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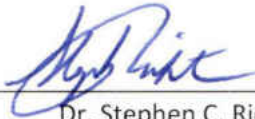
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AMPHIBIAN AND PLANT COMMUNITIES OF NATURAL AND CONSTRUCTED UPLAND-
EMBEDDED WETLANDS IN THE DANIEL BOONE NATIONAL FOREST

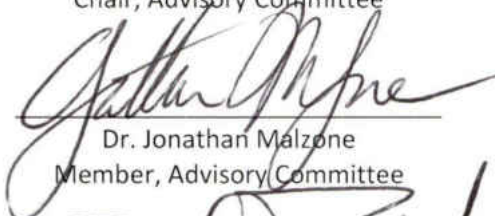
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AMPHIBIAN AND PLANT COMMUNITIES OF NATURAL AND CONSTRUCTED UPLAND-
EMBEDDED WETLANDS IN THE DANIEL BOONE NATIONAL FOREST

BY

RACHEL B. FEDDERS

Submitted to the Faculty of the Graduate School of
Eastern Kentucky University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

2018

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DEDICATION

This thesis is dedicated to my family. Your wisdom, humor, patience, and great kindness have enabled my progress and successes. To my parents, James and Barbara Fedders, for your constant steadfast support, for sparking my interest in the natural world at a young age, and for all those weekend wildflower hikes that finally sunk in! To my sisters, Anna and Emily Fedders, for your encouragement (and commiseration) regarding learning and working in the sciences. To my partner, Jackson Napier, for your patience and for having confidence in me to complete this endeavor.

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ABSTRACT

Wetlands fulfill many vital ecological functions, including providing habitat for amphibians and plants. Some wetlands, known as upland-embedded wetlands (UEWs), are depressional wetlands surrounded completely by upland habitat. This wetland type has been constructed in many areas for conservation and mitigation purposes, but constructed UEWs often do not function equivalently to natural wetlands, and often have different physical and chemical characteristics. In the Daniel Boone National Forest (DBNF), numerous UEWs have been constructed on ridge-tops to benefit game and bat species. Previous studies have shown that many of these constructed wetlands have permanent hydroperiods and different amphibian communities than co-occurring natural ephemeral wetlands. Wood frog and marbled salamander larvae are found almost exclusively in natural wetlands and green frog larvae and eastern newts are found in constructed wetlands. It is currently unknown whether plant communities at these constructed wetlands are similar to those of co-occurring natural wetlands. My objectives were to a) gain a more complete understanding of the amphibian communities in the ridge-top wetland system of the DBNF, b) to determine if previous amphibian findings are generalizable across the large number of UEWs that have been constructed, c) to determine if plant communities differ between natural and constructed UEW sites, d) to understand the environmental and habitat variables that influence plant communities, and e) to synthesize previous findings with my own

research to make management and research recommendations for the constructed UEW system in the DBNF.

I measured amphibian catch-per-unit effort and wetland habitat variables at 48 wetlands (10 natural, 6 previously-studied constructed, and 32 randomly-selected constructed). I used Kruskal-Wallis tests, generalized linear models, and nonmetric multidimensional scaling to compare conditions among wetland types and to visualize amphibian communities. Natural wetlands were associated with wood frogs (*Lithobates sylvaticus*) and marbled salamanders (*Ambystoma opacum*) and constructed wetlands were associated with green frogs (*L. clamitans*), eastern newts (*Notophthalmus viridescens*), and spotted/Jefferson salamanders (*A. maculatum*, *A. jeffersonianum*). Four-toed salamanders (*Hemidactylium scutatum*), cricket frogs (*Acris crepitans*), toads (*Anaxyrus* spp.), and chorus frogs (*Pseudacris* spp.) showed no clear patterns related to wetland construction history. Constructed wetlands had higher amphibian richness and diversity than natural wetlands. Hydroperiod was a major driver of community composition. The introduction of permanent water sources has allowed permanent-wetland obligate species, including newts and green frogs, to colonize the UEW system. These species prey on wood frog eggs and larvae and increase the threat of disease introduction and transmission. My findings supported previous research in the system, indicating that this pattern is representative of the more than 500 constructed wetlands throughout the Cumberland Ranger District. With amphibian declines due to habitat loss, constructed and restored wetlands provide important breeding habitat. Under

some climate models, hydroperiods of existing ephemeral wetlands are projected to shorten, disrupting breeding cycles and causing larval death. It is important that constructed wetlands provide habitat that is both structurally and functionally similar to natural reference habitat.

I evaluated differences in plant communities at 10 natural and 10 constructed upland-embedded wetlands in the DBNF. I estimated cover class of each understory species in several plots at each wetland and performed visual surveys to capture total species richness at each site. I also measured habitat variables at these sites. Using Mann-Whitney U tests, I found that natural and constructed wetlands differed significantly ($\alpha = 0.05$) regarding total and nonnative species richness, which were higher at constructed wetlands; and mean coefficient of conservatism, floristic quality, and percent canopy closure, which were higher at natural wetlands. Using cluster analysis and nonmetric multidimensional scaling (NMDS) with post-hoc PERMANOVA comparisons, I determined that understory vegetative communities were significantly different between wetland types. Permanent hydroperiod and a history of disturbance at constructed wetlands have resulted in these sites having lower floristic quality, lower ecological conservatism, and more invasive species than natural wetlands. Closed canopy at natural sites increases presence of shade-tolerant understory species. More research is needed to separate the effects of construction history, canopy closure, and hydroperiod on understory communities, richness, and floristic quality.

Management and additional research are recommended in the UEW system in the DBNF. Research should address amphibian and plant communities at natural and constructed UEWs throughout all districts of the DBNF, including population dynamics of marbled salamanders, effects of landscape and geologic features on wetland hydrology, and detection and mapping of undocumented UEW sites. Management should focus on conserving existing natural UEWs, reducing the number and density of constructed UEWs, altering a subset of constructed wetlands to encourage natural-type conditions, and removing invasive species from wetland sites. Amphibian community and habitat characteristics should be assessed to select candidate wetlands for alteration or removal. Methods could include draining wetlands by altering dams and shortening hydroperiods by decompacting soil, lowering dams, and planting trees. Post-alteration, plant and amphibian communities should be monitored for at least six years. Prudence and planning are urged in all wetland construction and alteration projects to ensure that the constructed wetlands will meet desired ecological goals and not disrupt existing ecosystem structures.

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Introduction

Wetlands perform many vital chemical, physical, and biological functions, including filtering impurities from water, acting as natural reservoirs, trapping sediment, lessening effects of flooding, and providing diverse habitat for a myriad of species (Mitsch & Gosselink, 2007). Some wetlands, known as ephemeral wetlands or vernal pools, have a temporary hydroperiod and dry in the summer and fall. In the eastern United States, these wetlands provide vital breeding habitat for many amphibian species, including wood frogs (*Lithobates sylvaticus* LeConte) and marbled salamanders (*Ambystoma opacum* Gravenhorst; Brown & Richter, 2012; Calhoun & deMaynadier, 2008). In some contexts, vernal pools may serve as keystone ecosystems. That is, they may have an inordinate effect on the surrounding landscape by acting as bastions of species richness and secondary productivity (Calhoun & deMaynadier, 2008).

Efforts to improve wildlife habitat and mitigate for wetland loss have led to attempts to construct vernal wetlands; however, hydroperiod of constructed wetlands often does not mimic that of natural ephemeral wetlands. Constructed wetlands often have longer hydroperiods than natural wetlands, despite sometimes being smaller in surface area (Denton & Richter, 2013; Drayer & Richter, 2016; Gamble & Mitsch, 2009). Depression depth, underlying soil type, soil compaction, groundwater

connectivity, and evapotranspiration of local vegetation affect pool hydrology (Brooks & Hayashi, 2002; Calhoun & deMaynadier, 2008; Calhoun et al., 2014; Gamble & Mitsch, 2009).

One of the most important factors determining breeding success of vernal pool obligate amphibians is hydroperiod, in which obligate populations are positively associated with yearly pool drying (Denton & Richter, 2013; Drayer & Richter, 2016; Calhoun et al., 2014). Semi-permanent wetlands, which dry occasionally but retain water for multiple years at a time (Calhoun & deMaynadier, 2008), and permanent wetlands, especially, are associated with populations of large ranid larvae (green frogs [*L. clamitans* Latreille] and bullfrogs [*L. catesbeianus* Shaw]) and eastern newts (*Notophthalmus viridescens* Rafinesque) (Denton & Richter, 2013; Drayer & Richter, 2016), which prey upon eggs and larvae of salamanders and anurans (Boone et al., 2004; Jennette, 2010; Kross and Richter, 2016). Due to these populations of predatory species, some constructed wetlands serve as reproductive sinks for wood frogs due to predation of eggs and larvae (Kross & Richter, 2016).

Amphibian diversity and richness are affected by habitat heterogeneity at the local scale and by wetland density and habitat connectivity at the landscape scale. Habitat heterogeneity has a positive effect on amphibian species diversity (Tews et al., 2004). Shrub cover and underwater vegetation provide sites for amphibian oviposition (Egan & Paton, 2004), and coarse woody debris provides cover and feeding grounds for amphibian species (Maser et al., 1979). More connected ecosystems have higher rates

of recolonization and often display higher species richness (Calhoun & deMaynadier, 2008). However, species richness alone does not indicate wetland success (Calhoun et al., 2014). High wetland density may aid dispersal of wetland-breeding amphibians; however, construction of wetlands at densities greater than historic or natural levels, especially when constructed wetlands are permanent, may increase predation pressure (Kross & Richter, 2016; McTaggart, 2016) and risk of disease introduction at nearby natural wetlands (Calhoun et al., 2014; Richter et al., 2013).

In the Cumberland District of the Daniel Boone National Forest (DBNF) in eastern Kentucky, hundreds of ridge-top wetlands have been constructed, primarily to enhance habitat for turkey, deer, and bats (Brown & Richter, 2012). Most constructed wetlands have permanent or semi-permanent hydrological regimes and populations of green frogs and eastern newts (Denton & Richter, 2013; Drayer & Richter, 2016). Although some constructed wetlands exhibit 'natural-type' temporary hydroperiods and host amphibian communities that are somewhat similar to natural ridge-top wetlands, these wetlands still have lower numbers of wood frog and marbled salamander larvae than natural wetlands (Denton & Richter, 2013; Drayer & Richter, 2016). Previous research in this system found that wood frog larvae are almost exclusively found in natural wetlands, that green frogs, bullfrogs, and eastern newts are almost exclusively found in constructed wetlands, and that spotted salamanders, Jefferson salamanders, spring peepers, mountain chorus frogs, American toads, Fowler's toads, and four-toed salamanders are found in both natural and constructed

wetlands and most do not show clear patterns of presence or abundance between wetland types (Denton & Richter, 2013; Drayer & Richter, 2016). Previous studies have been limited in geographic scope, and a broader random sample across the entire District is necessary to determine if previous findings are generalizable. I integrated additional assessment of the ridge-top wetland environment and surveys of amphibian species. I assessed this new information along with existing amphibian data to evaluate the generalizability of previously observed amphibian community composition patterns across the ridge-top wetland system and to investigate whether constructed wetlands are functioning similarly to the natural wetlands in the area.

My objectives were to collect amphibian diversity and abundance data at a greater number of randomly-selected constructed wetlands than have previously been studied (i.e., Denton & Richter, 2013; Drayer & Richter, 2016; Kross & Richter, 2016) and across the entire District to gain a more complete understanding of the amphibian communities in the ridge-top system, and to determine if previous findings are generalizable across the Cumberland District of the DBNF.

Materials and Methods

Study area

My study sites consisted of 48 ridge-top wetlands in the Cumberland District of the Daniel Boone National Forest (Figure 1-1). Wetlands were located in Mixed Mesophytic forest type (R. L. Jones, 2005) in the Western Allegheny Plateau Ecoregion

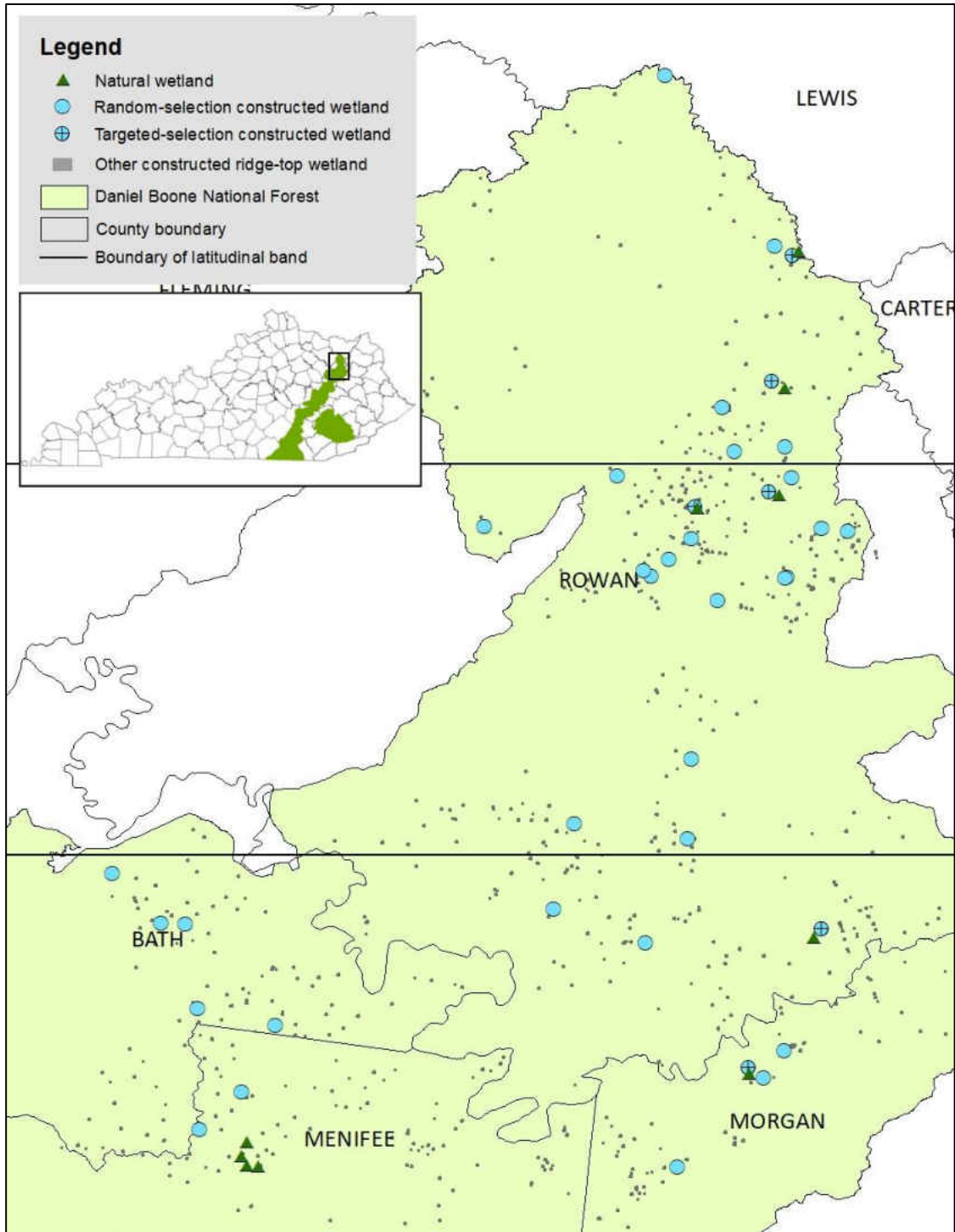


Figure 1-1. Locations of natural and constructed ridge-top wetland sites studied during the 2016 field season. Sites were located in the Cumberland District of the Daniel Boone National Forest, in the area indicated in the inset map. Horizontal lines represent boundaries between latitudinal bands used in random site selection.

