and 28-day control samples did not detect any significant changes. A small subset of samples returned net zero rates of carbon loss. This was attributed to lysis of bacterial cells during filtering, which has recently been highlighted as a concern for bioavailability studies using filters with a 0.2-μm pore size (Smith et al., 2017), and thus, these samples were excluded from analysis. Results from this study were compared with published results from similar bioassay experiments.

2.4 | Landscape analysis

The watersheds were delineated within ArcMap ver. 9.3 (Environmental Systems Research Institute, Redlands, CA) using 1-m light detection and ranging-derived digital elevation models (Lang et al., 2012). Cropland cover was determined using the 2006 Multi-Resolution Land Characteristics Consortium National Land Cover Database (Fry et al., 2011). Mean watershed TWI (Beven & Kirkby, 1979) was calculated from digital elevation models for each watershed delineated following Lang, McCarty, Oesterling, and Yeo (2013).

2.5 | Temporary stream connectivity

We measured wetland connectivity status using site visits and flow status loggers (described in McDonough et al. (2015) deployed in 24 temporary streams that link forested wetlands to perennial channels in the Tuckahoe and nearby Corsica River watersheds (Epting et al., 2018; McDonough et al., 2015). Site visits occurred at least monthly throughout the study, and flow status loggers were deployed at 12 sites from January 2009 to December 2010 and from October 2014 to September 2015 at all 24 sites. Loggers recorded presence or absence of surface water in the temporary channels, and site visits supported inferring flow from water presence. The later data informed a model of temporary channel connection status that could be applied to the perennial stream DOM sampling dates or locations where we did not have direct measurements of flow status. We used a binomial autoregressive dynamic lagged time series generalized linear model fit to surface water presence data using least absolute shrink and selection operator (lasso) regularization (Buckland, Burnham, & Augustin, 1997; Friedman, Hastie, & Tibshirani, 2010). Lasso regression is similar to linear regression, but with the addition of regularization, which improves variable selection and model fit when models with large numbers of variables are needed. Daily weather station data were obtained from Tuckahoe, MD (Western Regional Climate Center) including mean temperature, precipitation, solar irradiance, mean wind speed, mean relative humidity, and cooling degree days (at 65 °F). Additional precipitation gauge data from Royal Oak, MD, and Greensboro, MD, were obtained from NOAA National Centers for Environmental Information (https://www.ncdc.noaa.gov/). Each weather station variable was lagged up to 30 days. In addition to weather station data, watershed size and wetland area within a watershed were also used as predictor variables (Table S1). An autoregressive term for temporary stream flow status on the previous day ("1" or "0") was also included. Model selection was evaluated using *k*-fold cross-validation ($k = 10$) to evaluate classification accuracy. The final model had a cross-validation misclassification rate of 0.0488, meaning that on more than 95% of days, the model correctly predicted whether a given temporary stream was flowing. All analyses were conducted in R 3.3.3 (R Core Team, 2016) with the *glmulti* package (Calcagno, 2013).

2.6 | Statistical analysis

2.6.1 | Question 1: DOM and wetland type

To determine if DOM in water exported from forested, agricultural, and restored wetlands differed, two analyses were performed. First, linear discriminant analysis (LDA) was applied as factor analysis to determine if water samples from different wetland types could be differentiated on the basis of DOM composition. LDA was conducted in R 3.3.3 using the *MASS* package (Venables & Ripley, 2002). For the discriminant analysis, an initial model was computed that included per cent fluorescence of the four PARAFAC components, S_R, FI, $SUVA_{254}$, and log-transformed DOC concentration (Question 1). Log-transformed DOC concentration, FI, and $SUVA_{254}$ did not contribute to the model and were removed. Using the R package *Ellipse* (Murdoch & Chow, 2013), 95% confidence ellipses were calculated for each of the three categories of wetlands. Samples collected from perennial stream sites were subsequently applied to the discriminant model, and the resulting discriminant function scores were plotted to visualize similarities between Delmarva Bay and perennial stream DOM over time in support of Question 2.

Second, repeated-measures mixed-effects models were computed to test for differences in DOM composition among the three wetland types using R package *lme4* (Bates, Mächler, Bolker, & Walker, 2015). For the repeated-measures mixed-effects analysis, models followed the formula $Y = f$[wetland_type(fixed/categorical) + site(random/categorical)] with Y representing the range of DOM variables tested. An α level of 0.05 was selected a priori, compound symmetry covariance was assumed, and *p* values were reported with Kenward–Roger approximation (Kuznetsova, Brockhoff, & Christensen, 2016). Model residuals were evaluated for normality and heteroscedasticity and, in the case of DOC yield, log-transformed to meet model assumptions. For the models that returned a significant main effect for sampling date, significant

