



# Patterns of vegetation and soil properties in a beaver-created wetland located on the Coastal Plain of Virginia

Suzanne Dee<sup>1</sup> · Alicia Korol<sup>1</sup> · Changwoo Ahn<sup>1</sup> · Jung A. Lee<sup>1,2</sup> · Mary Means<sup>1</sup>

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## Abstract

This study investigated vegetation and soil properties in a beaver-created freshwater wetland located on the Coastal Plain of Virginia near Washington, DC. We focused on the associations among floristic quality, soil physicochemistry, denitrification, and hydrologic conditions of the wetland to understand links between the effects of beaver engineering and ecosystem function. The floristic quality assessment index (FQI) and denitrification are two important indicators often used to examine overall habitat quality and ecosystem functioning of a wetland. Samples were collected from ten plots (10 m × 10 m each) in August 2014. Vegetation attributes included total percent cover, species richness (*S*), diversity, FQI, and prevalence index (PI). Soil attributes included organic matter (OM), total carbon, total nitrogen, gravimetric moisture (GM), pH, bulk density ( $D_b$ ), and denitrification potential (DP). FQI was greater in the higher of the two standing water level categories, where  $D_b$  was lower, and was negatively associated with  $D_b$  but no other soil nutrient properties. DP was positively associated with soil nutrients, OM, and GM, but not with measured vegetation attributes nor standing water levels. We found higher soil GM, lower plant community PI, and lower plot *S* in this study compared to our previous study, with no changes to other vegetation or soil attributes, indicating enduring beaver activity and a resilient plant community. The outcome of the study includes regression models that best explain the association between structural and functional attributes of the ecosystem, which can be applicable to the study of other beaver-created wetlands. The study also provides partial evidence for the notion that low-lying areas dug out by beaver positively impact the FQI of wetlands.

**Keywords** Denitrification potential · Floristic quality · Plant diversity · Regression model · Wetland soil

## Introduction

The ecosystem engineering activity of beaver (*Castor Canadensis* Kuhl) has been well documented with studies conducted on hydrology, biogeochemistry, and plant and animal species composition (Naiman et al. 1986; Burns and McDonnell 1998; Meentemeyer and Butler 1999; Wright et al. 2002). Vegetation composition and diversity (Shannon-Weiner diversity index; *H'*) can be altered due to beaver foraging, while water level varies both in response to dam creation and subsequent natural deconstruction after

beaver abandonment (Mitchell and Niering 1993; Vandervalk et al. 1994; Sturtevant 1998; Rejmankova et al. 1999; Ray et al. 2001; Hudon 2004; Wright et al. 2004). A mixture of heterogeneous successional habitats can co-exist across beaver-engineered landscapes on a spectrum from low *H'* ponds to higher *H'* wet meadow or forested ecosystems of different ages and developmental states (Vandervalk et al. 1994; Wright et al. 2003; Hudon 2004).

The health and developmental state of beaver-created wetlands can be assessed using information on the floristic attributes of the vegetation community (Swink and Wilhelm 1994; Lopez and Fennessy 2002). Communities with more numerous and locally specialized species reflect greater habitat stability and heterogeneity, which are important characteristics for small, fragmented ecosystems. The Floristic quality assessment index (FQI) measures floristic quality in terms of species nativeness by incorporating both biodiversity and “species conservatism” of a site (Swink and Wilhelm 1994). To derive the

✉ Changwoo Ahn  
cahn@gmu.edu

<sup>1</sup> Department of Environmental Science and Policy, George Mason University, 4400 University Drive, Fairfax, VA 22030, USA

<sup>2</sup> Present Address: Department of Forestry and Landscape Architecture, Konkuk University, Seoul, South Korea

latter, a species is assigned a coefficient of conservatism ( $C_n$ ) that reflects its tolerance to disturbance and fidelity to specific habitat integrity (Swink and Wilhelm 1994). As the FQI has been found to be a useful indicator of wetland integrity when tracking wetland restoration project progress over time, it should also be useful for the study of ecosystem responses to large hydrological fluctuations associated with beaver activity. Study of FQI in conjunction with wetland biogeochemistry has been limited. Lopez and Fennessy (2002) found that FQI was positively associated with soil organic carbon (C), phosphorous, and calcium in depressional wetlands in Ohio.

Wetlands are recognized for their high rates of denitrification, a vital microbial function that reduces modern nitrogen (N) surplus from the environment and prevents the eutrophication of downstream ecosystems (Vitousek et al. 1997; Saunders and Kalff 2001).

Wetlands provide favorable conditions for denitrification by providing extensive anoxic conditions and abundant organic nutrients associated with water-logged soils (Groffman 1994; Hunter and Faulkner 2001; Hill and Cardaci 2004; Mitsch and Gosselink 2007). Both soil bulk density ( $D_b$ ) and organic matter (OM) content can be significant predictors of denitrification function (Wolf et al. 2011; Dee and Ahn 2012, 2014) that reflect long-term saturation levels and the physical suitability of soil for N cycling. These physical properties of a wetland develop slowly over time with localized influences of the plant community. The necessary physicochemical conditions for microbial N transformations (e.g., labile C, oxygen, and dissolved N) are proximately controlled by the types and behavior of plants which facilitate greater ecosystem complexity and nutrient functioning (Booth et al. 2005; Wallenstein et al. 2006; Ballantine et al. 2012). Ecological theory indicates a causal, positive relationship between plants and denitrification whereby diverse plant communities maximize community productivity, and in turn, augment stores of decomposed organic material and nutrients, but empirical studies suggest the observed relationships are driven by multiple mechanisms (Olde Venterink et al. 2003; Bouchard et al. 2007; Dee and Ahn 2012; Schultz et al. 2012).