(U.S. Environmental Protection Agency, 2013) and the Allegheny Plateau Physiographic Province (R. L. Jones, 2005). Wetlands were primarily rainwater-fed. In addition to rainwater, some wetlands received local surface and groundwater input, but these additional water sources are charged by precipitation (J. Malzone, unpubl. data, 2017). Sixteen of these sites, 10 natural and 6 targeted-selection (TS) constructed wetlands, had been previously surveyed for wood frog eggs, larvae of all amphibian species, and adult eastern newts (Denton & Richter, 2013; Drayer & Richter, 2016).

The remaining 32 randomly-selected (RS) constructed wetlands were previously unstudied and were randomly selected from three latitudinally stratified groups to ensure even distribution across the Cumberland District. The number of wetlands selected from each stratified group was proportional to the total number of constructed wetlands in that group (Figure 1-1). There were five RS constructed wetlands in group one (northern portion of District), 15 RS constructed wetlands in group two (central portion), and 12 RS constructed wetlands in group three (southern portion). This arrangement reflected the higher quantity of constructed wetlands in the middle and southern portions of the Cumberland District. The ten natural wetlands and 6 TS constructed wetlands served as a focal study group, where additional habitat information was collected (see 'habitat characterization' below).

Amphibian richness and abundance

I visited all RS constructed wetlands once between 20 February and 17 March 2016 to ground-truth the sites and count wood frog egg clutches. I counted clutches by

walking around the pool perimeter and recording any clutches observed. I wore polarized sunglasses to reduce surface glare and make the clutches easier to see. If a second observer was present, each observer recorded counts independently and the counts were averaged for analysis. Dipnet surveys occurred in two rounds: 15 April to 4 May 2016 and 23 May to 29 May 2016. During each survey, I took a dipnet sample every five meters around the pool perimeter; a dipnet sample consisted of placing the dipnet 1.5 m from the shore of the wetland and sweeping through the water toward the wetland margin. Each sweep included the top few centimeters of wetland substrate. I identified and counted all amphibian larvae in each dipnet sample. Due to the difficulty in distinguishing between young larvae in the field of spotted and Jefferson salamanders, spring peeper (*Pseudacris crucifer* Weid-Neuweid) and mountain chorus frogs (*Pseudacris brachyphona* Cope), and American and Fowler's toads (*Anaxyrus americanus* Holbrook, *A. fowleri* Hinckley), these species pairs were each grouped.

Habitat characterization

I recorded the following metrics at each wetland in conjunction with each amphibian dipnetting event: depth at the deepest point in the pool, depth in the cardinal directions at one and two meters from shore (which I converted to littoral slope), water temperature, conductivity, pH, dissolved oxygen, and oxidation-reduction potential (ORP). I measured physicochemical water characteristics using a YSI 556 multiparameter water meter (Yellow Springs Instruments, Yellow Springs, OH).

At each of the 16 focal wetlands, I recorded canopy closure using a spherical densiometer during full leaf-out, between 6 June and 20 June 2016. Canopy closure was measured in each cardinal direction by counting the number of closed dots in the densiometer. This was converted to a percentage, and the four measurements were averaged at each site. I also measured coarse woody debris (CWD) along four 50-m linear transects extending perpendicular from the pool boundaries in each cardinal direction (Denton & Richter, 2013; Waddell, 2002; Warren & Olsen, 1964). For any piece of CWD ≥ 10 cm in diameter at its narrow end that intersected a transect, I measured total length of the segment and diameter at each end. I assigned a decay class to each CWD fragment on a five-point scale (Waddell, 2002). I calculated the volume of each CWD piece using the formula

$$V_m = \frac{\left(\frac{\pi}{8}\right)(D_s^2 + D_L^2)l}{10,000} \quad (1)$$

where V_m = volume of the log in cubic meters, D_s = the diameter of the small end of the log in cm, D_L = the diameter of the large end of the log in cm, and l = length of the log in meters (Waddell, 2002). I calculated cubic meters of CWD per hectare using the formula

$$V_m \text{ per hectare} = \left(\frac{\pi}{2L}\right) \left(\frac{V_m}{l_i}\right) 10000m^2 / \text{hectare} \quad (2)$$

where L = the total length of the transect line, V_m = volume in cubic meters of the individual piece of CWD, and l_i = length of that individual piece. I summed values to the plot level (Waddell, 2002).

Analyses

I calculated amphibian species richness for each wetland site based on the total number of taxa that were observed at each site. Note that reported taxon richness is an underestimate of true species richness because some species were combined for richness estimates (i.e. spotted and Jefferson salamanders, spring peepers and mountain chorus frogs, and American and Fowler's toads). I calculated catch-per-unit-effort (CPUE) of each amphibian species by dividing the number of larvae captured by the number of dipnet samples collected and summed this across both sampling events at each site. CPUE served as a standardized index of abundance. I calculated Shannon's diversity index (H) for each site based on amphibian richness and CPUE. I performed Kruskal-Wallis (K-W) tests using the R statistical package in R version 3.3.2 (R Core Team, 2018) to compare richness, diversity, number of wood frog clutches, amphibian CPUE, and habitat characteristics among natural, TS constructed, and RS constructed wetlands. If the K-W test was significant ($\alpha = 0.05$) I applied a post-hoc Dunn comparison with Benjamini-Hochberg adjustment (Benjamini & Hochberg, 1995) using package `dunn.test` (Dinno, 2017).

I used generalized linear modeling and Akaike Information Criterion (AIC) model selection in IBM SPSS Statistics (IBM Corp., 2016) to examine which habitat variables best explained presence, abundance, and diversity of amphibians. Candidate models were developed from combinations of the following habitat characteristics: wetland type (natural, RS constructed, TS constructed), pH, dissolved oxygen,

conductivity, oxidation-reduction potential, wetland maximum depth, littoral slope, and water temperature. Wetland maximum depth and littoral slope were highly correlated ($r > 0.80$), and therefore were not included in any models together (Appendix A, Table A-1). Widespread and abundant species (eastern newt, green frog, spotted/Jefferson salamander) were modeled using a Tweedie distribution with a log-link function, where CPUE served as the response variable. Because eastern newts only occurred at constructed sites and green frogs were only found at one natural site, I excluded natural sites from modeling for these species. I also used the Tweedie distribution to model Shannon's Diversity Index (H).

For less widespread and abundant species (wood frog, marbled salamander, combined *Anaxyrus*, cricket frog [*Acris crepitans* Baird], combined *Pseudacris*, and four-toed salamander [*Hemidactylium scutatum* Temminck]), I modeled presence using binomial logistic regression. For marbled salamanders, I limited the 'type' variable to two levels (natural and constructed) to aid in model convergence. For both Tweedie and logistic regression results, I used Akaike information criterion adapted for small sample sizes (AIC_c) to rank the candidate models (Mazerolle, 2006). When more than one model had a difference in AIC_c value (Δ_i) of less than two, model averaging was used to evaluate the relative importance of each parameter included in the top models (Mazerolle, 2006). I calculated variable weight, model-averaged estimates, unconditional standard error and 85% confidence intervals for each variable. Eighty-five percent confidence intervals were used to ensure that variables from the set of

top models that had lower AIC values were not erroneously discarded (Arnold, 2010).

A variable was considered significant when its 85% CI did not overlap zero.

I evaluated amphibian community data with nonmetric multidimensional scaling (NMDS) using the metaMDS function in package vegan (Oksanen et al., 2018) in R version 3.3.2 (R Core Team, 2018). I chose a three-axis NMDS plot to minimize stress while maintaining visual interpretability. I performed permutational multivariate analysis of variance (PERMANOVA) using the ADONIS function in the vegan package (Oksanen et al., 2016) in R version 3.3.2 (R Core Team, 2016). The PERMANOVA compared community composition among the three site types (natural, TS constructed, and RS constructed). If the PERMANOVA was significant ($\alpha < 0.05$), I performed post-hoc pairwise contrasts and applied a Bonferroni adjustment ($\alpha_{\text{adjusted}} = 0.017$).

Results

Amphibian metrics

I surveyed 33 constructed and six natural sites for wood frog egg clutches (Table 1-1). I did not survey nine of my study wetlands (five constructed and four natural) for wood frog clutches because clutches had degraded to an undistinguishable point before I could visit these sites. I combined RS and TS constructed sites into a single constructed group for wood frog clutch analyses. I found wood frog clutches at a

Table 1-1. Number of ridge-top wetland sites in the Daniel Boone National Forest surveyed for wood frog clutches, number (percent) of sites where wood frog clutches were found, mean (SE) number of clutches found, and number (percent) of sites where wood frog larvae were found. Means in the same row with different letters are significantly different (Mann-Whitney U Test; $\alpha = 0.05$).

	natural	constructed	<i>p</i>
no. sites surveyed for clutches	6	33	-
no. sites with wood frog clutches (%)	6 (100%)	18 (54.5%)	-
mean (SE) no. clutches found	45.6 (22.4) ^a	10.5 (3.18) ^b	0.008
no. sites with wood frog larvae (%)	5 (83.3%)	5 (15.2%)	-

greater percentage of natural sites than constructed sites, and natural sites contained significantly more clutches than constructed sites (Table 1-1). Wood frog survival to the larval stage was higher in natural than constructed sites. I found wood frog larvae at 83% of natural wetlands that had contained wood frog eggs, and at 15% of constructed wetlands that had contained wood frog eggs.

I captured 7,603 amphibians representing 10 taxa. Richness estimates included three species pairs. Mean species richness across all sites ($n = 48$) was 3.59 (SE = 0.18). All wetlands contained at least one species of amphibian. RS constructed wetlands had the greatest mean richness, followed by TS constructed and natural wetlands, but this difference was not significant (Table 1-2). Shannon's diversity index (H) differed significantly among the groups ($p = 0.004$). Natural wetlands had significantly lower diversity than both types of constructed wetlands, and RS and TS constructed sites were not significantly different (Table 1-2). I only captured bullfrog larvae at one site, so I excluded bullfrogs from further analyses.

Table 1-2. Mean (SE) richness and H (Shannon-Weiner diversity) for amphibians captured in each of three ridge-top wetland groups. Means with different letters in the same row were significantly different from each other (Kruskal-Wallis test with post-hoc Dunn comparisons, Benjamini-Hochberg adjustment applied; $\alpha = 0.05$). TS= targeted-selection, RS= random-selection, H = Shannon-Weiner diversity index. Significance indicated by *

	Natural	TS constructed	RS constructed	<i>p</i>
Richness	3.3 (0.6)	4.4 (0.8)	4.0 (0.2)	0.067
H	0.32 (0.11) ^a	0.93 (0.10) ^b	0.79 (0.05) ^b	0.004*

Natural wetlands had significantly greater CPUE of wood frogs, and significantly less CPUE of green frogs, eastern newts, and spotted/Jefferson salamanders than both types of constructed wetlands. Natural wetlands had greater CPUE of marbled salamanders than TS constructed, but not RS constructed wetlands. Although there was a significant difference among groups for spring peeper/mountain chorus frog CPUE, the post-hoc Benjamini-Hochberg comparisons were not significant. There was not a significant difference in CPUE among wetland types for cricket frogs, toads, or four-toed salamanders. There was not a significant difference in larval CPUE between the constructed groups in any case (Figure 1-2, Table 1-3).

Habitat variables

Natural wetlands had lower pH than TS constructed wetlands but not RS constructed wetlands, and shallower maximum depth, shallower littoral slope, and lower dissolved oxygen than both constructed groups. Natural wetlands had higher canopy closure than TS constructed wetlands (Figure 1-3, Table 1-4). There were no significant differences among wetland groups in water temperature, conductivity, ORP,

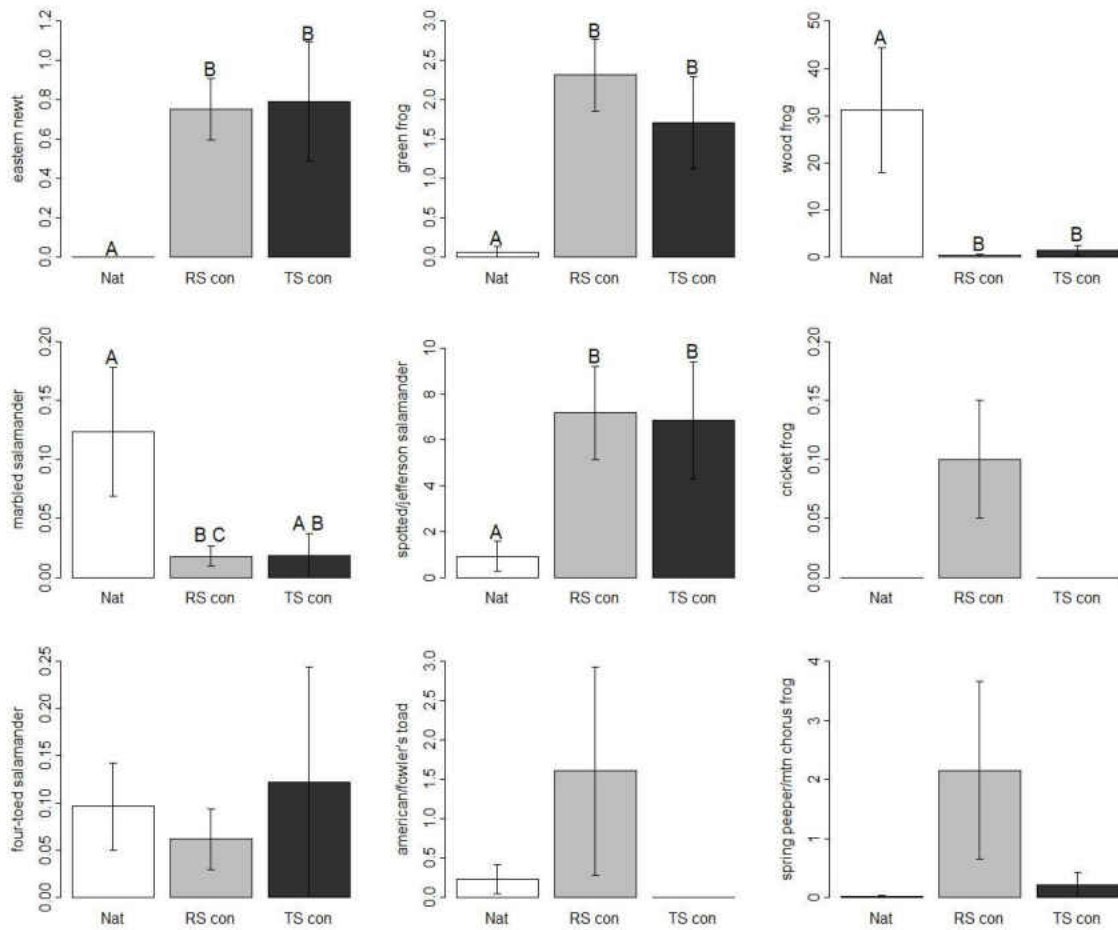


Figure 1-2. Mean (\pm SE) catch-per-unit-effort of each amphibian species at different ridge-top wetland types in the Daniel Boone National Forest. Nat = natural wetlands ($n = 10$), RS con = randomly-selected constructed wetlands ($n = 32$), TS con = targeted-selection constructed wetlands ($n = 6$). Bars with different letters within the same plot were significantly different from each other (Kruskal-Wallis test with post-hoc Dunn comparisons, Benjamini-Hochberg adjustment applied; $\alpha = 0.05$).