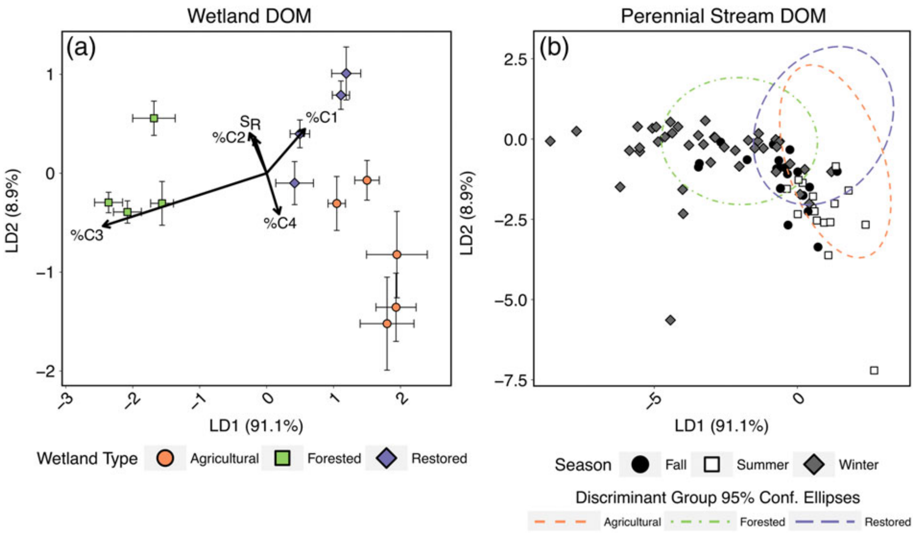

FIGURE 3 (a) Linear discriminant analysis (LDA) biplot of wetland dissolved organic matter (DOM) composition. Wetland samples used to generate the LDA model were plotted using linear discriminant functions 1 (LD1) and 2 (LD2). For each wetland site, the mean of repeated samples is reported with error bars representing standard error of the mean. Arrows represent the loadings of the five DOM compositional metrics used for LDA. (b) Samples from perennial streams located downstream of wetlands are plotted with the 95% confidence ellipses of the three discriminant groups generated from samples collected in wetlands for Question 1

differences between wetland type were calculated using Tukey's honestly significant difference multiple mean comparisons.

2.6.2 | Question 2: Perennial stream DOM

To determine if perennial DOM was related to connectivity, we evaluated DOM quantity and quality when wetlands were versus were not connected using connectivity status from the temporary flow logger data. On the basis of prior work, we included catchment attributes including wetland influence (% wetland cover; TWI) and surrounding land use (wetland and cropland). We used repeated-measures mixed-effects models to ask if DOM (composition and yield) and TDN yield were significantly related to watershed attributes and date. Models generated include the following preselected combinations of independent variables: "% Cropland + Date", "% Wetland + Date," " Watershed TWI + Date," "% Cropland," "% Wetland," and "TWI." Model selection was conducted following an information-theoretic approach (Anderson, 2008). Residuals were evaluated for normality, and heteroscedasticity and DOC yield, DOC concentration, TDN concentration, per cent wetland cover, and per cent cropland cover were base-10 log-transformed to meet model assumptions. All potential models were evaluated for statistical interactions and, when no interactions were found for any models, this term was removed. For each dependent variable, the model with the smallest second-order corrected Akaike information criterion value was selected as the model of best fit (Mazerolle, 2016). For each model selected by corrected Akaike information criterion, Kenward–Roger *p* values were calculated. For the models that returned a significant main effect for sampling date, significant differences between dates were calculated using Tukey's honestly significant difference multiple mean comparisons.

To further evaluate the potential sources of DOM in perennial streams, we compared composition of perennial stream DOM with wetland DOM. We projected DOM quality metrics from perennial streams using the linear discriminant functions developed with wetland data from Question 1. To assess the similarity of DOM from wetlands to downstream perennial streams over time, we included the 95% confidence ellipses for each of the three categories of wetland.

2.6.3 | Question 3: Microbial availability

To determine how DOM composition influences lability of DOM for microbial heterotrophy, we compared per cent bioavailable DOC with DOM composition—as measured by PARAFAC components—using linear regression. For this study and each published study included in our comparison, per cent bioavailable DOC was regressed against per cent humic-like fluorescence and per cent protein-like fluorescence using R 3.3.3.

3 | RESULTS

3.1 | Question 1: DOM from different wetland types

3.1.1 | Wetland DOM composition

The LDA using per cent fluorescence of each PARAFAC component and S_R reliably differentiated between forested, agricultural, and restored wetlands on the basis of carbon characteristics (Figure 3a), properly classifying 90% of forested wetland DOM samples (Table 4). Discrimination between agricultural and restored DOM in export was less

TABLE 4 Actual Delmarva Bay wetland type compared with the classification predicted by LDA

		Predicted		
		Forested	Agricultural	Restored
Actual	Forested	74	1	8
	Agricultural	0	29	26
	Restored	6	12	69

Note. Class predictions were generated from jackknifed models. LDA = linear discriminant analysis.

successful with only 53% and 79% respectively correctly identified by the model. Forested wetland DOM had higher levels of Component C3 and lower levels of Component C1. Agricultural wetland DOM contained higher levels of protein-like fluorescence (tryptophan; Component C4) than other wetland types, and restored wetlands were linked to higher S_R than other wetlands.