Denitrification can be approximated through measurements such as denitrification enzyme activity (DEA), which has been used as an index of denitrification potential (DP) rate in numerous studies (Groffman 1994; Jordan et al. 2007; Hopfensperger et al. 2009). DEA represents the relative activity of denitrifying enzymes in situ (i.e., enzymes active at the time of sampling), which is a sensitive measure of environmental factors (e.g., oxygen content and C availability) that exert immediate and prolonged control over denitrification (Tiedje et al. 1989). In anaerobic environments without C limitations, the amount of enzyme produced is proportional to the concentration of nitrate ( $\text{NO}_3^-$ ) available,

and the rate of denitrification is proportional to the enzyme content (Tiedje et al. 1989).

The goals of the study were to assess patterns and relationships in attributes of the plant community [e.g., species richness ( $S$ ),  $H'$ , cover], soil physicochemical properties (e.g., soil C, N, OM), and soil processes (i.e., denitrification) in a beaver-created wetland located on the Coastal Plain geologic province of Virginia, USA. We focused on floristic quality and DP as two proxies of vegetation quality and nutrient removal ability of wetlands. Specific objectives for this study included:

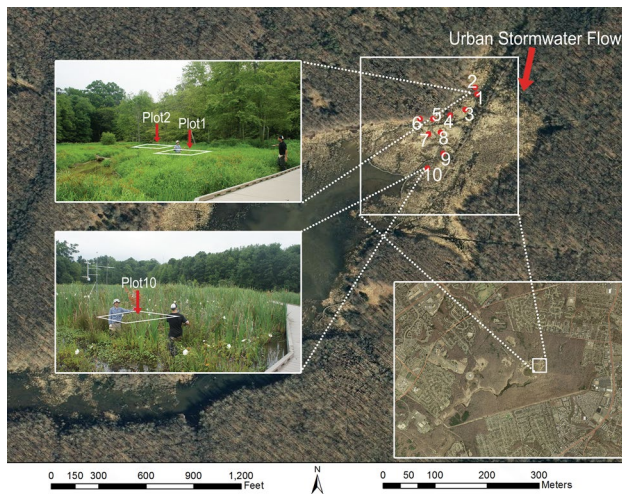
1. Conducting a survey of wetland attributes to describe plant  $H'$ , floristic quality, soil physicochemistry, and DP;
2. Evaluating the effect of standing water depth on plant and soil measurements;
3. Investigating associations between all structural and functional attributes and constructing linear regression models for two functional attributes of wetlands, floristic quality and denitrification, to assess ecosystem functions for management purposes.

## Materials and methods

### Site description

Huntley Meadows Park is a 576-ha park surrounded by significant suburban development, located near Alexandria in Fairfax County, Virginia ( $38^\circ 45' 10''\text{N}$ ,  $77^\circ 06' 25''\text{N}$ ). The park lies close to the eastern margin of the Coastal Plain geologic province, distinguished by soils of primarily marine origin, but the wetland area of study contains alluvial, metamorphic soils originating from western geologic provinces (Soil Survey Staff 2016). Thus, the studied wetland shares soil characteristics with other wetlands of the eastern Piedmont geologic province also in Northern Virginia.

Huntley Meadows Park has undergone dramatic changes in recent history. Trends observed in the wetland area of the park from 1959 to 1993 indicate that wetness of the park increased over this period with concomitant changes in the distribution and composition of the plant community (TAMS Consultants 1993). The central 16-ha Huntley Meadows wetland, where sampling was conducted, was a moist-soil area directly affected by beaver activity and was composed predominantly of herbaceous and woody shrub wetland species, accessible to visitors via boardwalk and trails (Fig. 1). Huntley Meadows supports a wide variety of wetland, pond, and forest habitat, which in turn sustain a wide array of wildlife. The central wetland of Huntley Meadows was formed when beavers dammed a second-order stream, Barnyard Run, which drastically increased the volume of water within the wetland and raised the



**Fig. 1** Landscape-level context for Huntley Meadows in terms of development intensity and storm water flow (*right insets*). Beaver-created marsh area and sampling plot locations (*main image*) with images of plots 1, 2 and 10 (*left insets*)

water table in the nearby forest (TAMS Consultants 1993; Fairfax County Park Authority 2017). By 2005, beavers had exhausted the food supply in the central impoundment area and subsequently moved out of the area for some time, yet returned and established new small dams in different areas within the wetland between 2005 and 2014 (Changwoo Ahn, personal observation). With greater hydrologic connectivity, silt and debris naturally fill in the central wetland, resulting in impacts on soil composition, water depths, and the value of wetland wildlife habitat (Fairfax County Park Authority 2017).