Table 1-3. Mean (SE) CPUE of larval amphibians at natural (n = 10), TS constructed (n = 6), and RS constructed (n = 32) ridge-top wetlands, and number (%) of sites at which each species was found. Means with different letters in the same row were significantly different from each other (Kruskal-Wallis test with post-hoc Dunn comparisons, Benjamini-Hochberg adjustment applied; $\alpha = 0.05$). TS = targeted-selection, RS = random-selection, CPUE = catch per unit effort.

species	<i>Natural</i>		<i>TS constructed</i>		<i>RS constructed</i>		CPUE <i>p</i>
	Mean (SE)	n sites (%)	Mean (SE)	n sites (%)	Mean (SE)	n sites (%)	
green frog	0.07 (0.06) ^a	1 (10%)	1.72 (0.53) ^b	6 (100%)	2.25 (0.45) ^b	27 (84%)	< 0.001
eastern newt	0.00 (0.00) ^a	0 (0%)	0.79 (0.28) ^b	5 (83%)	0.73 (0.15) ^b	29 (91%)	< 0.001
wood frog	31.21 (12.49) ^a	9 (90%)	1.56 (0.93) ^b	2 (33%)	0.37 (0.28) ^b	3 (9%)	< 0.001
spotted/ jeff. salamander	0.92 (0.61) ^a	7 (70%)	6.87 (2.33) ^b	6 (100%)	7.12 (1.97) ^b	30 (94%)	0.007
marbled salamander	0.12 (0.05) ^a	5 (50%)	0.02 (0.02) ^{a, b}	1 (17%)	0.02 (0.01) ^{b, c}	4 (13%)	0.030
cricket frog	0.00 (0.00)	0 (0%)	0.00 (0.00)	0 (0%)	0.10 (0.05)	7 (22%)	0.137
American/ Fowler's toad	0.23 (0.17)	2 (20%)	0.00 (0.00)	0 (0%)	1.56 (1.28)	7 (22%)	0.456
spring peeper/ mtn. chorus frog	0.01 (0.01)	1 (10%)	0.21 (0.19)	1 (17%)	2.09 (1.46)	16 (50%)	0.049 ^ψ
four-toed salamander	0.10 (0.04)	4 (40%)	0.12 (0.11)	1 (17%)	0.06 (0.03)	6 (19%)	0.404

^ψ These variables were not measured at RS constructed sites

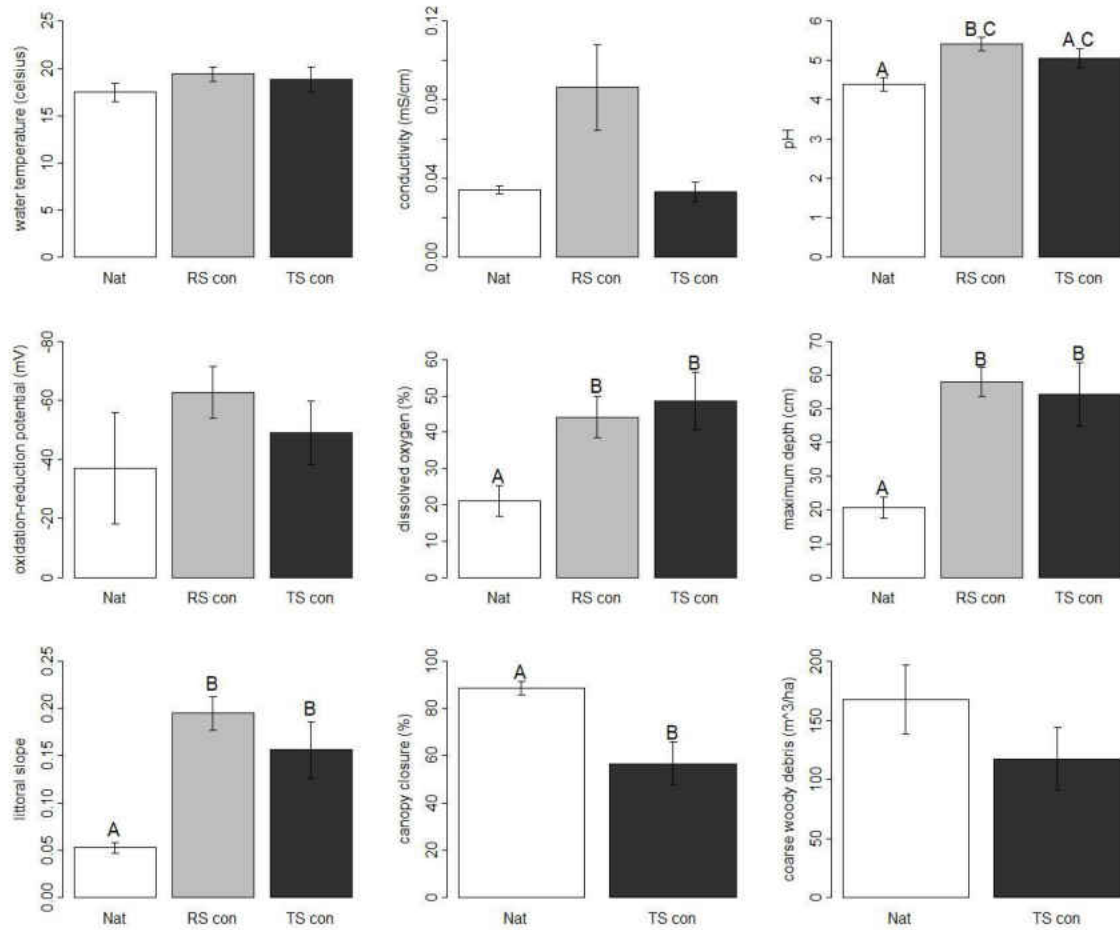


Figure 1-3. Mean (\pm SE) values of each habitat variable at different ridge-top wetland types in the Daniel Boone National Forest. Nat = natural wetlands ($n = 10$), RS con = randomly-selected constructed wetlands ($n = 32$), TS con = targeted-selection constructed wetlands ($n = 6$). Bars with different letters within the same plot were significantly different from each other (Kruskal-Wallis test with post-hoc Dunn comparisons, Benjamini-Hochberg adjustment; $\alpha = 0.05$). Canopy closure and CWD were only measured at natural and TS constructed sites.

Table 1-4. Mean (SE) values of habitat variables at natural (n = 10), TS constructed (n = 6), and RS constructed (n = 32) ridge-top wetlands in the Daniel Boone National Forest. Values in the same row with different letters are significantly different from each other (Kruskal-Wallis test with post-hoc Dunn comparisons, Benjamini-Hochberg adjustment; $\alpha = 0.05$). TS = targeted selection, RS = random selection, ORP = oxidation-reduction potential, DO % = percent saturation of dissolved O₂, CWD = coarse woody debris.

habitat variable	Natural (SE)	TS constructed (SE)	RS constructed (SE)	<i>p</i>
maximum depth (cm)	20.8 (3.0) ^a	54.3 (8.6) ^b	57.9 (4.2) ^b	< 0.001
water T (°C)	17.48 (0.93)	18.85 (1.18)	19.41 (0.75)	0.481
specific conductivity (mS/cm)	0.034 (0.002)	0.033 (0.004)	0.086 (0.022)	0.781
pH	4.40 (0.16) ^a	5.06 (0.23) ^{a, c}	5.42 (0.17) ^{b, c}	0.004
ORP (mV)	-37.0 (18.0)	-49.1 (9.7)	-62.7 (8.5)	0.264
DO (% saturation)	21.0 (4.0) ^a	48.5 (7.3) ^b	44.2 (5.7) ^b	0.027
littoral slope ($\Delta y/\Delta x$)	0.05 (0.01) ^a	0.16 (0.03) ^b	0.20 (0.02) ^b	< 0.001
canopy closure (%) ^ψ	88.7 (2.6) ^a	56.6 (8.4) ^b	-	0.009
CWD (m ³ /ha) ^ψ	167.6 (28.1)	117.3 (24.2)	-	0.428

and CWD volume. There were no significant differences between TS and RS constructed wetland groups for any habitat variables.

Model results

For all species evaluated with Tweedie regression models and for diversity modeling, multiple models had similar AIC_c values, and multiple models had $\Delta i \leq 2$ (Table 1-5). Therefore, I model-averaged the variables included in the top models (Table 1-6). Eastern newts were negatively associated with temperature and positively associated with ORP and littoral slope. Green frog larvae were negatively associated with conductivity. Spotted/Jefferson salamanders were positively associated with maximum depth and negatively associated with conductivity. Diversity was negatively associated with natural wetland type (Table 1-6).

For all species evaluated with binomial logistic regression, multiple models had similar AIC_c values and $\Delta_i \leq 2$ (Table 1-7). I model-averaged the variables included in the top models for each species (Table 1-8). Wood frog larvae were negatively associated with ORP, conductivity, RS constructed pond type, and DO. Marbled salamanders were negatively associated with constructed wetlands. Combined *Pseudacris* were positively associated with maximum depth. Cricket frogs were positively associated with littoral slope and DO. No habitat variables were significant in explaining presence of combined *Anaxyrus* species or four-toed salamanders.

Nonmetric Multidimensional Scaling

In the full NMDS, the 48 wetlands clustered in distinct groups of natural and constructed wetlands (Figure 1-4). Natural and Constructed groups differed primarily along NMDS axis 1, with natural wetlands occurring toward the negative end of the axis, and constructed wetlands occurring around zero and toward the positive end of the axis. RS and TS constructed wetlands overlapped and did not show distinct differences. NMDS species scores appeared to follow a hydroperiod gradient along NMDS axis 1, with ephemeral-wetland obligate amphibians occurring toward the negative end of axis 1, and permanent-wetland obligate amphibians occurring toward the positive end, with generalists in the middle. Species composition differed among the groups (PERMANOVA, $F_{2, 45} = 5.89$, $p < 0.001$). Post-hoc comparisons confirmed that species composition was significantly different between natural wetlands and

Table 1-5. Top Tweedie regression models ($\Delta_i < 2$) explaining the effects of habitat variables on CPUE (catch-per-unit-effort) of eastern newts, green frogs, and spotted/Jefferson salamanders; and on diversity (Shannon's H) at ridge-top wetlands in the Daniel Boone National Forest. Because newts and green frogs were rarely found at natural sites, only the constructed sites were used to inform these models. Spotted and Jefferson salamanders were distributed evenly across wetland types, so the full dataset was used to inform these models. Model weights (w_i) and relative likelihood values are also reported. Cond = conductivity, maxdep = maximum depth, slope = slope of the littoral zone, ORP = oxidation-reduction potential, T = water temperature, type = wetland type (targeted-selection constructed and random-selection constructed).

data	Response variable	model	K	log-likelihood	AIC _c	Δ_i	w_i	relative likelihood
cons	eastern newt	ORP, T	3	-45.587	100.387	0	0.1724	1
		ORP	2	-47.118	100.942	0.555	0.1306	0.758
		T, slope	3	-46.767	101.534	1.147	0.0972	0.564
		slope	2	-47.55	101.806	1.419	0.0848	0.492
		T	2	-47.574	101.855	1.468	0.0828	0.480
		intercept	1	-48.907	102.151	1.764	0.0714	0.414
cons	green frog	cond	2	-76.914	160.534	0	0.1627	1
		intercept	1	-78.1	160.542	0.008	0.1620	0.996
		type	3	-77.846	162.398	1.864	0.0641	0.394
		ORP	2	-77.855	162.416	1.882	0.0635	0.390
all	spotted/Jefferson salamander	maxdep	2	-125.473	257.491	0	0.3375	1
		cond, maxdep	3	-124.508	257.947	0.456	0.2687	0.796
		pH, maxdep	3	-125.232	259.394	1.903	0.1303	0.386
all	Shannon's H	type	4	-18.131	45.19	0	0.462	1
		type, littoral slope	5	-17.776	46.98	1.79	0.189	0.409

Table1-6. Model-averaged estimates and 85% confidence intervals of top variables explaining amphibian CPUE (catch-per-unit-effort) in ridge-top wetlands in the Daniel Boone National Forest. Values derived from Tweedie regression. Model-averaged variables are those included in models that had a $\Delta_i < 2$. Significant confidence intervals (those not overlapping zero) are indicated by '*'. T = water temperature, ORP = oxidation-reduction potential, slope = slope of littoral zone, cond = conductivity, maxdep = maximum depth, TS constructed = targeted-selection constructed wetland, RS constructed = random-selection constructed wetland.

data	Response variable	Parameter Name	Variable weight (w)	Model-averaged Estimate	Unconditional SE	85% Confidence Interval		
cons	eastern newt	T	0.391	-0.072	0.046	-0.138	-0.005*	
		ORP	0.363	0.009	0.005	0.002	0.016*	
		slope	0.225	2.998	2.028	0.078	5.918*	
cons	green frog	ORP	0.118	0.002	0.004	-0.003	0.007	
		cond	0.311	-2.770	1.870	-5.463	-0.077*	
		type	0.113					
		TS constructed		-	-	0.000	0.000	
		RS constructed		0.311	0.428	-0.305	0.928	
all	spotted/Jefferson salamander	maxdep	0.974	0.034	0.008	0.022	0.045*	
		cond	0.454	-3.920	2.537	-7.573	-0.267*	
		pH	0.317	0.368	0.320	-0.093	0.829	
all	Shannon's H	type	0.997					
		natural		-1.070	0.264	-1.451	-0.690*	
		TS constructed		-	-	0.000	0.000	
		RS constructed		-0.170	0.194	-0.450	0.109	
		slope	0.231	0.699	0.819	-0.479	1.876	

Table 1-7. Top Binomial logistic regression models ($\Delta_i < 2$) explaining the effects of habitat variables on CPUE. Model weights (w_i) and relative likelihood values are also reported. Cond = conductivity, DO = % saturation dissolved O₂, type = wetland type (natural, RS constructed, TS constructed), maxdep = maximum depth, slope = slope of littoral zone, type = wetland type (natural, targeted-selection constructed, or random-selection constructed), temperature = water temperature, global lacking slope = model contains pH, DO, cond, maxdep, ORP, water temperature, and type. ϕ 'type' variable for marbled salamanders contained two levels, natural and constructed.

Species	Model	K	-2 log			w_i	relative likelihood
			likelihood	AICc	Δ_i		
wood frog	pH, DO, cond, maxdep	5	36.888	48.28	0	0.225	1
	type	4	39.879	48.79	0.51	0.175	0.777
	global lacking slope	10	23.73	49.52	1.24	0.122	0.539
	pH, DO, ORP, cond	6	35.924	49.92	1.64	0.099	0.440
marbled sal. ϕ	type	3	42.258	51.17	0	0.175	1
American/ Fowler's toad	cond	2	44.083	48.34	0	0.194	1
	cond, maxdep	3	43.507	50.04	1.70	0.083	0.428
	slope	2	45.885	50.14	1.80	0.079	0.406
cricket frog	pH, DO, cond, slope	5	25.766	37.16	0	0.243	1
	DO, pH	3	31.283	37.82	0.65	0.175	0.721
	pH, DO, cond, maxdep	5	27.537	38.93	1.77	0.100	0.413
	DO	2	34.89	39.15	1.99	0.090	0.370
spring peeper/ mtn. chorus frog	maxdep	2	57.087	61.35	0.00	0.375	1
four-toed salamander	cond, maxdep	3	55.517	62.05	0.70	0.264	0.704
	DO, pH	3	45.373	51.91	0	0.180	1
salamander	DO	2	48.093	52.35	0.45	0.144	0.800
	pH	2	48.597	52.86	0.95	0.112	0.621
	ORP, DO	3	46.626	53.16	1.25	0.096	0.534
	cond, DO, pH	4	44.911	53.82	1.91	0.069	0.384

Table 1-8. Model-averaged estimates and 85% confidence intervals of top variables explaining amphibian CPUE (catch-per-unit-effort) at ridge-top wetlands in the Daniel Boone National Forest. Values derived from binomial logistic regression. Model-averaged variables are those included in models that had a $\Delta i < 2$. Significant confidence intervals (those not overlapping zero) are indicated by an *. DO = % saturation of dissolved O₂, cond = conductivity, T = water temperature, ORP = oxidation-reduction potential, maxdep = maximum depth, slope = slope of littoral zone, type = wetland type (natural, targeted-selection (TS) constructed, random-selection (RS) constructed). ^ϕ 'type' variable for marbled salamanders contained only two levels: natural and constructed.