Repeated-measures mixed-effects models confirmed the relationships found by LDA. Per cent fluorescence of Components

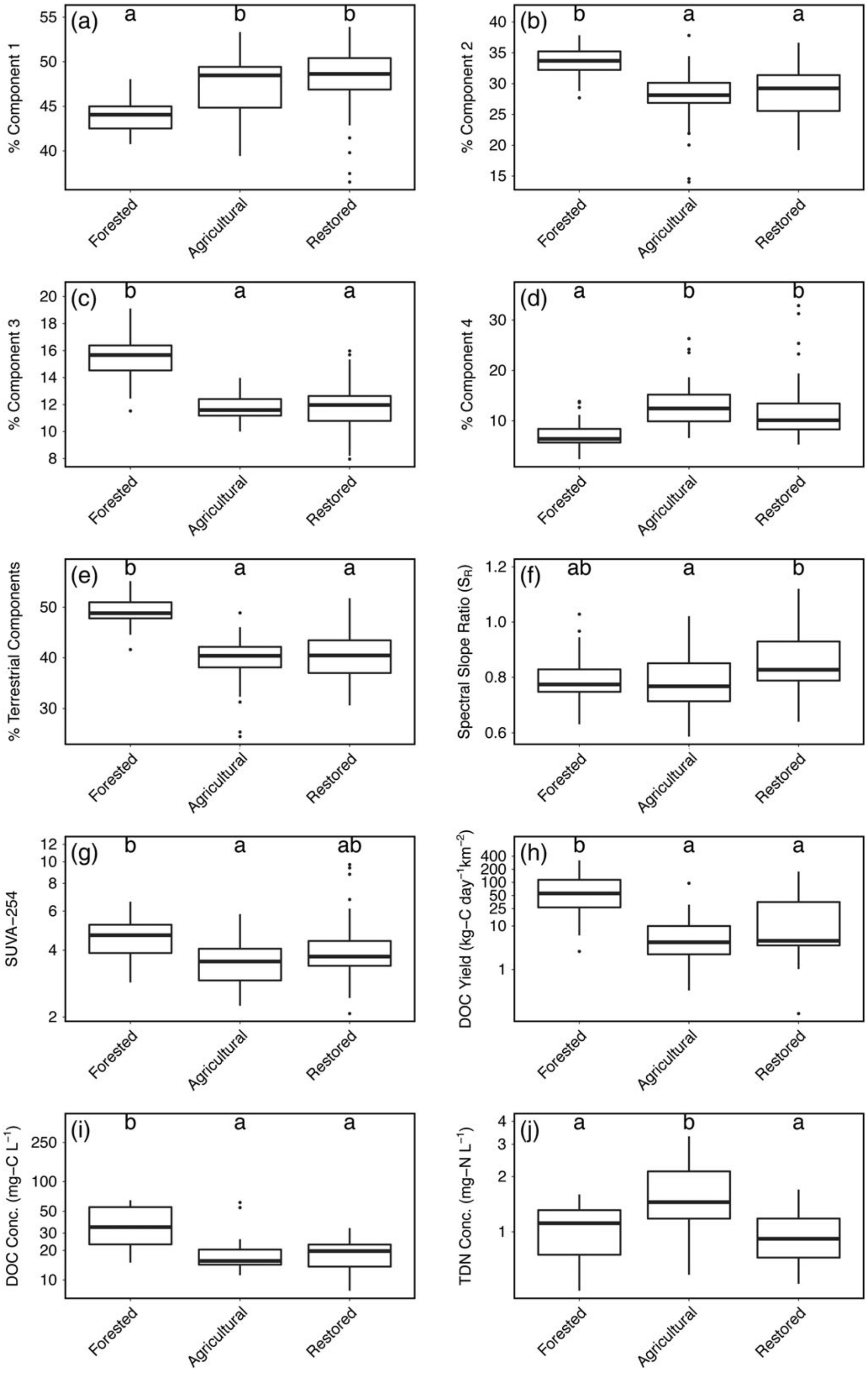

FIGURE 4 Boxplots of dissolved organic matter (DOM) composition across the three classes of Delmarva wetlands studied. Metrics reported were (a) C1 per cent fluorescence, (b) C2 per cent fluorescence, (c) C3 per cent fluorescence, (d) C4 per cent fluorescence, (e) % terrestrial (humic like) components (C2 and C3), (f) S_R, (g) $SUVA_{254}$, (h) dissolved organic carbon (DOC) concentration, (i) DOC yield, and (j) total dissolved nitrogen (TDN) concentration