## Fieldwork

### Study area and hydrologic regime of study plots

We made field measurements and soil collections in Huntley Meadows Park on 5 August 2014. We delineated ten study plots ( $10 \times 10$  m each) adjacent to the viewing boardwalk to be representative of central wetland hydrology, and subdivided each into quadrants to collect four random samples for all attributes of vegetation, soil, and water level (Fig. 1). Plot spacing ( $>$  minimum 7 m) should preclude spatial dependence for the measured soil and vegetation attributes. The hydrologic regime of each plot was categorized into one of these groups: (1) standing water  $< 2.5$  cm deep, including no standing water; and (2) standing water  $\geq 2.5$  cm deep. Whereas soils were completely covered by water in category 2 plots, soils in category 1 plots with standing water were not necessarily covered due to surface microtopography.

## Vegetation community survey

We conducted vegetation surveys for species identity and percent cover using a  $1\text{-m}^2$  quadrat embedded with a 100-cell string grid (i.e.,  $10 \times 10$ -cm cells). Vegetation was identified to the species level and percent cover was estimated using ten-level cover classes (Peet et al. 1998). To increase efficiency and accuracy in our measurements, we created a species identification guide in advance using authoritative online sources (Tenaglia 2007; National Resources Conservation Service, US Department of Agriculture 2014) and published field guides (Newcomb 1977; Strausbaugh and Core 1977).

## Soil sampling

We collected the top 10 cm of soil using both metal soil samplers and disposable syringes for a suction-based retrieval. Because we were interested in plant–soil relationships, sampling to 10 cm provided strong measures of organic-related soil properties that had the greatest potential to reflect influences of the current plant community. Three soil cores were taken at quadrant locations matched to vegetation sub-plots and allotted for lab measurement of soil gravitational moisture (GM), pH, total C (TC) and total N (TN), and OM. For DP, we further collected a composite sample of three soil cores for each quadrant; a composite sample for denitrification was chosen due to its high spatial heterogeneity. Soil for  $D_b$  was collected in 195-mL metal containers (7.2-cm diameter  $\times$  4.8-cm depth).

## Lab analyses for soil physicochemistry and DP

Soils for physicochemistry measurements were laid to air dry in ambient laboratory conditions prior to measurement. For GM, soils were homogenized, massed wet, and dried at  $105^\circ\text{C}$  for 48 h, then massed dry and sub-sampled for further testing. Soil pH was measured with a Hach pH electrode in the laboratory with  $\sim 10$  g of dry soil in a 1:1 soil to water solution. OM was measured by loss-on-ignition where soils dried to  $105^\circ\text{C}$  were combusted in a furnace at  $500^\circ\text{C}$  for 1 h (Nelson and Sommers 1996). Soil TC and TN (i.e., inorganic and organic) were measured by combustion in a Perkin Elmer 2400 Series II Element Analyzer (Nelson and Sommers 1996).

Soil denitrification was measured using the DEA assay (Smith and Tiedje 1979; Tiedje et al. 1989; Groffman 1999) as DP 3 days after sampling. Field-moist soil ( $\sim 25$  g wet weight) was weighed into 125-mL flasks and mixed to form slurries with 25-mL solutions of dextrose ( $1\text{ g L}^{-1}$ ), potassium nitrate ( $1.01\text{ g L}^{-1}$ ), and chloramphenicol ( $0.1\text{ g L}^{-1}$ ) in deionized water. The headspace was flushed with nitrogen gas ( $\text{N}_2$ ) to ensure an anoxic environment in each flask.

Acid-scrubbed acetylene (10 mL) was then injected into the flask headspace to inhibit the reduction of nitrous oxide ( $\text{N}_2\text{O}$ ) to  $\text{N}_2$  at time 0. Flasks were incubated in a reciprocal shaker and 2-ml gas samples withdrawn at 45 and 105 min.  $\text{N}_2\text{O}$  concentrations were measured by gas chromatography on a Shimadzu GC-8A equipped with a Supelco Haysep Q 80/100 packed column (1 m  $\times$  1/8 in  $\times$  2.1 mm) and an electron-capture detector.

## Data analysis

We calculated values not directly measured for several plant community and soil attributes: total cover,  $S$ ,  $H'$ , prevalence index (PI), FQI, OM, GM,  $D_b$ , and DP (see Dee and Ahn 2012).

Total cover was the sum total of species cover for a sample, allowing for overlap, as measured by the mid-point of cover classes [trace (1), 0–1% (2), 1–2% (3), 2–5% (4), 5–10% (5), 10–25% (6), 25–50% (7), 50–75% (8), 75–95% (9), > 95% (10)].  $H'$  is a function of  $S$  and evenness with the highest  $H'$  values obtained under conditions where there are several species with even distributions (i.e.,  $H'_{\max} = \log S$ ):  $H' = -\sum p_i \log p_i$ , where  $p_i$  is the sample proportional percent cover of species FQI (Andreas et al. 2004).