Response variable	Parameter Name	Variable weight (w)	Model-average Estimate	Unconditional SE	85% Confidence Interval	
wood frog	DO	0.70	-0.09	0.05	-0.16	-0.02*
	pH	0.69	-0.19	0.88	-1.46	1.07
	cond	0.67	-38.85	23.54	-72.75	-4.96*
	type	0.41				
	Natural		0.00	0.00	0.00	0.00
	TS constructed		-2.37	1.99	-5.24	0.49
	RS constructed		-3.33	1.56	-5.57	-1.08*
	T	0.38	0.19	0.37	-0.34	0.73
marbled salamander ^ϕ	ORP	0.38	-0.05	0.03	-0.09	-0.01*
	maxdep	0.29	-0.03	0.03	-0.07	0.01
	type	0.33				
	Natural		0.00	0.00	0.00	0.00
	Constructed		-2.03	0.92	-3.35	-0.70*
American/ Fowler's toad	conductivity	0.45	-3.84	3.11	-46.76	6.46
	max depth	0.20	0.00	0.02	-0.02	0.03
	littoral slope	0.16	-4.01	4.61	-10.66	2.63
cricket frog	DO	0.72	0.05	0.03	0.01	0.08*
	pH	0.66	1.09	0.93	-0.25	2.44
	cond	0.46	-6.19	8.66	-18.67	6.28
	slope	0.33	17.57	11.28	1.32	33.81*
	maxdep	0.22	0.04	0.03	0.00	0.09
spring peeper/ mtn chorus frog	maxdep	0.83	0.03	0.01	0.01	0.06*
	cond	0.33	-4.33	3.80	-9.80	1.14
four-toed salamander	DO	0.56	-0.03	0.02	-0.06	0.00
	pH	0.48	-0.69	0.48	-1.38	0.01
	cond	0.21	-6.49	10.50	-21.61	8.63
	ORP	0.18	0.01	0.01	0.00	0.02

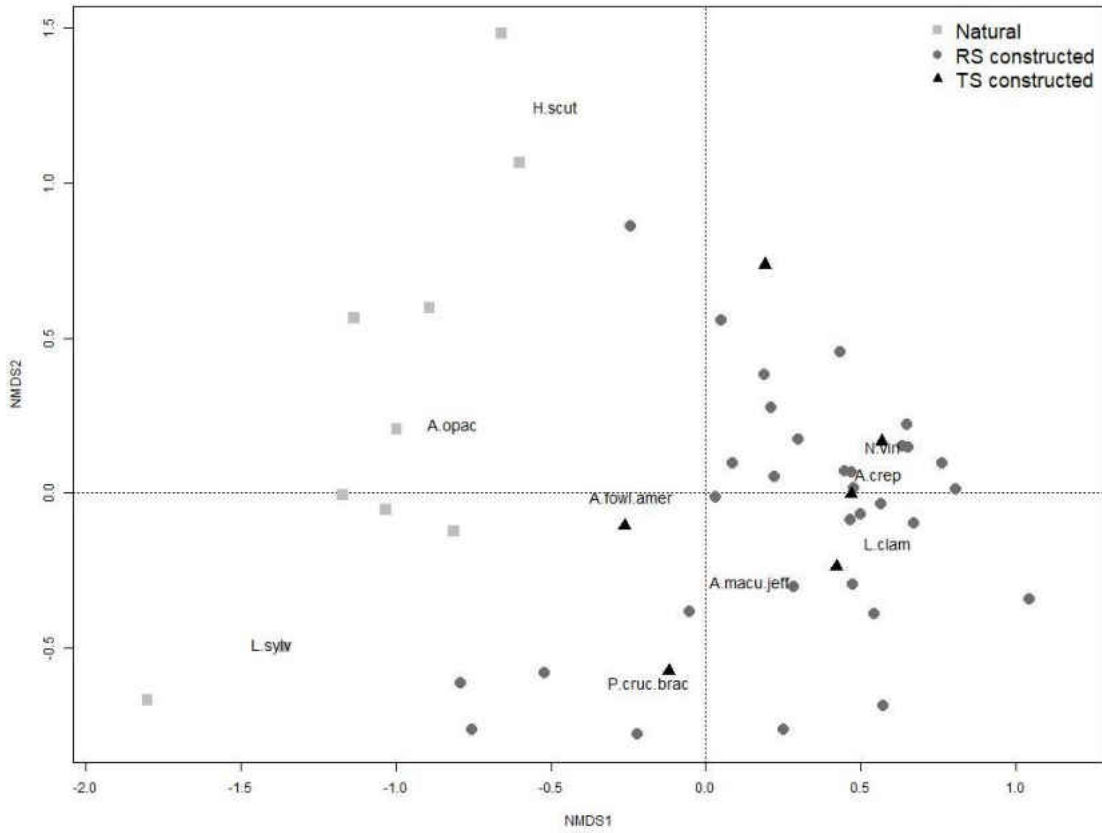


Figure 1-4. Nonmetric multidimensional scaling (NMDS) biplot of ridge-top wetland sites and amphibian community composition in the Daniel Boone National Forest. Species labels are the first letter of the genus and first four letters of the species (if taxa were grouped, both species are indicated). Dimensions = 3; stress = 0.11.

both constructed groups, but that community composition did not differ significantly between constructed groups (Table 1-9).

Discussion

Hydroperiod plays a major role in amphibian community composition in upland-embedded wetlands. Permanent wetlands host newts and large ranid frogs, while ephemeral wetlands exclude these species and provide habitat for wood frogs, marbled salamanders, and other species adapted for shorter hydroperiods. Wood frogs are negatively impacted by high abundance of newts and large ranids (Boone et al., 2004; Jennette, 2010; Kross & Richter, 2016; Vasconcelos & Calhoun, 2006). Lower richness and diversity at natural ephemeral wetlands is a function of hydroperiod (Babbitt et al., 2003) and is not a sign of low ecological value. Many species found at permanent constructed wetlands are cosmopolitan and/or typical of lowland wetland habitat such as marshes, streams, and ponds. Natural ephemeral wetland sites are vital to survival of ephemeral wetland-obligate species, especially in areas where

Table 1-9. Post-hoc contrasts (Bonferroni adjustment, $\alpha_{\text{adjusted}} = 0.017$) of PERMANOVA comparisons of amphibian community composition among three groups of ridge-top wetlands in the Daniel Boone National Forest. Nat = natural wetlands, TS con= targeted-selection constructed wetlands, RS con = random-selection constructed wetlands. Significance indicated by *.

contrast	df _{error}	F	p
natural/ TS constructed	14	5.67	0.001*
natural/ RS constructed	40	10.62	0.001*
RS constructed/ TS constructed	36	0.42	0.920

constructed wetlands have introduced novel hydroperiods and high concentrations of predators.

Species associations

Constructed wetlands consistently failed to recruit wood frogs in numbers comparable to those of natural ridge-top wetlands in the DBNF, even in some constructed wetlands where 40 or more clutches were deposited, similar to the findings of Kross & Richter (2016). The majority of constructed wetlands did not support any wood frog larvae, and when wood frogs were present at constructed wetlands, their numbers were usually much lower than at natural wetlands. Wood frog eggs are abundant and easily accessible to predatory green frogs and eastern newts, which almost exclusively inhabit permanent wetlands. Constructed wetlands where I found wood frog larvae successfully developing had distinct characteristics that set them apart from typical constructed wetlands: these wetlands either dried completely, had portions that dried, had shallow areas with lots of vegetative cover to provide refuge from predation, or lacked newts and/or large ranids. Wood frogs' negative association with dissolved oxygen content is likely a function of their habitat requirements, as natural and ephemeral wetlands have been found to have lower dissolved oxygen levels than constructed wetlands and permanent wetlands (Babbitt et al., 2003; Korfel et al., 2010).

Although my methods did not account for detection probability, it is clear that wood frogs do not experience equal reproductive success and recruitment in

constructed ridge-top wetlands as in natural wetlands. Under natural conditions, wood frog larvae are conspicuous due to their abundance (Denton & Richter, 2013; Drayer & Richter, 2016), and if wood frog larvae were not present in conspicuous quantities at a site, it is likely that they were not present in large enough numbers for significant reproductive and metamorphic success at that site. As an r-selected species, wood frogs rely on production of large numbers of eggs and larvae to sustain population levels (Berven, 1990). Wood frogs and other amphibians that breed in ephemeral wetlands have highly variable reproductive success from year to year, and juvenile recruitment can fluctuate by more than two orders of magnitude from one year to the next (Berven, 1990; Pechmann et al., 1991; Richter et al. 2003). Thus, it is possible that wood frog larvae could be present at other constructed ridge-top wetlands in detectable numbers during other years. However, surveys of targeted constructed wetlands in 2010, 2013, and 2014 also revealed low abundance or absence of wood frog larvae compared to high abundance of wood frog larvae at natural wetlands (Denton & Richter, 2013; Drayer & Richter, 2016; Kross & Richter, 2016).

My observations of marbled salamander presence and abundance fit their life history. Marbled salamanders require basins that dry partially or completely during the late summer and fall, and fill over the late winter and spring (Petranka & Petranka, 1981). Therefore, the permanent hydroperiod of most constructed wetlands is likely not conducive to successful hatching and larval development. In addition to hydroperiod, canopy closure and CWD volume appeared to play a role in marbled

salamander presence at a site; however, I did not measure these variables at enough sites to draw broad conclusions. Thus, this is an area for future research. Female selection of oviposition sites in the wetland basin is of crucial importance to the survival of the offspring, as eggs placed in the deepest part of the basin may hatch prematurely, and eggs placed near the pool edges may freeze or never become inundated (Jackson et al., 1989; Petranka & Petranka, 1981). Permanent wetlands were historically absent from the ridge-top system in the DBNF, and it is unknown whether marbled salamanders have adapted to selecting oviposition sites in permanent constructed wetlands.

Many constructed ridge-top wetlands serve as population sinks for wood frogs (Kross & Richter, 2016). It is unknown whether they also serve as sinks for marbled salamanders. Marbled salamanders are currently widespread and common in the eastern US (Hammerson, 2004). However, many of the seasonal wetlands and intact forests that marbled salamanders rely on have been destroyed and fragmented, and it is likely that marbled salamander populations will undergo decline (Hammerson, 2004; Scott, 2005). Restoring constructed wetlands to a more natural function is important to maintain and improve breeding habitat for ephemeral wetland-obligate species.

Observed patterns of eastern newt and green frog abundance can largely be explained by life history. Adult newts are aquatic and are most common in permanent wetlands (Harding & Holman, 1992). Littoral slope, which is closely linked with maximum depth and hydroperiod, was positively associated with newt abundance.

Newts' negative association with water temperature is likely tied to water depth and hydroperiod as well. Although newts were positively associated with ORP, the effect size was small. It is possible that ORP is correlated with other habitat variables that I did not measure, such as presence of dissolved metals or salts, or prevalence of pathogens (Suslow, 2004), that may affect newt abundance. Green frog larvae take up to two years to metamorphose (Harding & Holman, 1992), and thus seldom survive to metamorphosis in ephemeral wetlands. The two natural sites known to have green frog larvae in the Cumberland District dry occasionally but not annually (Richter, pers. comm., 2016).

Spotted and Jefferson salamanders appear to be able to reproduce, hatch, and survive the larval stage in constructed wetlands just as well as, if not better than, in natural sites. This is likely due to the thick jelly layer of the clutches, which makes their eggs difficult for newts and green frog larvae to prey upon (Gibbs, 2007; Harding & Holman, 1992), and larval behavior. Greater water depth at constructed wetlands also provides more volume for eggs and larvae to occupy. Despite higher larval abundance at constructed sites, these sites still may not provide optimal habitat, as ambystomatid salamanders also rely on high canopy closure, habitat connectivity, and coarse woody debris, which provide suitable local conditions and migration corridors (deMaynadier & Hunter, 1999; Rubbo & Kiesecker, 2005). Despite these potential detriments, spotted and Jefferson salamanders appear to maintain viable populations in both

constructed and natural wetland types (Denton & Richter, 2013; Drayer & Richter, 2016; Petranka et al., 2003).

Pseudacris spp., cricket frogs, four-toed salamanders, and toads displayed few clear patterns explaining their presence in wetlands. *Pseudacris* spp were positively associated with depth, and egg morphology likely protects *P. crucifer* from predation by newts and green frogs in permanent wetlands, as their eggs are small and are laid singly or in small groups (Harding & Holman, 1992) making them difficult to prey upon. The eggs of *P. brachyphona* are laid in clutches of 10–50 eggs attached to vegetation (Green, 1938), and it is unknown whether green frog or newt predation impacts *P. brachyphona*. Four-toed salamander presence and abundance is likely more dependent on presence and quality of moss habitat than wetland type, hydroperiod, or presence of newt/ranid predators (Blanchard, 1923; King, 2012). Cricket frogs were only found at constructed sites and were grouped close to permanent-wetland obligate species in the NMDS, but were not found at enough sites to draw definitive conclusions. Cricket frogs use permanent wetlands for breeding, but are susceptible to predation by bullfrogs (Lannoo, 1998). It is unknown whether newts or green frogs prey on cricket frogs. American and Fowler’s toads are known to be generalists (Hecnar & M’Closkey, 1997), although Petranka et al. (1994) found that toads avoid depositing eggs in pools inhabited by wood frog larvae. This interaction potentially

contributes to the non-significant difference in larval toad abundance between natural and RS constructed wetlands.

Wood frogs, green frogs, and spotted/Jefferson salamanders were all negatively associated with conductivity in model averaging. This supports the findings of McTaggart (2016) who found a negative association between green frogs and conductivity. However, other research has shown that conductivity of 0.5 mS/cm did not significantly impact survival of larval green frogs or wood frogs (Karraker, 2007; Karraker, Gibbs, & Vonesh, 2008). Spotted salamanders have been shown to be more sensitive to conductivity than wood and green frogs, suffering significant mortality at 0.5 mS/cm (Karraker, Gibbs, & Vonesh, 2008).

These perceived negative associations may be due to a combination of actual conductivity effects and site associations. Wood frogs' perceived negative association with conductivity may be due to differences in conductivity between constructed and natural sites (RS constructed sites had higher conductivity than naturals, although this difference was not significant). Two constructed sites had conductivity levels higher than the recommended amphibian husbandry maximum conductivity value of 0.24 mS/cm (Poole & Grow, 2012), and it is possible that low green frog and spotted/Jefferson salamander abundances at these sites contributed to the negative association. Ridge-top wetlands in the DBNF are not typically impacted by road salt or other anthropogenic sources of dissolved solids, and conductivity in this system is mostly a function of local geology and solute accumulation due to lack of outflow.

With the exception of a few constructed sites with high conductivity values, it is unlikely that conductivity significantly impacts amphibian presence and abundance in the ridge-top system at this time.

Comparison with previous research

Constructed ridge-top wetlands in the Cumberland District of the Daniel Boone National Forest do not have amphibian communities or habitat characteristics that are ecologically equivalent to those of natural ridge-top wetlands in the District. Overall, my research supported previous findings in the ridge-top wetland system that wood frogs and marbled salamanders either do not use constructed wetlands or seldom survive to metamorphosis in these sites, that eastern newts and green frogs are found nearly exclusively in constructed wetlands, and that spotted/Jefferson salamanders survive to the larval stage successfully in both wetland types but are found in greater abundance in constructed wetlands (Denton & Richter, 2013; Drayer & Richter, 2016; Kross & Richter, 2016). Also similar to previous research, four-toed salamanders were found in low abundance in both natural and constructed wetlands, and no clear pattern was evident regarding abundance of toads, *Pseudacris* spp., and cricket frogs (Denton & Richter, 2013; Drayer & Richter, 2016).

Contrary to previous research in this system which found no wood frog larvae at constructed sites (Denton & Richter, 2013; Kross & Richter, 2016), I did find wood frog larvae in a small number of constructed wetlands. However, these constructed sites contained wood frog larvae in lower abundance than natural wetlands and were

the exception rather than the rule. Differences in wood frog presence and abundance compared to previous years is likely due to differences in sites sampled as well as natural variation in wood frog reproduction from year to year (Berven, 1990).