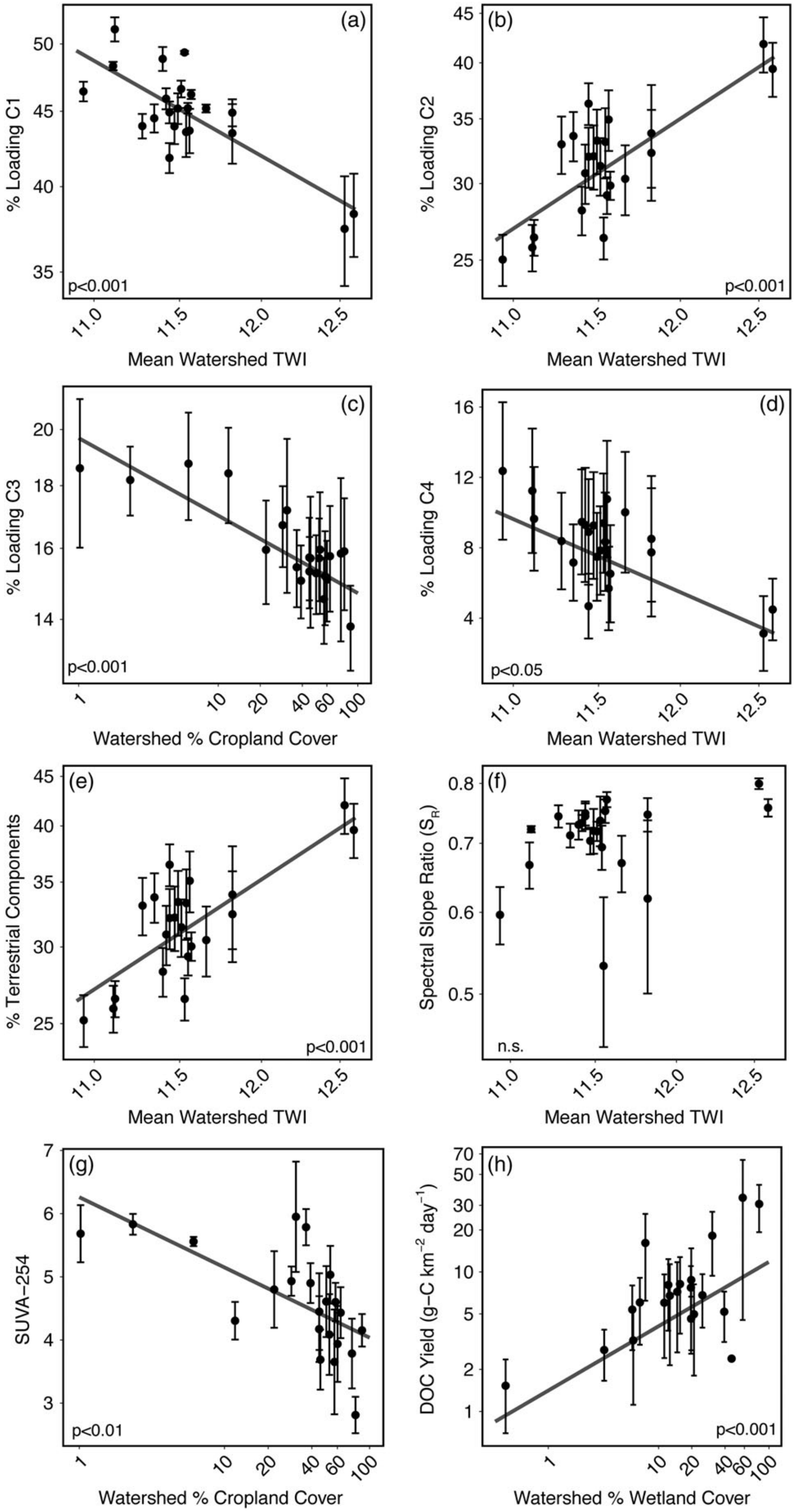

FIGURE 5 Relationships between landscape metrics and (a) C1 per cent fluorescence, (b) C2 per cent fluorescence, (c) C3 per cent fluorescence, (d) C4 per cent fluorescence, (e) per cent fluorescence of terrestrial (humic like) components (C2 and C3), (f) spectral slope ratio (S_R), (g) $SUVA_{254}$, and (h) dissolved organic carbon yield. TWI = topographic wetland index

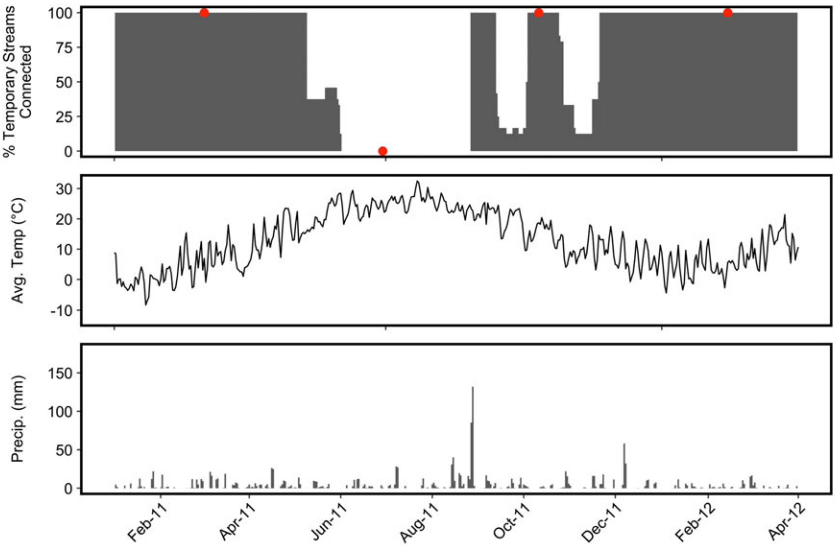

FIGURE 6 A plot of the per cent of temporary streams that were flowing and connecting forested Delmarva wetlands to perennial streams ($n = 30$) during this study based on a binomial autoregressive generalized linear model validated with surface water presence loggers and site visits. Points indicate dates on which perennial streams were sampled. Average daily temperature and precipitation in Tuckahoe, MD, are reported (Western Regional Climate Center)

C1 ($p < .001$) and C4 ($p < .01$) was significantly higher in DOM from both agricultural and restored wetlands than forested wetlands (Figure 4a,d). By contrast, Components C2 and C3 were significantly higher in forested wetland DOM than either agricultural or restored ($p < .001$; Table S2 and Figure 4b,c). S_R was the only variable that was significantly different between agricultural and restored Delmarva Bay classes ($p < .05$; Figure 4f); values were the lowest in agricultural wetlands and the greatest in restored wetlands. $SUVA_{254}$ was higher for DOM from forested wetlands than from other systems (Figure 4g).