Floristic quality index (FQI) is a measure of natural character calculated as a function of the  $C_n$  for each species and the total number of native species present in a given sample or set of samples (Swink and Wilhelm 1979, 1994).  $C_n$  values range from 0 to 10 with 0 associated with non-native species adapted to disturbed conditions, and 10 to the most sensitive native species (Swink and Wilhelm 1979, 1994).  $C_n$  values assigned by a regional panel of experts in a 2006 study sponsored by the Virginia Department of Environmental Quality were used to calculate FQI:  $\text{FQI} = \sum C_n / (N)^{1/2}$ , where  $N$  is the total number of native species (Davis and Harold 2006; US Environmental Protection Agency 2002). FQI and  $S$  were calculated at the scale of the subplot, plot, and wetland level per standard practice.

PI is a function of species wetland indicator status (WIS) and proportional percent cover (Cronk and Fennessy 2001). WIS values range from 1 to 5 [obligate (1), facultative wet+ (1.5), facultative wet (2), facultative wet– (2.5), facultative (3), facultative upland (4), upland (5)] with 1 being assigned to taxa found greater than 99% of the time in wetlands and 5 assigned to taxa found less than 1% of the time in wetlands (Cronk and Fennessy 2001). PI values less than three are reflective of an overall wetland status of Facultative to Obligate (i.e., majority of species are found in wetlands). PI was calculated using the equation:  $\text{PI} = \sum A_i W_i$ , where  $A_i$  is the proportional percent cover of species  $i$  and  $W_i$  is the WIS of species  $i$  (Cronk and Fennessy 2001).

GM was calculated as the difference between wet and dry mass as a percentage of the dry mass, while  $D_b$  was

measured as dry mass per collection volume, and OM was the percentage of mass loss after ignition. Rates of DP were expressed per mass of dry soil as  $\mu\text{g N-N}_2\text{O kg}^{-1} \text{ h}^{-1}$  adjusting for soil moisture and  $D_b$ .

We screened the data for appropriate use in statistical testing. Visual assessments of normal probability and residual plots were used to determine uni- and multivariate normality and linearity (Mertler and Vannatta 2010). We compared mean differences in vegetation and soil variables by water level category using either the parametric independent  $t$ -test or the nonparametric Mann–Whitney–Wilcoxon test (Mertler and Vannatta 2010). To investigate which multiple vegetation and physicochemical gradients contributed most to the patterns observed in FQI and DP variability across the wetland, linear models were constructed for FQI and DP predictions using least squares linear regression with all subsets selection. Model selection criteria included the coefficient of determination (adjusted  $R^2$ ), Mallows'  $C_p$ , Bayesian information criterion, and variance inflation factors. We assessed the linear relationships among all variables with Pearson correlation to select input variables for regression. All statistical analyses were conducted in R version 3.2.1 with  $\alpha$  set at 0.05 (R Core Team 2015).

## Results

### Vegetation community

A tally of observed plant species, their WIS, and their  $C_n$  are presented in Appendix Table 6. A total of 17 species were found across the ten plots, while six species were seen outside of the plots for a wetland with  $S$  of 23 and FQI of 20.5. Ten of the 23 species had a  $C_n$  value of 5 or greater, indicative of a wetland ecosystem with conditions supporting more sensitive species (Swink and Wilhelm 1979, 1994). *Leersia oryzoides* L. (rice cutgrass) and *Saururus cernuus* L. (lizard's tail) were dominant across the samples with importance percentages of 46 and 33%, respectively, representative of the large relative influence of these plants in the community. Four of the ten plots were monotypic for *L. oryzoides* (plots 1, 2, and 4) or *S. cernuus* (plot 7) with mean (plot) percent cover greater than 85%. Nine of the 17 species found in study samples had obligate (OBL) WIS, seven were facultatively wet (FACW), and only one was facultative (FAC), leading to a plot PI range of 1.00–1.20, where the PI of plot 1 was highest (Table 1).

Mean values for sample  $S$  and FQI were smaller than the broad-scale plot values (Tables 1, 2). From calculations of the total species in each plot, which differed from the mean species in each plot,  $S$  ranged from 2 to 7 along with FQI values from 4.9 to 13.2 (Table 2). Mean values



**Table 1** Huntley Meadows vegetation and soil attributes by plot

	Plot number										Mean	Coefficient of variation
	1	2	3	4	5	6	7	8	9	10		
Vegetation attributes												
Total cover (%)	135	104	129	140	152	125	124	136	105	83	123	0.17
<i>S</i>	2.5	1.8	3.3	3.5	3.8	3.3	3.0	3.5	3.0	5.3	3.3	0.28
FQI	5.7	4.7	7.5	7.9	8.9	8.0	7.8	8.7	9.4	9.7	7.8	0.20
<i>H'</i>	0.5	0.1	0.8	0.7	1.1	0.9	0.4	0.8	0.5	1.1	0.7	0.44
PI	1.20	1.03	1.02	1.02	1.00	1.00	1.02	1.01	1.01	1.04	1.04	0.06
Soil attributes												
TC (%)	2.3	2.4	4.0	2.4	2.0	2.0	6.1	4.7	2.9	2.1	3.1	0.45
TN (%)	0.18	0.20	0.28	0.20	0.17	0.17	0.49	0.38	0.24	0.19	0.25	0.43
DP <sup>a</sup>	172	278	475	399	205	325	943	752	487	70	411	0.65
<i>D</i> <sub>b</sub> (g cm <sup>−3</sup> )	0.59	0.63	0.36	0.30	0.35	0.39	0.32	0.29	0.28	0.22	0.37	0.36
GM (%)	76	75	110	107	72	66	175	151	105	63	100	0.38
pH	4.05	4.29	3.96	3.97	3.75	3.98	4.05	3.94	4.01	4.38	4.04	0.04
OM (%)	7.5	8.8	13.1	11.5	9.1	7.3	18.9	15.5	9.7	8.1	10.9	0.35