There were also differences between this research and findings from the London District of the DBNF, which has far fewer constructed wetlands than the Cumberland District. McTaggart (2016) found that *Pseudacris* spp. were positively associated with natural wetlands in the London District, whereas I found the difference in *Pseudacris* spp. abundance was not significant among wetland types. Additionally, wood frogs coexisted with large ranids and newts at both natural and constructed wetlands in the London District (McTaggart, 2016). Differences in amphibian communities between the London and Cumberland Districts is likely due to a combination of lower constructed wetland density in the London District and differences in natural wetland size and hydroperiod between the districts. Natural wetlands in the London District tend to be larger than in the Cumberland and some have semipermanent hydroperiods (McTaggart, 2016). Semi-permanent hydrology of natural wetland sites in the London District may mean that newts and large ranids were historically present at these sites, which may have allowed wood frogs to adapt to avoid predation in order to coexist. The overall abundance of newts and large ranid larvae is much lower in the London District, which also reduces predation pressure and allows coexistence of these species with wood frogs.

Amphibian impacts and concerns

Disturbed ecosystems often have species compositions that differ from those of undisturbed systems (Fuller et al., 2011; MacDougall & Turkington, 2005). According to Dix et al. (2010), a key source of anthropogenic forest disturbance arises from management efforts intended to mitigate the effects of prior disturbance. In the case of the ridge-top wetland system, wetland construction undertaken to improve habitat for game species has negatively affected the historical amphibian species composition of the ridge-tops by providing habitat that facilitates the introduction of permanent-wetland-obligate newts and large ranids. Introduction of these species is an amphibian health concern because ranavirus and *Batrachochytrium dendrobatidis* fungus (Bd) are emerging amphibian diseases that have been documented in Kentucky wetlands (McTaggart, 2016; Richter et al., 2013; Stasiak et al., unpubl. data). There is concern that eastern newts and green frogs serve as reservoirs for these diseases (Brunner et al., 2004; Daszak et al., 2004; Gahl et al., 2012; Richter et al., 2013).

Amphibian populations are experiencing global declines due to climate change, disease, pollution, habitat destruction, and other factors (Houlahan et al., 2000; Nowakowski et al., 2017; Scheele et al., 2017; Waldman & Tocher, 1998). Habitat loss in the form of wetland destruction has been rampant across the US, with $\geq 53\%$ of wetlands lost in the conterminous U.S. since 1780 (Dahl, 1990), and Kentucky alone experiencing more than 81% loss in total wetland area since 1780 (Dahl, 1990; Dahl, 2000). The percent of ephemeral wetlands that have been destroyed is unknown

because seasonal water bodies are not always recognized as wetlands for assessment purposes (Cowardin et al., 1979; Dahl, 2000). Further loss of ephemeral wetlands in eastern North America will likely occur due to global climate change. Under some models, climate-change-induced reduction in late spring and summer precipitation combined with increased evapotranspiration rates is expected to shorten hydroperiods of ephemeral wetlands, making them unsuitable for amphibian larval survival and metamorphosis (Brooks, 2009; Greenberg et al., 2015). Preserving wetlands with a range of hydroperiods is important to provide refugia for species under varying climatic conditions (Lowe, Castley, & Hero, 2014). With climate change and other anthropogenic disturbances, continued monitoring of amphibian populations is necessary to detect declines of sensitive species and potential invasions of tolerant and historically-absent species.

Introduction

Upland-embedded wetlands (UEWs), also referred to in the literature as geographically-isolated wetlands, are depressional wetlands surrounded completely by uplands. These wetlands receive water via precipitation, runoff, and/or groundwater and subsurface connections (Mushet et al., 2015; Tiner, 2003). UEWs in the US support many at-risk plant species and communities (Comer et al., 2005). This wetland type has been constructed in many areas of the US for mitigation and conservation purposes (Biebighauser, 2003; Calhoun et al., 2014). Numerous studies have documented the differences in amphibian communities between natural and constructed UEWs (e.g. Calhoun et al., 2014; Denton & Richter, 2013; Drayer & Richter, 2016; King, 2012; Kross & Richter, 2016). However, the majority of studies regarding plant communities at constructed wetlands focus on large and/or lowland sites (e.g. Balcombe et al., 2005; Moore et al., 1999; Moreno-Mateos et al., 2012; Thompson, Miller, & Culley, 2007; Zedler & Callaway, 1999), and relatively little literature exists regarding vegetation comparisons of small (< 0.1 ha) natural and constructed UEWs (e.g. Ciccotelli et al., 2011; Hartzell, Bidwell, & Davis, 2007; Vasconcelos & Calhoun, 2006). Thus, many questions remain about whether the structure and ecological function of vegetation at small constructed UEWs adequately approximates that of their naturally-occurring counterparts.

Factors including, but not limited to, disturbance, canopy closure, hydrologic regime, and soil characteristics influence wetland plant diversity and community composition (Billups & Burke, 1999; Burke & Eisenbies, 2000; Cronk & Fennessy, 2001; Cutko & Rawinski, 2007). Low-to-moderate levels of disturbance are important to maintain species diversity in many systems (Petraitis et al., 1989; Sousa, 1984); however, anthropogenic disturbance can negatively impact plant communities by disrupting native assemblages and exacerbating invasion by aggressive native and nonnative species (MacDougall & Turkington, 2005). In natural UEWs, one of the defining sources of disturbance is seasonal flooding. In constructed wetlands, disturbance arises from excavation and/or dam construction, soil compaction, permanent flooding, and removal of trees and other vegetation (Biebighauser, 2003).

Although plant communities at constructed wetland sites sometimes come to emulate natural communities over time (National Research Council, 1992), plant communities in constructed wetlands are often dissimilar to those of natural wetlands, even many decades after construction (Balcombe et al., 2005; Moreno-Mateos et al., 2012; Zedler & Callaway, 1999). Less-disturbed systems, early-successional communities, and sites close to natural wetland areas are more rapidly restored to natural ecological function than severely disturbed, isolated, and/or climax communities (National Research Council, 1992). Although plant diversity is sometimes higher at constructed wetland sites than at natural wetlands, constructed wetlands

typically have more nonnative species and lower average ecological conservatism (Balcombe et al., 2005).

Measures of ecological conservatism and floristic quality are useful in assessing wetland condition, disturbance, and habitat quality (Andreas, Mack, & McCormac, 2004; DeBerry & Perry, 2015; Gianopulos, 2014; Miller & Wardrop, 2006). Ecological conservatism is represented through Coefficients of Conservatism (C), values which are assigned *a priori* on a scale of 0–10 based on vegetative species' tolerance of disturbance and specificity of habitat requirements (Andreas et al., 2004; Gianopulos, 2014; Taft et al., 1997). Mean C reflects vegetative quality and site disturbance but is not recommended as the sole measure of vegetative quality at a site (Miller & Wardrop, 2006; Taft et al., 1997). The Floristic Quality Assessment Index (FQAI), based on \bar{C} and richness of native plant species (Swink & Wilhelm, 1979, 1994), is commonly used to assess wetland condition and floristic quality (DeBerry & Perry, 2015; Stefanik & Mitsch, 2012). However, although FQAI scores are correlated with quality and disturbance, these values do not adequately provide for comparison among sites where species richness differs greatly (Miller & Wardrop, 2006). FQAI also does not take into account presence of nonnative species, because nonnatives are not assigned C values. The Adjusted Floristic Quality Index (*I'*) is recommended as an improved version of FQAI to better compare floristic quality between sites of differing richness and to take nonnative species into account (Miller & Wardrop, 2006).

Wetland vegetation affects other wetland organisms. Variations in macro- and micro-topography, including tree mounds, moss clumps, and tussock- and hummock-forming vegetation encourage diversity of both plant and animal communities (Calhoun et al., 2014; USDA NRCS, 2008; Vivian-Smith, 1997). Shrub cover and underwater vegetation provide sites for amphibian oviposition (Egan & Paton, 2004). Coarse woody debris provides cover and feeding grounds for amphibian species (Maser et al., 1979). Many pool-breeding amphibians require vegetated upland habitat to support their terrestrial life stage (Semlitsch, 1998). Vegetated buffer zones can help to mitigate the effects of habitat loss on amphibians (Castelle, Johnson, & Conolly, 1994; Houlahan & Findlay, 2004) .

Woodland vernal pools are one of the wetland types included in the 'upland-embedded' category (Tiner et al., 2002). Vernal pools are wetlands that have ephemeral (seasonal to semi-permanent) hydroperiods and lack fish. Due to these unique conditions they provide habitat for many species of plants, amphibians, and aquatic invertebrates (Calhoun & DeMaynadier, 2001; Calhoun et al., 2014). Vernal pools in the eastern US are not characterized by any particular plant community. Rather, vegetative structure and composition are influenced by biogeography, hydroperiod, basin size, canopy closure, and substrate (Calhoun & DeMaynadier, 2001; Cutko & Rawinski, 2007). Few vernal pool obligate plant species occur in the eastern US (Calhoun et al., 2014; Cutko & Rawinski, 2007).

There are currently over 6 million ha of UEWs in the US, comprising about 8.3 million individual wetland sites and 16% of the total freshwater wetland habitat (Lane & D'Amico, 2016). In Kentucky, there are about 46,500 ha of UEWs, comprising over 180,000 individual wetlands and making up 13% of the total freshwater wetland area (Lane & D'Amico, 2016). Kentucky has lost over 80% of its wetlands since European colonization, but the loss of UEW habitat is unknown (Dahl, 1990; Dahl, 2000). Wetland construction and restoration are important parts of conservation, and it is important to better understand plant communities at constructed wetlands to improve wetland construction techniques and management of constructed sites for conservative species.

In the Daniel Boone National Forest, small ephemeral UEWs occur naturally at low density on ridge-tops, and hundreds of UEWs have been constructed to create water sources for deer, turkeys, and bats, greatly increasing wetland density on the ridge-tops (Brown & Richter, 2012). Constructed wetlands were often built near forest roads or in the roadbed of decommissioned logging roads, which are potential sources of invasive plant introduction (Buckley et al., 2003). Some wetlands have been impacted by nearby logging operations, and some are located in maintained forest openings that are occasionally mowed. However, most constructed wetlands have suffered relatively little anthropogenic disturbance after the initial construction event.

Research in the DBNF ridge-top system has revealed that constructed ridge-top wetlands have longer hydroperiods, are deeper, have less canopy closure, and host

different amphibian communities than their natural counterparts (Denton & Richter, 2013; Drayer & Richter, 2016; Kross & Richter, 2016; McTaggart, 2016; thesis chapter 1); however, little is currently known about the plant assemblages at these sites. Some constructed wetland sites were vegetated as part of the construction process, but many were not, and site-specific records are not available (T. Biebighauser, personal communication). There have been no comparisons to date of plant communities at natural and constructed ridgetop wetlands in the DBNF. My objective was to evaluate plant communities to determine whether there were differences in vascular species richness, nonnative species richness, mean coefficients of conservatism, floristic quality, and overall vegetative community composition between natural and constructed wetlands.

Materials and Methods

Study sites

Vegetative study sites consisted of ten natural and ten constructed UEWs in the Cumberland District of the DBNF (Table 2-1, Figure 2-1). Wetlands were located in Mixed Mesophytic forest type (Jones, 2005) in the Western Allegheny Plateau Ecoregion (U.S. Environmental Protection Agency, 2013) and the Allegheny Plateau Physiographic Province (Jones, 2005). All wetlands were classified as palustrine forested wetlands

Table 2-1. Names, abbreviations, and coordinates of natural and constructed wetland study sites in the Cumberland District of the Daniel Boone National Forest.

site	abbreviation	Latitude	Longitude	USGS quad
Elk Lick Natural	ELN	38.3309	-83.3628	Soldier
Elk Lick Constructed	ELC	38.32934	-83.36508	Soldier
Gas Line Natural	GLN	38.28457	-83.36876	Soldier
Gas Line Constructed	GLC	38.28543	-83.37197	Soldier
Big Perry Natural	BPN	38.24559	-83.36975	Haldeman
Big Perry Pine (constructed)	BPP	38.25257	-83.37874	Haldeman
977 Natural	977N	38.24027	-83.39843	Morehead
977 Constructed	977C	38.2408	-83.39998	Morehead
Jones Ridge Natural	JRN	38.08853	-83.35832	Wrigley
Jones Ridge Constructed	JRC	38.09244	-83.3548	Wrigley
High Energy Natural	HEN	38.04227	-83.3799	Bangor
High Energy Constructed	HEC	38.04296	-83.38072	Bangor
Dark Cave 2 Natural	DC2	38.01191	-83.55956	Salt Lick
Dark Cave 4 Natural	DC4	38.01688	-83.5575	Salt Lick
Dark Cave 5 Natural	DC5	38.00941	-83.55719	Salt Lick
Dark Cave 6 Natural	DC6	38.00846	-83.55291	Salt Lick
3-02 Constructed	3-02	38.02155	-83.57388	Salt Lick
3-03 Constructed	3-03	38.03461	-83.55899	Salt Lick
3-08 Constructed	3-08	38.09392	-83.58762	Salt Lick
3-10 Constructed	3-10	38.05831	-83.5473	Salt Lick

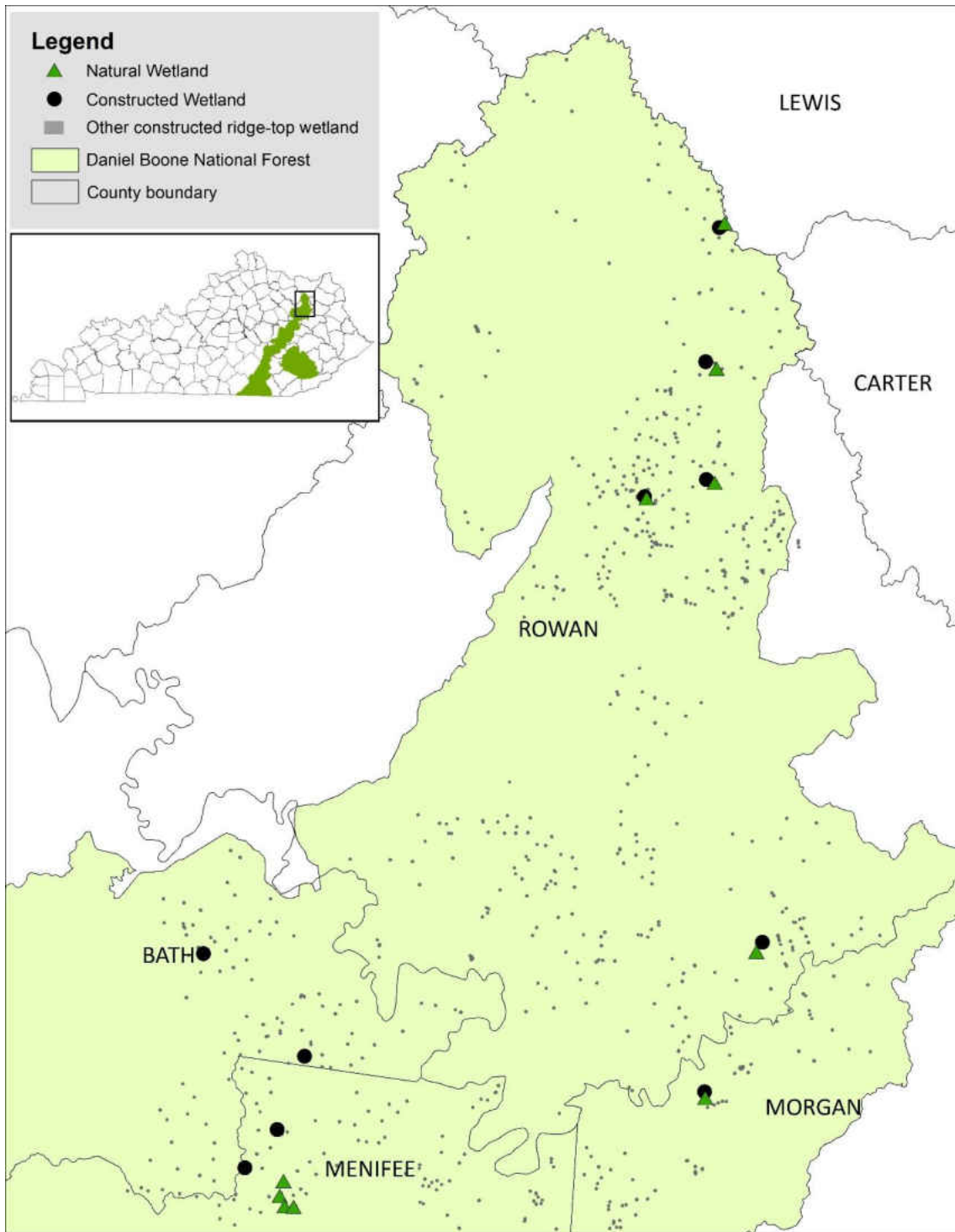


Figure 2-1. Locations of natural (n = 10) and constructed (n = 10) upland-embedded wetlands where vegetative surveys took place during the 2016 field season. Wetlands were located in the Cumberland District of the Daniel Boone National Forest, in the area of Kentucky indicated in the inset map.

according to Cowardin et al. (1979). All were less than 0.1 ha in size and located in deciduous forest on ridge-tops between 285 and 405 m in elevation. Six natural sites were paired with and located within 1 km of a constructed site. Four natural sites had no constructed sites within a 1 km radius, so four additional constructed sites were randomly selected from constructed sites of similar latitude. Six constructed wetlands were known to have permanent hydrology, (Denton & Richter, 2013; Drayer & Richter, 2016; Kross & Richter, 2016), and three constructed wetlands were suspected to be Permanent based on water depth, amphibian community, and landscape placement (see chapter 1). One constructed site and all ten natural sites were ephemeral to semi-permanent, drying annually or biennially.