The highest DOC watershed yields (Figure 4h) and concentrations (Figure 4i) were found for forested wetlands. TDN was higher in agricultural wetlands than either forested or restored wetlands (Figure 4j).

3.2 | Question 2: Perennial stream DOM

3.2.1 | Relationship to landscape attributes

For all variables except S_R, a significant correlation was found with watershed attributes (Figure 5 and Table S3). Mean watershed TWI was negatively correlated to Components C1 ($p < .001$; Figure 5a) and C4 ($p < .001$; Figure 5d) and positively correlated to DOM Component C2 ($p < .001$; Figure 5b). Per cent cropland cover was negatively related to the relative amount of Component C3 ($p < .001$; Figure 5c) and values for $SUVA_{254}$ in perennial streams ($p < .01$; Figure 5g). DOC yield was positively related to log-transformed per cent wetland cover ($p < .001$; Figure 5h).

3.2.2 | Relationship to connectivity

We found that connectivity between forested wetlands and perennial streams via temporary channels was high for three out of the four dates on which perennial streams were sampled. Our analysis indicated that 100% of the temporary streams studied were connected on March 2, 2011, October 11, 2011, and February 14, 2012 (Figure 6). By contrast, during the June 2011 sampling date, all temporary streams were dry (Figure 6). All DOM metrics were significantly related to sampling date (Figure 7). Watershed DOC yield was significantly higher on winter and autumn sampling dates, when forested wetlands were connected to perennial stream networks; DOC yields were far lower in June 2011—when Delmarva Bays were disconnected—than for other dates ($p < .001$; Figure 7h). The two PARAFAC components linked to wetland DOM—C2 and C3—were both significantly lower in June 2011 than all other sample dates (Figure 7b,c). By contrast, protein-like fluorescence (Component C4) was significantly greater in June 2011 than on other dates (Figure 7 d). Values for autochthonous Component C1 were significantly lower in February 2012 than on other dates but were otherwise relatively consistent (Figure 7a). Photodegradation metric S_R was the lowest in June 2011, but differences with subsequent sampling events in October 2011 and February 2012 were not significant (Figure 7f).

3.2.3 | Seasonal relationship between perennial stream and wetland DOM

Plotting DOM composition using the linear discriminant function developed with wetland data from Question 1 (Figure 3a) showed that 75% of perennial stream DOM samples collected during the summer (June 2011) fell within the 95% confidence ellipse for DOM found in agricultural wetlands (Figure 3b). Perennial stream DOM samples collected during the fall, shortly after forested temporary stream flow resumed, were less protein-like and more humic-like beginning to resemble forested wetland DOM more than agricultural DOM—70% of fall perennial stream samples fell within the 95% confidence ellipse for forested DOM. For both winter samplings, when forested wetlands were the deepest and forested temporary stream discharge was the highest, DOM composition in perennial streams was the most similar to material found in forested Delmarva wetlands. Only 62% of perennial stream samples fell within the 95% confidence ellipse for forested DOM. This percentage was low only because DOM composition for many winter perennial stream samples was even more enriched in Components C2 and C3 than typical forested wetland DOM.

3.3 | Question 3: Bioavailability

DOM bioavailability—defined as per cent DOC lost to microbial activity over a 28-day bioassay—was significantly related to DOM composition. Protein-like DOM, the most abundant in agricultural wetlands and perennial streams draining agriculturally dominated watersheds, was positively related to per cent bioavailable DOC ($p < .05$; Figure 8a).