Mean of four subsamples per plot

*S* Richness, *FQI* floristic quality index, *H'* Shannon-Weiner diversity index, *PI* prevalence index, *TC* total carbon, *TN* total nitrogen, *DP* denitrification potential, *D<sub>b</sub>* bulk density, *GM* gravitational moisture, *OM* organic matter

<sup>a</sup>μg N–N<sub>2</sub>O kg<sup>-1</sup> h<sup>-1</sup>

**Table 2** Huntley Meadows plot diversity indices of the study

Index	Plot number										Mean ± SE
	1	2	3	4	5	6	7	8	9	10	
<i>S</i>	4	2	5	6	5	5	6	7	7	7	5.4 ± 0.5
FQI	7.5	4.9	8.5	10.3	11.6	11.4	9.8	11.0	13.2	12.9	10.1 ± 0.8

Indices calculated with the full set of species in a plot (≠ mean of subsamples in a plot). For abbreviations, see Table 1

of vegetation attributes per plot in 2014 ranged from 83 to 152% for total cover, and 0.1–1.1 for *H'* (Table 1).

Plot-to-plot variation was highest for *H'*, with a coefficient of variation (CV) of 0.44, which was roughly twice as variable as *S*, FQI, and total cover with CVs of 0.28, 0.20, and 0.17, respectively (Table 1). Plots 4–6 and 8–10, each with from two to three species (i.e., *Hydrocotyle ranunculoides*, *Sagittaria latifolia*, *Sagittaria cernuus*) and with *C<sub>n</sub>* values equal to 6, had the highest FQI values (Tables 1, 2; Fig. 1; Appendix Table 6). Plot 10, which had the highest water levels and lowest total cover (83%), supported the highest levels of *S* (5.3), FQI (9.7), and *H'* (1.1). Lowest values for plant *H'* and quality [i.e., lowest mean *S* (1.8), FQI (4.7), and *H'* (0.1)] were found in plot 2 located furthest from the central ponded area at the interface of herbaceous and forested marsh (Fig. 1).

## Soil physicochemistry and DP

Measured soil properties were characteristic of freshwater marshes and were more variable overall than vegetation attributes (Table 1). High values of GM, OM, TC, and low values of *D<sub>b</sub>* for mineral soils reflect frequent waterlogging with accompanying OM build-up (Table 1). In the plots with the greatest standing water (plots 8, 9, and 10), an unconsolidated topsoil horizon exhibited the lowest *D<sub>b</sub>*. Low pH values, as measured in this study (3.75–4.38), are characteristic of soils with abundant OM. With the exception of pH, the properties TC, TN, DP, *D<sub>b</sub>*, GM, and OM had CVs larger than total cover, *S*, FQI, and PI (Table 1). DP was the most variable (CV = 0.65) soil or vegetation property measured, suggestive of the hot-spot nature of DEA (Table 1). The lowest plot value (70 μg N kg<sup>-1</sup> h<sup>-1</sup>) coincided with the highest

recorded water levels, possibly from  $\text{NO}_3^-$  limitation under continuous anoxic conditions; the highest plot values ( $752$  and  $953 \mu\text{g N kg}^{-1} \text{ h}^{-1}$ ) coincided with the highest measurements of TC, TN, and OM, the source material supporting the heterotrophic microbial process (Table 1).

**Table 3** Differences in Huntley Meadows vegetation and soil attributes (mean  $\pm$  SE) by water level

	Water level category		Statistic	<i>P</i>
	Standing water < 2.5 cm <i>n</i> = 7	Standing water ≥ 2.5 cm <i>n</i> = 3		
Vegetation attributes				
Total cover (%)	130 ± 6	108 ± 16	<i>t</i>	NS
S	3.0 ± 0.3	3.9 ± 0.7	<i>t</i>	NS
FQI	7.2 ± 0.6	9.2 ± 0.3	<i>t</i>	**
<i>H'</i>	0.6 ± 0.1	0.8 ± 0.2	<i>t</i>	NS
PI	1.04 ± 0.03	1.02 ± 0.01	<i>t</i>	NS
Soil attributes				
TC (%)	3.0 ± 0.6	3.2 ± 0.8	<i>U</i>	NS
TN (%)	0.24 ± 0.04	0.27 ± 0.06	<i>U</i>	NS
DP <sup>a</sup>	400 ± 99	436 ± 198	<i>t</i>	NS
D <sub>b</sub> (g cm <sup>−3</sup> )	0.42 ± 0.05	0.26 ± 0.02	<i>U</i>	*
GM (%)	97 ± 14	106 ± 25	<i>t</i>	NS
pH	4.01 ± 0.06	4.11 ± 0.14	<i>U</i>	NS
OM (%)	10.9 ± 1.5	11.1 ± 2.3	<i>U</i>	NS