Plant surveys

I surveyed plant plots between Jun 6 and 20, 2016 using a modified relevé method to survey the vascular plant understory (< 2 m tall) community at each of the 20 wetlands. I placed plots based on the vegetation present: I divided the pool and surrounding pool-influenced area into visually homogenous zones, and set up a survey plot in each zone, making sure that the plot fit within the watershed of the wetland site (Figure 2-2). Plots ranged in size from 3 x 4 meters to 5 x 5 meters (Barbour et al., 2005). Constructed wetlands were often situated within high berms or dams, resulting a very small watershed, which necessitated small and/or narrow plots in some cases. In the absence of multiple distinct vegetative zones, I surveyed five plots per pool, one at each bank in the cardinal directions, and one in the center of the pool.

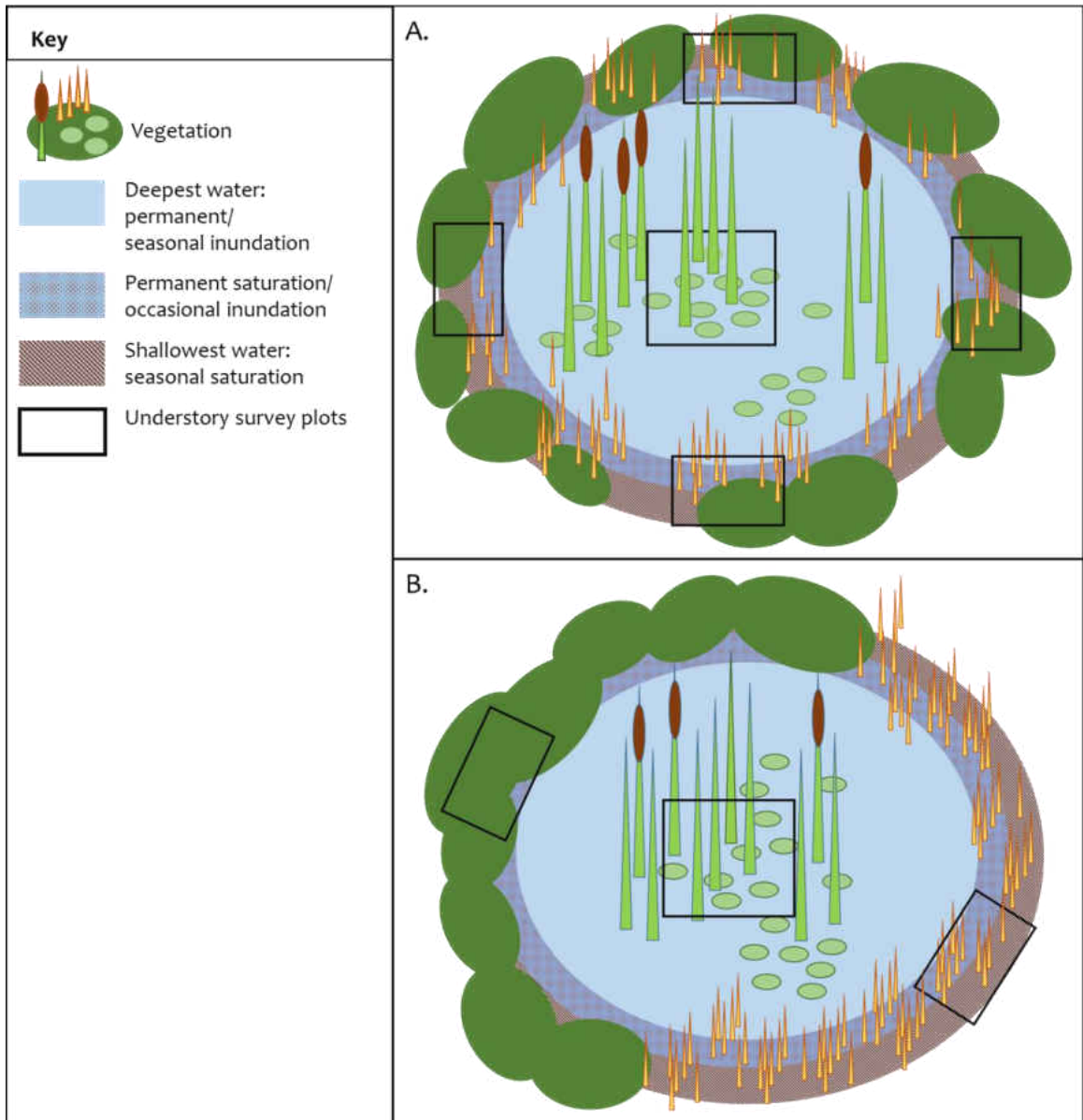


Figure 2-2. Placement of understory vegetation plots at natural and constructed wetland sites in the Cumberland District of the Daniel Boone National Forest. Plots were placed based on vegetative patterns. A. If vegetation was relatively homogenous around the entire wetland, plots were placed at the wetland edges in saturated/temporarily inundated areas in each of the cardinal directions and in the wetland center. B. If distinct zones of vegetation were apparent (e.g. one side of the wetland edge dominated by woody shrubs and the other by emergent graminoids), then a plot was placed in each zone, as well as in the wetland center.

I identified plants in the field using Jones (2005), and unidentified specimens were collected and identified in the lab using Jones (2005), Gleason (1958), Weakley (2015), and Flora of North America Editorial Committee (1993+). Taxonomy is based on that of Jones (2005). I consulted botanists for help with identification as needed. I collected voucher specimens of most plant species, including flowers/fruits when possible. I did not collect species that were present in low abundance (less than 20 herbaceous stems present) or irritants such as poison ivy. I found one endangered species, American chestnut (*Castanea dentata* [Marshall] Borkh.), at one wetland site. This species was not collected due to its endangered status. I pressed and dried vouchers and deposited these in the Ronald L. Jones Herbarium (Herbarium Code EKY) at Eastern Kentucky University. Plants that could not be identified to the species level due to lack of flowers/fruits were identified to genus and included in richness calculations but excluded from further analyses (Flinn et al., 2008).

Based on visual cover estimation, I assigned a cover class to all floating, emergent, and terrestrial vascular species in the plot understory using the Braun-Blanquet cover/abundance scale (Minnesota Department of Natural Resources, 2013; Mueller-Dombois & Ellenberg, 1974) (Table 2-2), which uses the following classes: 'OP'= species was located outside plot, but within 0.5 m of the plot boundary. 'R'= 1-3 individuals in plot. '+'= several individuals, but less than 1% cover, 1= $1 < c \leq 5\%$, 2= $5 < c \leq 25\%$, 3= $25 < c \leq 50\%$, 4= $50 < c \leq 75\%$, and 5= $c > 75\%$. Submerged aquatic vegetation was not recorded. I also performed a visual survey of each wetland and

Table 2-2. Braun-Blanquet cover/abundance scores, corresponding ordinal values for NMDS analysis, and cover value estimate.

Braun-Blanquet cover/abundance score	Ordinal value	Cover value
r	1	A few individuals
+	2	Several individuals, but less than 1% cover
1	3	1-5% cover
2	4	5-25%
3	5	25-50%
4	6	50-75%
5	7	75-100%

identified any species that occurred within five meters of the wetted pool area that were not included in the plots, as well as midstory and canopy species. I revisited each wetland between 23 Aug and 5 Sep 2016 and performed a second round of visual surveys to capture presence of late-blooming species that occurred in the maximum wetted area of the pool and within five meters of the wetland boundary.

Habitat variables and water parameters

I measured percent concentration of dissolved oxygen (DO), pH, specific conductivity, littoral slope, and canopy closure at each site between 6 and 20 June 2016. I used a spherical densiometer to measure canopy closure, taking a measurement in each cardinal direction by counting the number of closed dots in the densiometer, converting this to a percentage, and averaging the four measurements to obtain canopy closure for that wetland. I measured Coarse Woody Debris (CWD) along four 50-m linear transects extending perpendicular from the pool boundaries in each cardinal direction (Denton & Richter, 2013; Waddell, 2002; Warren & Olsen,

1964). For any piece of CWD ≥ 10 cm in diameter at its narrow end that intersected a transect, I measured total length of the segment and diameter at each end (Waddell, 2002). Individual volume of each CWD piece was calculated using the formula

$$V_m = \frac{\left(\frac{\pi}{8}\right)(D_s^2 + D_L^2)l}{10,000} \quad (1)$$

where V_m = volume of the log in cubic meters, D_s = the diameter of the small end of the log in cm, D_L = the diameter of the large end of the log in cm, and l = length of the log in meters (Waddell, 2002). I calculated cubic meters of CWD per hectare using the formula

$$V_m \text{ per hectare} = \left(\frac{\pi}{2L}\right) \left(\frac{V_m}{l_i}\right) 10000m^2 / \text{hectare} \quad (2)$$

where L = the total length of the transect line, V_m = volume in cubic meters of the individual piece of CWD, and l_i = length of that individual piece. Values were then summed to the plot level (Waddell, 2002). GIS coordinates were obtained using a Garmin etrex handheld GPS unit (Garmin International, Inc., Olathe, KS). Site elevation was determined using USGS 7.5-minute topographical maps (U.S. Geological Survey, 1970a, 1970b, 1970c, 1970d, 1970e, 1970f).

Plant community metrics

I calculated richness of vascular plant species at each of the 20 sites based on the full species list from each site, including understory, midstory, and canopy vegetation. I also calculated mean total richness, native richness, nonnative richness, and proportion of native and nonnative species at natural and constructed sites.

Nonnative species designations were obtained from the PLANTS database (NRCS, 2016). Mean C (\bar{C}) values were calculated for each pool's plant community based on C values presented in Gianopulos (2014) for the Interior Low Plateau ecoregion. If a species was not listed in Gianopulos (2014), I sourced additional C values from Taft et al. (1997) and Andreas et al. (2004). C values are not assigned to nonnative species (Gianopulos, 2014), thus nonnative species were excluded when calculating \bar{C} .

Nonnative species were those not native to the state of KY, and were based on US Department of Agriculture (USDA) PLANTS database listings (NRCS, 2016). I calculated adjusted FQAI (I') for each wetland based on the following formula:

$$I' = \left(\frac{\bar{C}}{10} \frac{\sqrt{N}}{\sqrt{N+A}} \right) \times 100 \quad (3)$$

where \bar{C} is the mean Coefficient of Conservatism of native plant species at a site, N is the native species richness of that site, and A is the number of nonnative species at that site (Miller & Wardrop, 2006). I chose I' as a metric of floristic quality because, unlike some other measures of floristic quality (e.g. FQAI), I' takes invasive species into account.

I assigned wetland indicator status (WIS) values (obligate wetland [OBL], facultative wetland [FACW], facultative [FAC], facultative upland [FACU], and upland [UPL]) based on the National wetland plant list (NWPL; Lichvar et al., 2016). Using the USDA PLANTS database (NRCS, 2016), I assigned functional groups to each plant species (woody, annual forb, perennial forb, graminoid, fern) (Little & Church, 2018).

Analyses

To compare \bar{C} between natural and constructed sites I performed a nested ANOVA where individual wetland was nested within wetland type using package lme4 (Bates et al., 2015) in R version 3.3.2 (R Core Team, 2018). I performed Mann-Whitney U tests in R version 3.3.2 (R Core Team, 2018) to compare pH, DO, ORP, conductivity, littoral slope, latitude, longitude, elevation, richness, CWD volume, canopy closure, I' , proportion of nonnative species, proportion of total richness represented by each vegetative functional group and proportion of total richness represented by each WIS class between natural and constructed sites.

I used R packages vegan (Oksanen et al., 2018) and cluster (Maechler et al., 2018) to perform multivariate community analyses. To prepare understory cover class data for multivariate analyses, I performed the following data management: plots were discarded from the analysis if they were 'empty', that is, if they contained no floating, emergent, or terrestrial vascular vegetation. If multiple plots from a single wetland were similar in composition, I randomly chose a single representative plot from among the similar plots for analysis. If plots were unique in composition, all plots were included. Braun-Blanquet cover/abundance scores were transformed to an ordinal scale (Table 2-2; Non & de Vries, 2013).

I described understory community composition using flexible- β Hierarchical Agglomerative Cluster (HAC) analysis (flexible $\beta = -0.25$) (Lance & Williams, 1967; Little & Church, 2018) and nonmetric multidimensional scaling based on Bray-Curtis

distances. I designated clusters visually based on natural breaks in the dendrogram, and then determined indicator species (Dufrêne & Legendre, 1997) for each cluster using R package labdsv (Roberts, 2016). Indicator species were selected based on indicator value > 0.4 and $p > 0.05$ (Little & Church, 2018). A two-dimensional NMDS was chosen to maximize interpretability of the two-dimensional biplot (NMDS stress = 0.13). Hulls were added in the biplot to delineate the clusters from HAC analysis.

I performed Permutational Analysis of Variance (PERMANOVA) using the vegan package (Oksanen et al., 2018) in R (R Core Team, 2018) to compare community data among natural edge, natural middle, constructed edge, and constructed middle plots, with 'middle' plots being those located entirely within a portion of the wetland in which there was standing water for at least part of the year (preferably as close to the wetland center as possible, but in the case of deep constructed wetlands where the center was inaccessible, 'middle' plots were placed in an accessible area of the wetland interior with representative vegetation). 'Edge' plots were those situated around the wetland margins in areas that are seasonally-to-permanently saturated, but that rarely have standing water. Post-hoc pairwise Permutational Analysis of Variance (PERMANOVA) comparisons were performed among all plot groups, and a Bonferroni adjustment was applied ($\alpha_{\text{adjusted}} = 0.008$).

Results

Environmental variables

Natural and constructed wetlands differed in several key ways. Natural wetlands had lower pH, shallower littoral slope, lower species richness, and higher percent canopy closure than constructed sites. There was not a significant difference in CWD (Table 2-3, Figure 2-3). Natural wetlands were also of higher elevation than the constructed sites.

Species richness

I identified 196 species representing 129 genera and 60 families (Table 2-4; appendix B, Table B-1). Natural wetlands had a cumulative richness of 98 and constructed wetlands had a cumulative richness of 169. Constructed wetlands had greater mean richness per site than natural wetlands (mean constructed richness \pm SE = 46.0 ± 2.06 ; mean natural richness = 27.0 ± 2.54 ; $p < 0.001$; Figure 2-3, Table 2-4).