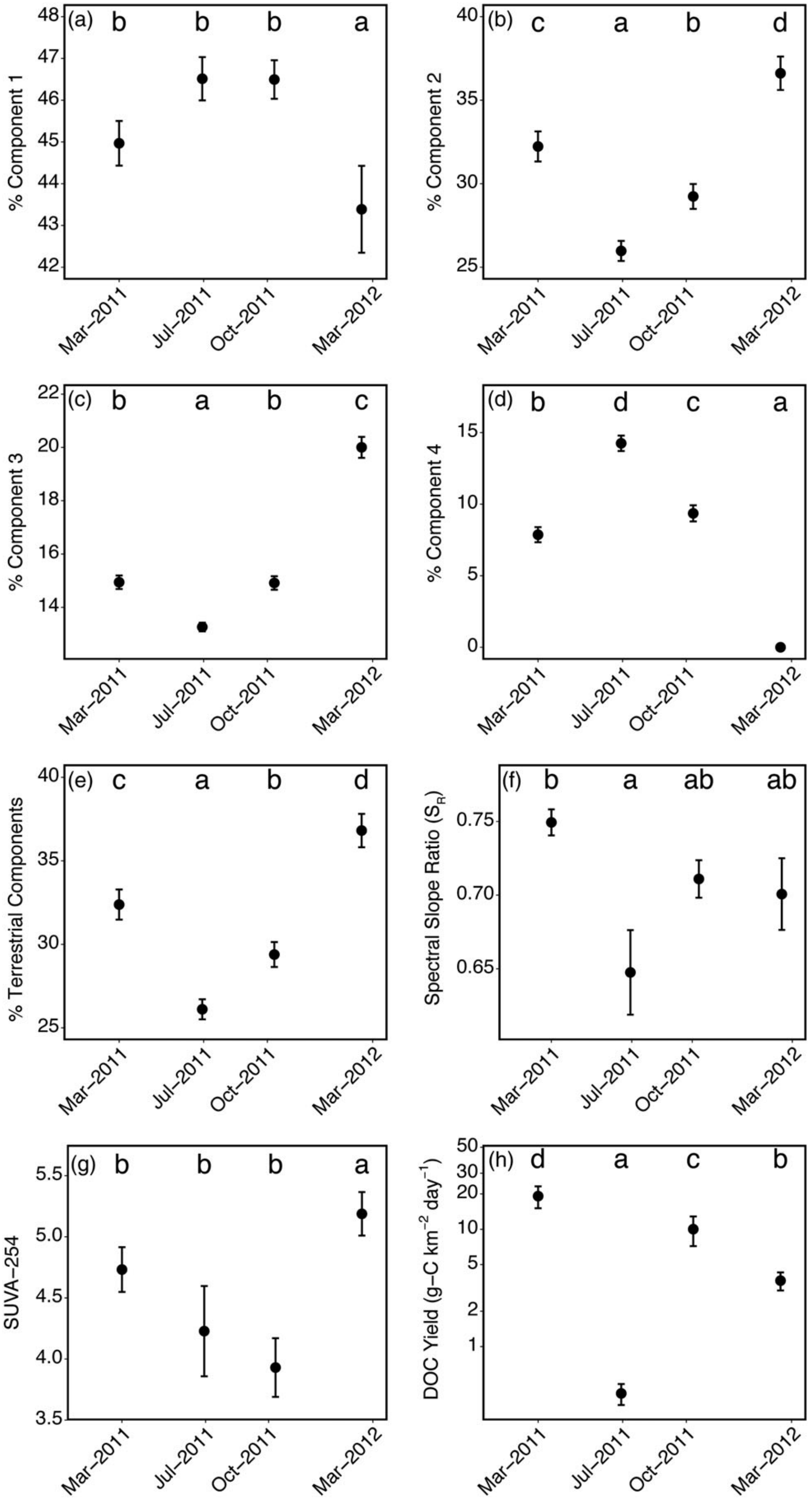

FIGURE 7 Perennial stream water chemistry over time for PARAFAC components (a) C1, (b) C2, (c) C3, (d) C4, (e) per cent terrestrial parallel factor analysis components, (f) S_R, (g) SUVA-254, and (h) dissolved organic carbon (DOC) yield. All metrics differed significantly between sampling dates. Letters indicate results of Tukey's honestly significant difference post hoc multiple mean comparisons. Full statistics are presented in Table S4

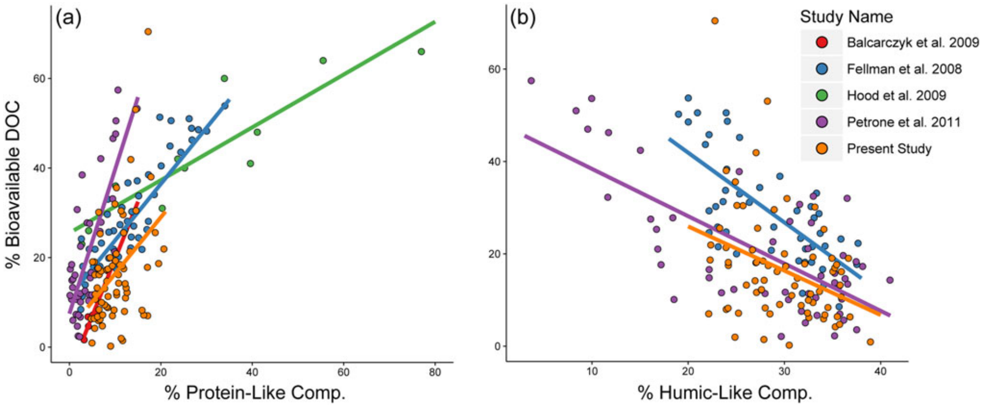

FIGURE 8 The relationship between dissolved organic matter (DOM) quality and per cent bioavailable dissolved organic carbon (DOC), as measured by bioassays. Per cent bioavailable DOC was compared with (a) per cent of protein-like parallel factor analysis (PARAFAC) components and (b) per cent of humic-like PARAFAC components. For this study, PARAFAC Component C4 represented protein-like DOM and Component C2 represented terrestrial, humic-like DOM

Humic-like DOM Component C2, which was the most common in forested wetlands and perennial streams with high levels of wetland land cover, was negatively correlated to DOC bioavailability ($p < .05$; Figure 8b).

4 | DISCUSSION

Wetlands are critical components of many landscapes providing benefits as diverse as coastal protection, water quality improvement, carbon sequestration, and support of biodiversity (Bobbink, Beltman, Verhoeven, & Whigham, 2007; Fisher & Acreman, 2004; Mitsch et al., 2013). Degradation and loss of wetlands primarily due to agricultural and urban activities have been a major concern for decades (Davidson, 2014), but less attention has been placed on changes in the spatiotemporal dynamics of wetlands (Bishop-Taylor, Tulbure Mirela, & Broich, 2017). Alterations to wetlands such as ditching and modifying the surrounding landscape matrix can result in fundamental changes in the hydrological connectivity among wetlands and with perennial waters (Boland-Brien et al., 2014) that influence ecological processes broadly. We provide empirical evidence that wetlands varying in surface hydrological connectivity to downstream waters can impact the amount and composition of DOM moving into stream networks. Total wetland cover in a watershed is known to influence the flux of DOM to downstream waters (Creed et al., 2003; Williams, Yamashita, Wilson, Jaffé, & Xenopoulos, 2010), but our work suggests that the pattern of surface hydrological connections may also influence fluxes. Further, it suggests that although upland wetlands often appear hydrologically isolated, they may play critical roles in carbon processes in streams and rivers much like many well-studied riparian wetlands and floodplains that also vary in connectivity to perennial streams (Cole et al., 2007). This is important given the abundance of upland wetlands worldwide (Cohen et al., 2016) and their high risk of loss or modification (Golden et al., 2017). It is also important given heated debates over the need for protection of wetlands designated as geographically isolated (Alexander, 2015; Creed et al., 2017).