$t$  Independent two-tailed  $t$ -test,  $U$  Mann–Whitney–Wilcoxon two-tailed test; for other abbreviations, see Table 1

\*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , NS not significant

<sup>a</sup> $\mu\text{g N-N}_2\text{O kg}^{-1} \text{ h}^{-1}$

## Differences in soil and vegetation attributes by water level categories

The sampling area within the central wetland of Huntley Meadows experiences moist-soil to shallow water regimes (no standing water to greater than 7.5 cm) due to heterogeneity in elevation and surface roughness. Because the median monthly precipitation for the growing season in 2014 (117 mm) prior to sampling was within the interquartile range for 30-year monthly values, sampled water levels represent typical short-term differences in wetness across the wetland (PRISM Climate Group 2017). Water level was an important factor explaining FQI and  $D_b$ , where FQI values were on average larger ( $0.56$ – $3.48$ ; 95% confidence interval) and  $D_b$  values were on average lower ( $0.03$ – $0.28 \text{ g cm}^{-3}$ ; 95% confidence interval) in the plots with deeper standing water (Table 3). Water level category, however, was not found to impact total cover, S,  $H'$ , PI, TC, TN, DP, GM, pH, or OM (Table 3).

## Associations of vegetation and soil attributes

The majority of correlations were found among but not between vegetation and soil variables. For vegetation attributes, S, FQI, and  $H'$  were all strongly positively associated ( $r \geq 0.72$ ); for soil attributes, TC, TN, OM, GM, and DP were even more strongly associated ( $r \geq 0.93$ ) (Table 4). Two soil attributes were found to correlate with vegetation attributes: pH was negatively correlated with total cover ( $r = -0.89$ ), and  $D_b$  was negatively correlated with S, FQI, and  $H'$  ( $r \leq -0.63$ ) (Table 4). Plots 7 and 8, which had the highest TC, TN, OM, GM, and DP, had plant  $H'$  and quality measures close to the grand mean across plots, but were not

**Table 4** Pearson correlation coefficient (two-tailed) matrix for vegetation and soil attributes

	Cover (%)	S	FQI	$H'$	TC	TN	DP	$D_b$	GM	pH
<b>Vegetation attributes</b>										
S	– 0.2									
FQI	– 0.08	0.81**								
$H'$	0.14	0.87***	0.72*							
<b>Soil attributes</b>										
TC (%)	0.12	– 0.11	0.07	– 0.26						
TN (%)	0.06	– 0.09	0.11	– 0.27	0.99***					
DP <sup>a</sup>	0.22	– 0.22	0.12	– 0.33	0.93***	0.94***				
$D_b$ ( $\text{g cm}^{-3}$ )	0.08	– 0.81**	– 0.94***	– 0.63*	– 0.26	– 0.29	– 0.29			
GM (%)	0.23	– 0.13	0.13	– 0.29	0.95***	0.95***	0.97***	– 0.33		
pH	– 0.89***	0.09	– 0.24	– 0.25	– 0.12	– 0.08	– 0.28	0.17	– 0.24	
OM (%)	0.23	– 0.04	0.13	– 0.19	0.96***	0.96***	0.93***	– 0.36	0.97***	– 0.21

For abbreviations, see Table 1

\*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$

<sup>a</sup> $\mu\text{g N-N}_2\text{O kg}^{-1} \text{ h}^{-1}$

dominated by lower quality species (i.e., plot 7 was dominated by the more sensitive *S. cernuus* with a  $C_n$  of 6).

**Table 5** Simple regression models of soil attributes for FQI and for DP

y	x	Equations	$R^2$	F	p
FQI	$D_b$ ( $\text{g cm}^{-3}$ )	$y = -11.03x + 11.92$	0.89	66.6	< 0.001
DP <sup>a</sup>	GM (%)	$y = 6.89x - 277.61$	0.94	120.1	< 0.001
	TN (%)	$y = 2336.76x - 169.97$	0.88	57.3	< 0.001
	TC (%)	$y = 179.45x - 143.82$	0.87	51.6	< 0.001
	OM (%)	$y = 65.41x - 305.51$	0.86	50.1	< 0.001

For abbreviations, see Table 1

<sup>a</sup> $\mu\text{g N-N}_2\text{O kg}^{-1} \text{ h}^{-1}$

## Linear models for FQI and DP

Of the multiple soil attributes that might explain patterns in FQI,  $D_b$  alone was the best predictor (Table 5). Higher water levels were previously shown to have a positive influence on FQI values; however, the similarity in water levels between plots in this study implies water level has lower predictive power at smaller scales than soil attributes.  $D_b$  was not only a strong predictor of FQI but linearly related to additional measures of  $S$  and  $H'$  (Table 5). For DP, the four highly correlated variables TC, TN, GM, and OM, were all found to be strong single predictors (Table 5). The generally higher variability in soil properties relative to the vegetation attributes as measured by CV contributes to the greater explanatory power of DP. These simple models indicate that multiple soil variables that are easily monitored in beaver-created