The most common species was red maple (*Acer rubrum* L.), which was found at all sites. Roundleaf greenbrier (*Smilax rotundifolia* L.), white oak (*Quercus alba* L.), poison ivy (*Toxicodendron radicans* [L.] Kuntze), blackgum (*Nyssa sylvatica* Marsh.), black oak (*Q. velutina* Lam.), northern red oak (*Q. rubra* L.), and common serviceberry (*Amelanchier arborea* [Michx. f.] Fern.) were found at $\geq 75\%$ of sites (Table 2-5).

Nonnative species comprised 5.6% ($n=11$) of total species richness. The most common nonnative species were Japanese stiltgrass (*Microstegium vimineum* [Trin.] A. Camus), which was found at four natural and nine constructed sites; and multiflora

Table 2-3. Mean \pm SE values of environmental variables measured at natural and constructed upland-embedded wetlands in the Daniel Boone National Forest. Significant difference (Mann-Whitney U Test, $\alpha= 0.05$) indicated by *. DO (%) = percent saturation of dissolved O₂, CWD= m³ of coarse woody debris per hectare, \bar{C} = mean coefficient of conservatism, I' = adjusted floristic quality assessment index.

Variable	Natural	Constructed	<i>p</i>
Water chemistry			
pH	4.40 \pm 0.16	5.36 \pm 0.21	0.006*
DO (%)	21.05 \pm 4.04	37.05 \pm 6.64	0.075
Conductivity (mS/cm)	0.035 \pm 0.003	0.069 \pm 0.020	0.364
ORP (mV)	-36.99 \pm 18.04	-57.55 \pm 7.31	0.123
Physical/geomorphological			
Littoral slope	0.05 \pm 0.01	0.19 \pm 0.03	<0.001*
Elevation (m)	372.1 \pm 7.38	339.5 \pm 9.37	0.028*
Latitude (dd)	38.1277 \pm 0.0393	38.1452 \pm 0.0354	0.353
Vegetation			
Canopy closure (%)	88.7 \pm 2.64	58.5 \pm 8.22	0.012*
Richness	27.0 \pm 2.6	46.0 \pm 2.1	<0.001*
Native richness	26.3 \pm 2.5	42.7 \pm 1.9	<0.001*
Nonnative richness	0.7 \pm 0.3	3.3 \pm 0.5	<0.001*
Percent native	97.7 \pm 1.1	92.9 \pm 1.0	0.016*
Percent nonnative	2.3 \pm 1.0	7.1 \pm 1.0	0.016*
CWD (m ³ /ha)	167.6 \pm 28.1	104.9 \pm 17.5	0.166
\bar{C} ϕ	4.6 \pm 0.1	4.1 \pm 0.1	0.004*
I'	45.2 \pm 1.3	39.16 \pm 0.9	0.002*

ϕ mean of means (SE of means) is reported for this variable

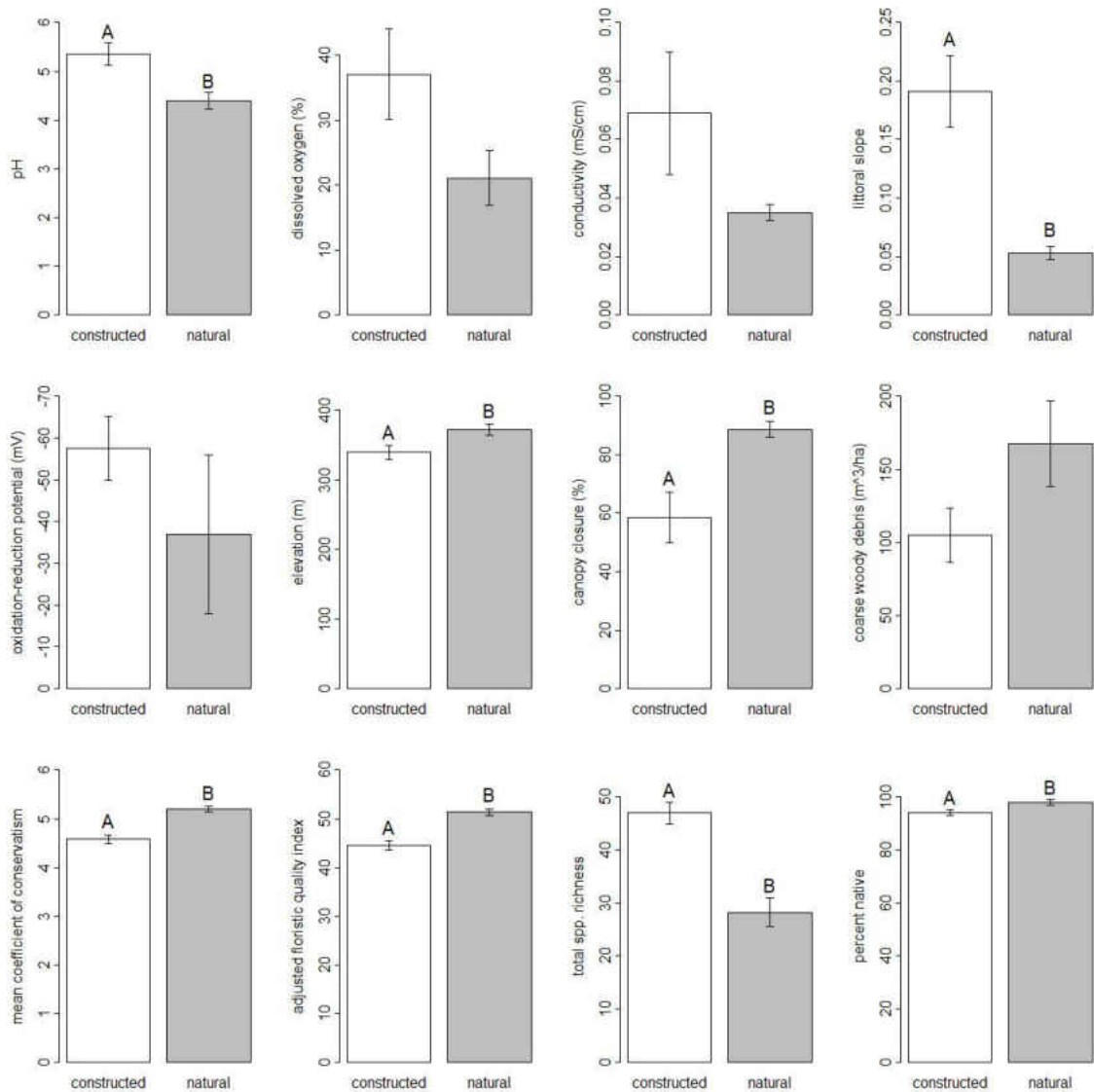


Figure 2-3. Mean (\pm SE) values of wetland and vegetative variables at natural and constructed upland-embedded wetlands in the Daniel Boone National Forest. Letters indicate significant difference between groups (Mann-Whitney U Test, $\alpha = 0.05$).

Table 2-4. Summary of the taxa treated in this text.

	ferns	gymnosperms	monocots	dicots	total
families	2	2	11	45	60
genera	4	2	27	96	129
native species	4	3	55	123	185
nonnative species	0	0	3	8	11
total species	4	3	58	131	196

Table 2-5. The 22 most common understory vascular plant species (those found at ten or more sites) at natural and constructed upland-embedded wetlands in the Daniel Boone National Forest. Number of natural (nat) and constructed (cons) wetlands, and total number of wetlands at which each species was present. WIS= Wetland indicator Status (OBL = obligate wetland species, FACW = facultative wetland species, FAC = facultative species, FACU = facultative upland species, UPL = upland species). Nonnative species are marked with an *.

Scientific name	Family	Common name	Functional group	WIS	Present at:		
					nat.	cons.	total
<i>Acer rubrum</i>	Sapindaceae	Red maple	woody	FAC	10	10	20
<i>Amelanchier arborea</i>	Rosaceae	Common serviceberry	woody	FAC	9	6	15
<i>Boehmeria cylindrica</i>	Urticaceae	False nettle	perennial forb	FACW	6	5	11
<i>Carya glabra</i>	Juglandaceae	Pignut hickory	woody	FACU	6	6	12
<i>Fraxinus pennsylvanica</i>	Oleaceae	Green ash	woody	FACW	4	6	10
<i>Liriodendron tulipifera</i>	Magnoliaceae	Tulip poplar	woody	FACU	5	7	12
<i>Lycopus virginicus</i>	Lamiaceae	American water horehound	perennial forb	OBL	4	8	12
<i>Lysimachia quadrifolia</i>	Onagraceae	Fourflower yellow loosestrife	perennial forb	FACW	6	6	12
<i>Microstegium vimineum</i> *	Poaceae	Japanese stiltgrass	graminoid	FAC	4	9	13
<i>Nyssa sylvatica</i>	Nyssaceae	Blackgum	woody	FAC	10	7	17
<i>Oxydendron arboreum</i>	Ericaceae	Sourwood	woody	UPL	7	4	11
<i>Parthenocissus quinquefolia</i>	Vitaceae	Virginia creeper	perennial forb	FACU	2	10	12
<i>Polystichum acrostichoides</i>	Dryopteridaceae	Christmas fern	fern	FACU	3	7	10
<i>Quercus alba</i>	Fagaceae	White oak	woody	FACU	8	10	18
<i>Quercus montana</i>	Fagaceae	Chestnut oak	woody	UPL	6	7	13
<i>Quercus rubra</i>	Fagaceae	Northern red oak	woody	FACU	9	6	15
<i>Quercus velutina</i>	Fagaceae	Black oak	woody	UPL	7	8	15
<i>Rosa multiflora</i> *	Rosaceae	Multiflora rose	woody	FACU	2	8	10
<i>Sassafras albidum</i>	Lauraceae	Sassafras	woody	FACU	8	5	13
<i>Smilax rotundifolia</i>	Smilacaceae	Roundleaf greenbrier	perennial forb	FAC	10	8	18
<i>Toxicodendron radicans</i>	Anacardiaceae	Poison ivy	perennial forb	FAC	8	9	17
<i>Vaccinium pallidum</i>	Ericaceae	Lowbush blueberry	woody	UPL	7	6	13

rose (*Rosa multiflora* Thunb. ex Murr.), found at two natural and eight constructed sites. At least one nonnative species was found at every constructed site (Table 2-6). Mean nonnative richness at constructed wetlands was 3.3 ± 0.5 , and mean percent nonnative richness at constructed wetlands was $7.1\% \pm 1.0$. Nonnative species were found at four natural wetlands, and no more than two nonnative species were found at any one natural wetland. Mean nonnative richness at natural wetlands was 0.7 ± 0.3 , and mean percent nonnative at natural wetlands was $2.3\% \pm 1.0$. Nonnative

Table 2-6. Nonnative species found at natural and constructed upland-embedded wetlands in the Daniel Boone National Forest. Functional group, wetland indicator status (WIS), family, scientific name, common name, and number of natural (nat.), constructed (cons.) and total number of wetlands where invasive species were present. WIS= Wetland Indicator Status, OBL = obligate wetland species, FAC = facultative species, FACU = facultative upland species, UPL = upland species.

scientific name	family	common name	Functional group	WIS	<i>present at:</i>		
					nat.	cons.	total
<i>Microstegium vimineum</i>	Poaceae	Japanese stiltgrass	graminoid	FAC	4	9	13
<i>Rosa multiflora</i>	Rosaceae	Multiflora rose	woody	UPL	2	8	10
<i>Lonicera japonica</i>	Caprifoliaceae	Japanese honeysuckle	woody	FAC	0	3	3
<i>Polygonum caespitosum</i>	Polygonaceae	Oriental lady's thumb	annual forb	FACU	1	2	3
<i>Typha angustifolia</i>	Typhaceae	Narrowleaf cattail	graminoid	OBL	0	3	3
<i>Daucus carota</i>	Apiaceae	Queen Anne's lace	annual forb	UPL	0	1	1
<i>Echinochloa crus-galli</i>	Poaceae	Barnyardgrass	graminoid	FAC	0	1	1
<i>Leucanthemum vulgare</i>	Asteraceae	Oxeye daisy	perennial forb	UPL	0	1	1
<i>Trifolium campestre</i>	Fabaceae	Field clover	annual forb	UPL	0	1	1
<i>Plantago major</i>	Plantaginaceae	broad-leaved plantain	perennial forb	FACU	0	1	1
<i>Coronilla varia</i>	Fabaceae	Crown-vetch	perennial forb	NA	0	1	1

richness and percent nonnative species were significantly higher at constructed wetlands than natural wetlands ($p < 0.001$, $p = 0.016$, respectively; Figure 2-3, Table 2-3).

Plant community analysis

A greater proportion of total richness was represented by woody species in natural than constructed wetlands (mean constructed = 0.40 ± 0.03 , mean natural = 0.60 ± 0.05 , $W = 15.0$, $p = 0.007$; Table 2-7, Figure 2-4). A greater proportion of total richness was represented by perennial and annual forbs in constructed than in natural wetlands (mean proportion of richness represented by annual forbs at constructed = 0.08 ± 0.01 , natural = 0.03 ± 0.01 , $W = 88.5$, $p = 0.004$; mean proportion of richness

Table 2-7. Mean \pm SE proportion of total richness represented by each functional group and each WIS (wetland indicator status) group at natural and constructed upland-embedded wetlands in the Daniel Boone National Forest. OBL= obligate wetland species, FACW= facultative wetland, FAC= facultative, FACU= facultative upland, UPL= upland. Significance (Mann-Whitney U test, $\alpha = 0.05$) indicated by *.

Group	Natural	Constructed	W	<i>p</i>
Functional group				
Woody	0.60 ± 0.05	0.40 ± 0.03	15.0	0.007*
Annual forb	0.03 ± 0.01	0.08 ± 0.01	88.5	0.004*
Perennial forb	0.16 ± 0.02	0.31 ± 0.02	97.0	<0.001*
Graminoid	0.20 ± 0.03	0.19 ± 0.02	58.0	0.571
Fern	0.02 ± 0.01	0.02 ± 0.00	59.5	0.467
WIS class				
OBL	0.08 ± 0.02	0.10 ± 0.02	61.5	0.405
FACW	0.16 ± 0.02	0.14 ± 0.01	36.5	0.326
FAC	0.30 ± 0.01	0.27 ± 0.02	29.0	0.120
FACU	0.27 ± 0.02	0.29 ± 0.01	61.5	0.406
UPL	0.19 ± 0.02	0.20 ± 0.02	52.5	0.880

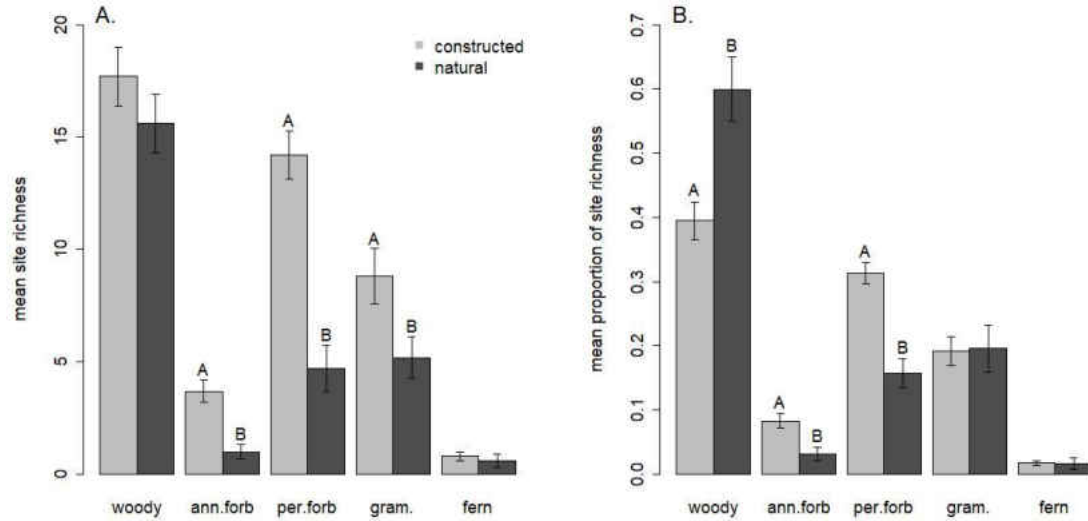


Figure 2-4. A.) Mean (\pm SE) richness-per-site of different vegetative functional groups at natural ($n = 10$) and constructed ($n = 10$) wetlands. B.) Mean (\pm SE) proportion of species richness-per-site represented by each group at natural and constructed wetlands. Ann.forb = annual forb, per.forb = perennial forb, gram. = graminoid. Columns with different letters within a pair are significantly different from each other.

represented by perennial forbs at constructed wetlands = 0.31 ± 0.02 , natural = 0.16 ± 0.02 , $W = 97.0$, $p < 0.001$). There were no significant differences in proportion of richness represented by each WIS class between natural and constructed sites (Figure 2-5).