Yields of DOC from the wetland-dominated watersheds in this study were significantly higher during winter and autumn sampling dates, when wetlands were connected to perennial stream networks (Figure 7h); and, composition of perennial stream DOM was the most similar to that characterizing the forested wetlands (Figure 7a–f), that is, dominated by aged, aromatic-rich compounds. Because these forested wetlands have water in the temporary channels that connect to the perennial network significantly more days per year than restored or agricultural wetlands (McDonough et al., 2015), this implies that forested wetlands contribute more DOM that is more aromatic to downstream waters than wetlands with altered land use or cover. Abundant research has shown that the amount and composition of DOM moving to streams influence microbial processes and aquatic food webs (Bernhardt & Likens, 2002; Fasching, Behounek, Singer, & Battin, 2014; Halbedel, Buettner, & Weitere, 2013; O'Brien et al., 2017), and the bioavailability assays in this study (Figure 8a,b) suggest GIW status (altered, restored, and natural) and connectivity contribute to this. During midsummer when wetlands were not connected to streams, the perennial stream DOM composition reflected other land uses in the watershed and was more similar to DOM found in agricultural wetlands at our sites. In addition to the relevance for stream ecosystems, understanding when and how isolated wetlands varying in levels of hydrological connectivity influence carbon dynamics may shed light on factors that influence long-term carbon storage in wetland soils; this could have major implications for climate change mitigation (Yu et al., 2017). Scholars have emphasized that one of the greatest uncertainties in regional and global C model estimates is associated with wetlands (e.g., Buffam et al., 2011).

4.1.1 | Wetland status and surrounding land cover influence wetland DOM

We show that not only do the restored and agricultural study wetlands differ significantly in hydrological connectivity from natural (forested) wetlands but also they differ significantly in terms of DOM quantity and composition. DOC concentration, PARAFAC components, SUVA_{254}, and S_R values indicated that forested wetlands have more DOM that is consistent with aged, aromatic DOM of terrestrial origin than either agricultural or restored wetlands (Figure 4). This is consistent with previous observations of increased DOM humic content and structural complexity in natural wetlands (Inamdar et al., 2012). Wetland cover has also been positively correlated with fluvial DOC quantity (Mulholland, 2003), whereas croplands tend to be associated with low stream DOC concentration and yields (Wilson & Xenopoulos, 2009). Here, agricultural wetlands maintain the depressional morphology of forested wetlands, but due to drainage, water residence time is very low, and thus, agricultural wetlands do not have time to develop reducing redox conditions (McDonough et al., 2015). This suggests that land use decisions including the loss or ditching of wetlands dating back to European settlement may have dramatically reduced the amount and altered the type of DOM reaching perennial waters.

Consistent with research showing slow restoration trajectories in agricultural areas (Moreno-Mateos, Meli, Vara-Rodríguez, & Aronson, 2015), we found little evidence that DOM in restored wetlands had returned to reference conditions and, in fact, restored DOM could not be distinguished from DOM in agricultural wetlands. Both LDA (Figure 3a) and univariate tests (Figure 4) confirmed that that forested wetland DOM was distinct from that in both agricultural and restored wetlands. Cultivation practices drive losses of soil organic matter (SOM; McLauchlan, 2006), and excavation during restoration may further decrease the amount of SOM in restored Delmarva wetlands (Fenstermacher, 2011). Other researchers have shown that restoration of natural SOM is slow, often requiring decades to centuries (Hossler & Bouchard, 2010) potentially explaining the relatively low DOC concentrations we found in restored wetlands, which were only 8–9 years postrestoration at the time of this study. This may be related to the lack of vegetative inputs to soils because the restored wetlands are surrounded by grasses and small, immature trees in contrast to forested wetlands (Yepsen et al., 2014). Additionally, higher light levels in restored wetlands, which lacked canopy cover, may have contributed to increased S_R values—an indicator of DOM photodegradation (Helms et al., 2008; Figure 4f). Forested wetland sites are protected from sunlight by the canopy and the high optical density of forested wetland DOM itself (Wetzel, 2001). Agricultural wetland sites also have high light exposure, however, very low water residence times in agricultural compared with forested or restored wetlands (McDonough et al., 2015) limit exposure time necessary to achieve photodegradation comparable with restored sites.

Overall, our work supports a growing consensus that restoration efforts may not compensate functionally for loss or alteration of natural wetlands (Moreno-Mateos et al., 2015; Yu et al., 2017); although see (Bortolotti et al., 2016). Legacies of past land use (e.g., agriculture) as well as existing broader watershed land use may limit full recovery for long periods of time or even indefinitely (Ducey et al., 2015).