**Table 6** Plant species observed in Huntley Meadows Park, Virginia

Scientific name	Common name	WIS <sup>a</sup>	$C_n$ <sup>a</sup>	Plot <sup>c</sup>									
				1	2	3	4	5	6	7	8	9	10
<i>Asclepias incarnata</i> L.	Swamp milkweed	OBL	5									X	
<i>Bidens cernua</i> L.	Nodding beggartick	OBL	4	X		X		X	X	X	X		
<i>Commelina communis</i> L. <sup>b</sup>	Asiatic dayflower <sup>b</sup>	FAC	0				X						
<i>Cyperus strigosus</i> L.	Straw-colored flatsedge	FACW	3	X	X		X				X		
<i>Hibiscus moscheutos</i> L.	Crimson-eyed rose-mallow	FACW	5						X		X	X	X
<i>Hydrocotyle ranunculoides</i> L.f.	Marsh pennywort	FACW	6							X	X	X	X
<i>Juncus effusus</i> L.	Common rush	FACW	3							X	X	X	X
<i>Leersia oryzoides</i> L.	Rice cutgrass	OBL	4	X	X	X	X	X	X	X	X	X	
<i>Ludwigia decurrens</i> Walter	Wingleaf primrose-willow	OBL	4	X									
<i>Mikania scandens</i> L. Willd.	Climbing hempvine	FACW	3			X							
<i>Persicaria hydropiperoides</i> Michx.	Mild water pepper	OBL	4										X
<i>Rosa palustris</i> Marshall	Swamp rose	OBL	6					X	X				
<i>Sagittaria latifolia</i> Willd.	Broadleaf arrowhead	OBL	6				X	X				X	X
<i>Saururus cernuus</i> L.	Lizard's tail	OBL	6			X	X	X	X	X <sup>c</sup>	X	X	X
<i>Scirpus cyperinus</i> L.	Woolgrass	FACW	3							X	X		
<i>Typha latifolia</i> L.	Broadleaved cattail	OBL	2			X		X	X				X
<i>Verbena hastata</i> L.	Swamp verbena	FACW	4							X			
Outside of plots													
<i>Alisma subcordatum</i> RAF.	American water plantain	OBL	6										
<i>Eleocharis obtusa</i> Willd.	Blunt spikerush	OBL	2										
<i>Lobelia cardinalis</i> L.	Cardinal flower	FACW+	7										
<i>Ludwigia palustris</i> L.	Marsh seedbox	OBL	2										
<i>Potamogeton diversifolius</i> Raf.	Waterthread pondweed	OBL	5										
<i>Sparganium americanum</i> Nutt.	Lesser bur-reed	OBL	6										
Wetland richness ( $S$ ) 23													
Wetland (FQI) 20.5													

OBL Obligate, FAC facultative, FACW facultatively wet

<sup>a</sup>Wetland indicator status (WIS) and coefficient of conservatism ( $C_n$ ) taken from the 2005 Virginia Wetland Plants C-Value List prepared by the Virginia FQAI Advisory Committee for the Virginia Department of Environmental Quality

<sup>b</sup>Low-ranking invasive species (Heffernan et al. 2014)

<sup>c</sup>Mean species % cover > 85% in study plot

wetlands are useful for predicting areas with high FQI and DP.

## Discussion

Huntley Meadows provided a great opportunity to study a mature, yet transitional wetland shaped by decades of beaver immigration and abandonment. Nine years after a major beaver dam breach and subsequent drawdown, changes to the plant community challenged our assumptions regarding the effects of continuously low water levels. Instead of seeing more FAC species, as would have been expected had the wetland remained drained, and which would have resulted in higher PI values, more OBL and FACW species coverage was seen in 2014. We calculated PI values of 1.0–2.1 in our 2005 study (Moser et al. 2007), which are slightly higher than 2014 values (1.0–1.2); we infer that the presence of *Microstegium vimineum* (Japanese stiltgrass), a species with a FAC indicator status, increased PI in 2005 (Moser et al. 2007). In 2005, like in 2014, both *L. oryzoides* and *S. cernuus* were dominant with mean percent cover of 30 and 12%, respectively. *M. vimineum*, a high ranking invasive, also had a high mean cover at 24% in 2005 (Moser et al. 2007), but was not observed in 2014, probably due to active invasive species management by the park. Continuing inundation from new beaver dam creation likely contributed to maintenance of an overall OBL WIS for the sampled area of the wetland (Fig. 1).

Changes to *S* further suggest little long-term impact by the dam breach 9 years earlier in 2005, when Moser et al. (2007) observed 26 species that are comparable to the number of species observed (23) in 2014. Yet within plots, *S* ranged from 8 to 14 in 2005 compared to 2–7 in 2014, which may also be a reflection of the greater number of FAC species present in 2005. We conclude that the presumed drier conditions immediately after the beaver dam breach may have disturbed the plant species composition, but these effects had likely reversed by 2014. That GM mean  $\pm$  SE levels were much lower in 2005 ( $32.4 \pm 0.5\%$ ) than in 2014 ( $100 \pm 12\%$ ) without substantial changes to soil TC or TN (varying from 0.7 to 7.7 and 0.06 to 0.39%, respectively), may further indicate that the water level drawdown was brief or had a variable impact depending on annual precipitation.