4.1.2 | Relative importance of ground versus surface water flows unknown

Although the focus of this study was on surface hydrological connectivity, results suggest that subsurface hydrological connections via groundwater likely influence perennial stream biogeochemistry at our sites. Watershed TWI was a consistent predictor of DOM quality across watersheds, even in the summer when temporary stream connections are dry but some wetlands remain inundated (Figure 6). The fact that wetland DOM was similar to perennial stream DOM composition even when surface connections were dry also suggests subsurface flow path connectivity. Although this is supported by other research from the study region (Phillips & Shedlock, 1993; Epting et al., 2018), understanding the relative contributions of ground versus surface water requires much more work including the use of isotopic signal studies as in Brooks et al. (2018).

Even with significant groundwater connectivity, surface water contributions from our study wetlands to streams was evident—terrestrial DOM levels were always the highest in perennial streams draining wetland-dominated catchments; however, levels were even higher during spring and summer when wetlands were connected to perennial channels and DOM composition also changed. Our results suggest that export of DOM to the study streams is related to total wetland watershed land cover in a catchment, reflecting the year-round influence of subsurface connectivity, but wetland surface may drive the timing and variability of peak carbon fluxes through streams. Verification of this will require sampling for much longer times than the short duration of this study. Such patterns will certainly be site specific and likely to vary significantly regionally as a function of hydrogeology and topography (Neff & Rosenberry, 2018).

The finding that upland wetlands contribute to downstream water quality via surface and potentially subsurface connections clarifies the biogeochemical connectivity of GIWs. Existing research on the importance of wetland connectivity has been seemingly contradictory. Some studies have reported that overall wetland coverage in a watershed, not connectivity or spatial arrangement of wetlands, drives downstream chemistry (Creed et al., 2003; Gergel et al., 1999; Richardson et al., 2010). Others report that GIWs are only important when surface water connectivity is high (Köhler, Buffam, Laudon, & Bishop, 2008; Laudon et al., 2011). Our findings indicate that surface and subsurface connections from GIWs influence stream DOM in different ways—groundwater flowpaths provide a consistent supply or DOM from upland wetlands to stream networks, but seasonal pulses of organic matter require surface connectivity (e.g., temporary streams). This framework unifies seemingly contradictory results (Laudon et al., 2011) in a way that can be used to improve understanding of when and where DOM is exported from watersheds.

4.1.3 | Ecological significance of surface connectivity and wetland DOM

Our findings that DOM bioavailability was higher when protein-like fluorescence is high (agricultural wetlands, Figure 8a) and lower for the humic-like fluorescent components (forested wetlands, Figure 8 b) are consistent with results from a variety of aquatic ecosystems: soil water (Fellman et al., 2008), streams draining permafrost (Balcarczyk, Jones, Jaffé, & Maie, 2009), glaciated rivers (Hood et al., 2009), and streams in agricultural and urbanized watersheds (Petrone, Fellman, Hood, Donn, & Grierson, 2011; Figure 8). Greater stream DOM bioavailability due to more agriculture in a wetland watershed could lead to shorter DOM uptake lengths along fluvial networks and increased rates of microbial respiration, with concomitant changes in the fluxes of dissolved or emitted CO_2 or CH_4 (Kayranli, Scholz, Mustafa, & Hedmark, 2010). Loss of DOM with high optical density can amplify the downstream delivery of labile DOM by stimulating autochthonous photosynthesis as more sunlight reaches stream benthic environments. This can cause environmental problems in larger water bodies because labile DOM from anthropogenic sources has been linked to increased estuarine eutrophication (Seitzinger, Sanders, & Styles, 2002).

Finding that perennial stream DOM composition shifted towards DOM of lower microbial bioavailability on sampling dates when temporary streams were most likely connected to forested wetlands (Figure 7) indicated that seasonal temporary stream flows of water from Delmarva wetlands have a significant impact not only on the composition and quantity of DOM but also on microbial function in downstream perennial networks. This finding is broadly relevant for understanding the biogeochemical and ecological role upland wetlands play in watersheds but has particular relevance in the United States where wetland protected status is often contingent upon a significant nexus existing with downstream navigable waters. This means that a water body must have a significant impact on the "chemical, physical, or biological integrity of traditional navigable waters or interstate waters" (McLaughlin et al., 2014; U.S. Environmental Protection Agency and Army Corps of Engineers, 2008) in order to be considered for protection. We argue that delivery of aromatic DOM from upland wetlands represents such a "significant nexus" that is relevant to perennial stream water quality and ecosystem function.

Results from this study also underscore that conversion of forested wetlands to land in crops alters perennial stream DOM quantity and quality, and wetland hydrological restoration does not reverse this, at least not within 8–9 years. This alteration in DOM may have an impact on downstream food web dynamics (Hall & Meyer, 1998), nutrient cycling (Bernhardt & Likens, 2002) and potentially emission of greenhouse gases (Kayranli et al., 2010). Beyond altering the bioavailability of DOM in downstream waters, the ecosystem-level influences of seasonal pulses of water from forested Delmarva wetlands connected to stream networks are largely unknown. The regular seasonality of DOM quantity and composition in Delmarva wetlands likely broadly changes the base of stream food webs and decreases light availability, decreasing aquatic photosynthesis and making food webs more dependent on terrestrial sources of organic matter (Hensley & Cohen, 2017; Sabo et al., 2018). Ultimately, such pulses of DOM from headwaters have far reaching implications for river networks in particular and the carbon cycle in general (Raymond, Saiers, & Sobczak, 2016).

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SUPPORTING INFORMATION

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