The range of FQI reported in the literature [9.6–35.3 (Fennessy 1998; Bried et al. 2013)] suggests ecological disturbance shapes the plant communities of Huntley Meadows Park. Beavers dredge channels into the bottom of wetlands, increasing soil microtopography, re-arranging hydrologic patterns, and creating pools of standing water during low water levels (Hood and Larsen 2015). Our finding that floristic quality was greater in sites with greater standing water levels provides some evidence that beaver

activity could impact the quality of the plant community. It has similarly been found that higher variation and relief in the microtopography of natural wetlands, which increases pools of standing water, is associated with higher plant *H'* (Moser et al. 2007, 2009). In addition to water level, FQI relates to other wetland characteristics. Dee and Ahn (2012) reported that FQI increased with aggregate soil conditions indicative of wetland maturity (i.e., greater OM, neutral pH, greater GM, and lower  $D_b$ ). In Huntley Meadows, FQI was directly and negatively associated with  $D_b$ , suggesting FQI was strongly responding to physical and hydrologic gradients and not to soil chemical gradients (e.g., OM accumulation). It was noteworthy that we found the lowest plot FQI score at the most upstream site of Barnyard Run, closer to the residential communities in the direction from which storm water runoff enters the site. Dee and Ahn (2012) also noted likely negative effects on created wetland vegetation *H'* from polluted storm water run-off at a site located adjacent to a highway and airport industrial area, in contrast to more rural sites. Though the effect of proximity was not studied, our findings of the sensitivity of FQI to water levels and soil disturbance may be one of the confounding factors that renders FQI less indicative of the disturbance of wetlands to surrounding land cover (Bried et al. 2013).

Environmental gradients in TC, TN, GM, and OM were found to positively explain DP variability in Huntley Meadows. These soil properties comprise typical biogeochemical controls on denitrification (e.g., Wolf et al. 2011). These findings are unsurprising, particularly because all our DP values fell mid-range within reported rates of DEA for natural freshwater wetlands (Groffman et al. 1996; Burgin et al. 2010). Water level category did not directly explain DP, but hydrologic condition was still likely influential. The lowest DP rate was found at the plot with highest standing water, and DP was still most strongly and positively associated with soil moisture (GM). The highly saturated soils in some of the plots and their low bulk densities possibly decoupled the association between GM and standing water levels. That all four predictors—GM, TC, TN, and OM—could almost equally well predict DP indicates a joint physicochemical gradient across the wetland. As this gradient was not related to water levels, a likely reason for this gradient might be plant productivity, which was not measured here, and can be negatively related to *H'* and quality measures of the plant community (Dee and Ahn 2012). The lack of a commonly found negative association between DP and  $D_b$  could in part relate to the shallower depth (< 5–10 cm) measurement of  $D_b$ ; thus, the insignificant relationships should not be construed as strong evidence of no relationship. Vertical stratification was observed most strongly in the wettest plots at a depth below sampling between non-clay and clay horizons, or a “friable-firm” divide (Robbins et al. 1992).



Beaver-created wetlands are distinguished by hydrologic and biological structuring forces different from those found in other common wetlands, such as bottomland swamps or fringe marshes of ponds. Understanding the impact of these forces on ecosystem attributes will be of increasing importance as management of wetlands within the Chesapeake Bay watershed continues to intensify. This study provides ecosystem structure–function relationships that will inform experimentation with wetland design and restoration (Hudon 2004; Mitchell and Niering 1993; Vandervalk et al. 1994).

Further, evidence was lacking that there had been major changes to the soil and plant attributes 9 years after a major dam breach in the wetland. These findings of wetland resilience in ecosystem structure inform the long-term management of beaver-created wetlands. Large variations in water levels from year to year will not necessarily alter the succession of the wetland or disrupt soil nutrient storage, and thus management of multi-year patterns should take priority over year-to-year changes.

## Conclusion

The study investigated the associations between heterogeneity in vegetation and soil biogeochemical properties, with a focus on floristic quality and denitrification, in a mature freshwater herbaceous wetland created by beavers located in the Coastal Plain region of northern Virginia. Beavers play an important role in structuring a wetland by their natural dam building activities as ecological engineers, yet often their abandonment of wetlands can disturb the established plant communities and associated biogeochemical functions that were once supported by the habitat. We found structural changes indicating a reversal of lowered water levels in the past that provides evidence for wetland resilience 9 years after a major dam breach. High water levels were associated with greater floristic quality (i.e., FQI) and lower  $D_b$ , but no other soil physicochemical properties. DP was not associated with water levels or plant community measures of  $H'$  and was instead positively associated with soil OM, C, N, and moisture, possibly attributable to plant productivity, which was not measured in this study.

The study is quite limited since all our sites were located in one contiguous wetland, thus study findings may not be representative of other beaver-created wetlands. It is rare to see a naturally occurring marsh type of wetland in northern Virginia other than the Huntley Meadow one described in this study. Further study may be necessary to include other beaver-created wetlands in different hydroscares and geological settings to tease out more generally applicable relationships between structure and function of this unique ecosystem. Nonetheless, all the structural and functional attributes studied, and the mathematical equations built for the relationships of these attributes, can be used in the studying

and monitoring of other beaver-created wetlands for their management and resilience to improve our understanding and management of beaver-created wetlands.

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## Appendix

See Table 6.

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