Mean C of plants at natural wetlands was greater than that of constructed wetlands (natural $\bar{C} = 4.96 \pm 0.17$, constructed $\bar{C} = 4.38 \pm SE=0.15$, $p = 0.0002$). Mean I' of plants at natural wetlands was greater than that of constructed wetlands (natural $\bar{I}' = 51.7 \pm 0.68$, constructed $\bar{I}' = 44.6 \pm 0.86$, $p < 0.001$; Table 2-3, Figure 2-3). In Hierarchical Agglomerative Cluster (HAC) analysis, data clustered into four distinct groups with one group of outliers (Figure 2-6). The outliers were plots that contained

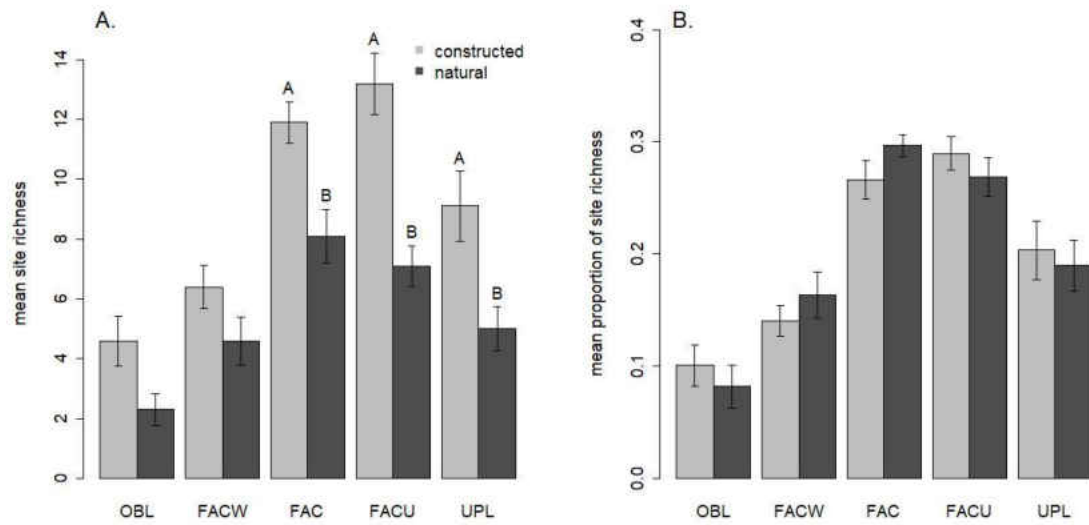


Figure 2-5. A.) Mean (\pm SE) richness-per-site of different wetland indicator status (WIS) groups at natural ($n = 10$) and constructed ($n = 10$) wetlands. B.) Mean (\pm SE) proportion of species richness-per-site represented by each WIS group at natural and constructed wetlands. OBL = obligate wetland species, FACW = facultative wetland species, FAC = facultative species, FACU = facultative upland species, UPL = obligate upland species. Columns with different letters within a pair are significantly different from each other.

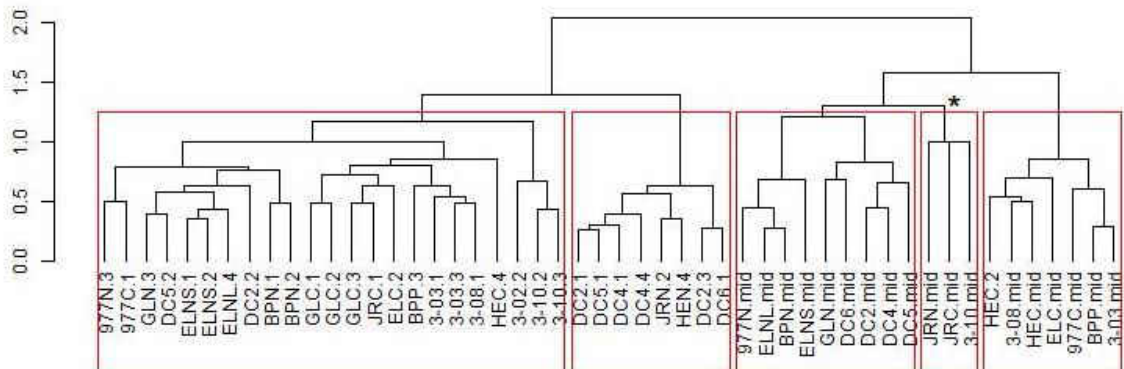


Figure 2-6. Cluster dendrogram based on hierarchical agglomerative cluster analysis (flexible- $\beta = -0.25$) of understory vegetation plots at natural and constructed upland-embedded wetlands in the Daniel Boone National Forest. Four main clusters and one outlying cluster are indicated by boxes. The outlying cluster is indicated by *.

only one species each and were dissimilar to other plots. The four main clusters matched well with most of the *a priori* plot groupings (natural edge, natural middle, constructed edge, and constructed middle), with the exception of cluster 1 (Table 2-8).

All but one constructed edge plot, and about half of the natural edge plots fell into cluster 1. Cluster 2 consisted solely of natural edge plots. Cluster 3 consisted solely of natural middle plots, and cluster 5 consisted mostly of constructed middle plots with one constructed edge plot from constructed wetland HEC. Edge plots from constructed wetlands 977C and HEC constructed wetlands clustered with natural edge plots.

Several species met the criteria for indicator species (Table 2-9). Narrowleaf cattail (*Typha. angustifolia* L.) and water shield (*Brasenia schreberi* J. F. Gmel.) were indicative of constructed wetland middles (cluster 5). Rice cutgrass (*Leersia oryzoides* [L.] Sw.) and Gray’s sedge (*Carex grayi* Carey) were indicative of natural wetland middles (cluster 3). Woody species, Sassafras (*Sassafras albidum* [Nutt. Nees),

Table 2-8. Groupings resulting from Hierarchical Agglomerative Cluster Analysis. The majority of plots in each cluster matched with the plot groupings based on wetland construction history (natural or constructed) and plot placement in wetland (edge or middle). ^φ cluster 4, consisting of 3 plots that contained one species each, was considered to be an outlier.

	n plots in <i>a priori</i> group	cluster 1	cluster 2	cluster 3	φ cluster 4	cluster 5
n plots in cluster	-	23	8	9	3	7
n (%) nat. edge plots in clust.	17	9 (39.1%)	8 (100%)	0 (0%)	0 (0%)	0 (0%)
n (%) nat. mid. plots in clust.	10	0 (0%)	0 (0%)	9 (100%)	1 (33.3%)	0 (0%)
n (%) con. edge plots in clust.	15	14 (60.9%)	0 (0%)	0 (0%)	0 (0%)	1 (14.3%)
n (%) con. mid. plots in clust.	8	0 (0%)	0 (0%)	0 (0%)	2 (66.7%)	6 (85.7%)

Table 2-9. Indicator species at each of 4 groups defined through Ward Hierarchical cluster analysis. Groups mostly aligned with *a priori* plot classifications based on wetland type and plot placement. Cluster 1 included constructed and natural edge plots. Cluster 2 consisted of natural edge plots. Cluster 3 consisted of natural middle plots, cluster 4 was considered to be an outlier. Cluster 5 consisted mainly of constructed middle plots. A species was deemed an indicator species for a cluster if that species had $p < 0.05$ and indicator value > 0.4 . Indicator values of indicator species are marked with *.

species	p	indicator value				
		cluster 1	cluster 2	cluster 3	cluster 4	cluster 5
<i>Acer rubrum</i>	0.001	0.3211	0.4587*	0.0437	0.0000	0.0000
<i>Brasenia schreberi</i>	0.001	0.0010	0.0000	0.0000	0.0000	0.9771*
<i>Carex grayi</i>	0.007	0.0308	0.0000	0.5994*	0.0000	0.0125
<i>Leersia oryzoides</i>	0.003	0.0091	0.0000	0.4972*	0.0000	0.0000
<i>Nyssa sylvatica</i>	0.026	0.2691	0.4185*	0.0000	0.0000	0.0000
<i>Oxydendrum arboreum</i>	0.006	0.0454	0.5932*	0.0000	0.0000	0.0000
<i>Parthenocissus quinquefolia</i>	0.008	0.5217*	0.0000	0.0000	0.0000	0.0000
<i>Quercus montana</i>	0.009	0.0697	0.5497*	0.0000	0.0000	0.0000
<i>Quercus rubra</i>	0.001	0.1010	0.6492*	0.0000	0.0000	0.0000
<i>Sassafras albidum</i>	0.001	0.0140	0.8929*	0.0000	0.0000	0.0000
<i>Smilax rotundifolia</i>	0.001	0.2759	0.4905*	0.0454	0.0000	0.0000
<i>Toxicodendron radicans</i>	0.023	0.4457*	0.0000	0.0000	0.0000	0.0302
<i>Typha angustifolia</i>	0.003	0.0020	0.0000	0.0000	0.0000	0.5452*
<i>Vaccinium pallidum</i>	0.001	0.0233	0.7578*	0.0000	0.0000	0.0000

blackgum (*Nyssa sylvatica* Marshall), roundleaf greenbrier (*S. rotundifolia*), red maple (*Acer. rubrum*), northern red oak (*Quercus rubra* L.), chestnut oak (*Quercus montana* Willd.), sourwood (*Oxydendrum arboreum* L. DC.), and blue ridge blueberry (*Vaccinium pallidum* Aiton), were indicative of some natural wetland edges (cluster 2). Virginia creeper (*Parthenocissus quinquefolia* [L.] Planch.) and poison ivy (*Toxicodendron radicans* L. Kuntze) were indicative of cluster 1, which largely consisted of constructed edge plots, but also contained natural edge plots. Due to the mixture of natural and

constructed edge plots in cluster 1, indicator species found in wetland centers may be more useful at this time for rapid assessment of natural vs. constructed wetland type.

Nonmetric multidimensional scaling (NMDS) revealed that the vegetative communities at natural and constructed wetlands fell into distinct groups (Figure 2-7). Wetland type and plot placement differed along both NMDS axes, with edge plots at constructed wetlands falling along the positive end of axis 2, and constructed middle plots falling along the positive end of axis 1. Natural edge plots fell along the negative end of axis 1, and natural middle plots fell along the negative end of axis 2. Woody and herbaceous species also differed along both axes, with most woody species occurring on the positive end of axis 2 (Figure 2-8). Most forbs and graminoids occurred on the negative end of axis 2. An initial PERMANOVA comparison found the difference among the four groups to be significant ($p = 0.001$), and post-hoc pairwise PERMANOVA comparisons with a Bonferroni adjustment ($\alpha_{\text{adjusted}} = 0.008$) indicated that all groups were significantly different from each other ($p = 0.001$) (Table 2-10).

Discussion

Disturbance, hydroperiod, and canopy closure are all major factors influencing wetland plants (Cronk & Fennessy, 2001; Cutko & Rawinski, 2007). In contrast to amphibian communities, which in this system are primarily driven by length of hydroperiod (Calhoun et al., 2014; Denton & Richter, 2013; Drayer & Richter, 2016), drivers of plant community composition are more complex. Plant communities at constructed wetlands appear to be primarily affected by disturbance arising from the

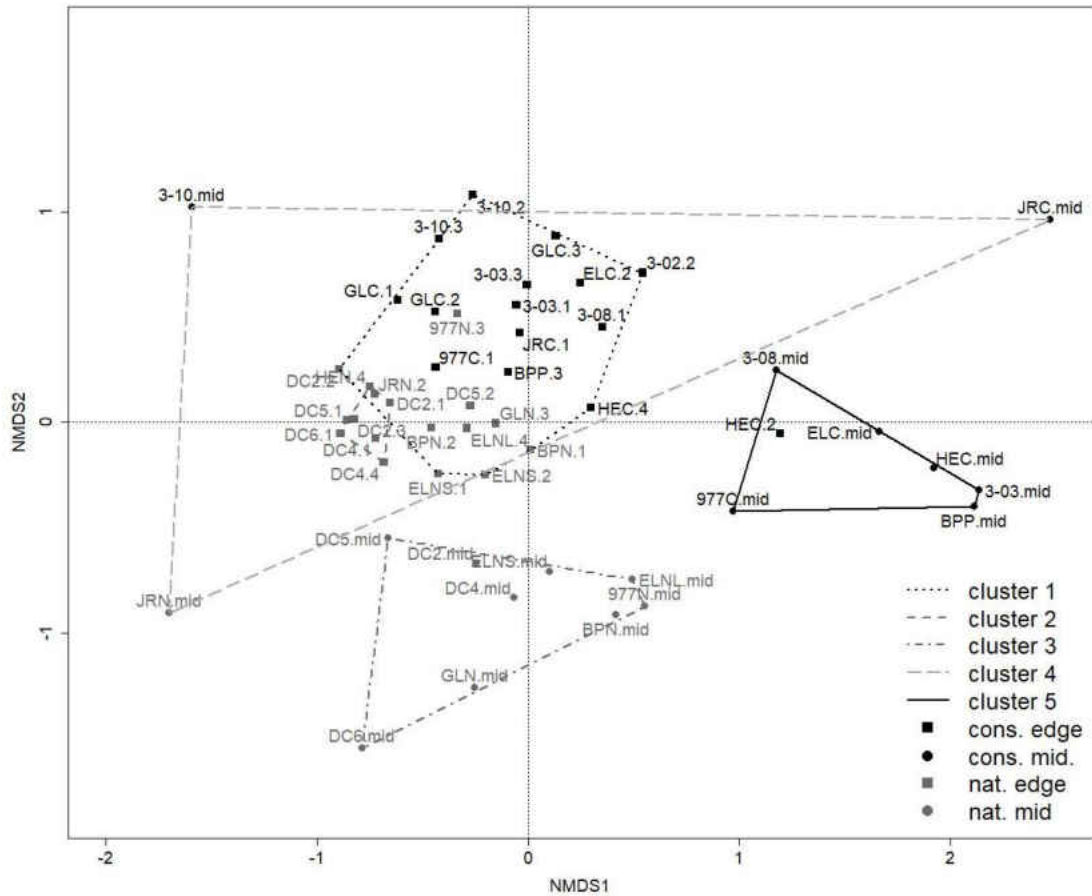


Figure 2-7. Plot of Nonmetric multidimensional scaling (NMDS) site scores from vegetation survey plots at natural and constructed upland-embedded wetlands in the Daniel Boone National Forest. NMDS is based on a Bray-Curtis dissimilarity matrix of ordinally-transformed Braun-Blanquet cover/abundance scores. Symbology indicates whether the plot was located at a natural or constructed wetland site, and whether the plot was located at the edge of the wetland or in the wetland center. Hulls are based on hierarchical agglomerative cluster analysis, and indicate which plots clustered together. Plots JRN.mid, 3-10.mid, and JRC.mid contained only one species each. They were considered outliers and excluded from cluster groupings. Stress = 0.13, dimensions = 2.

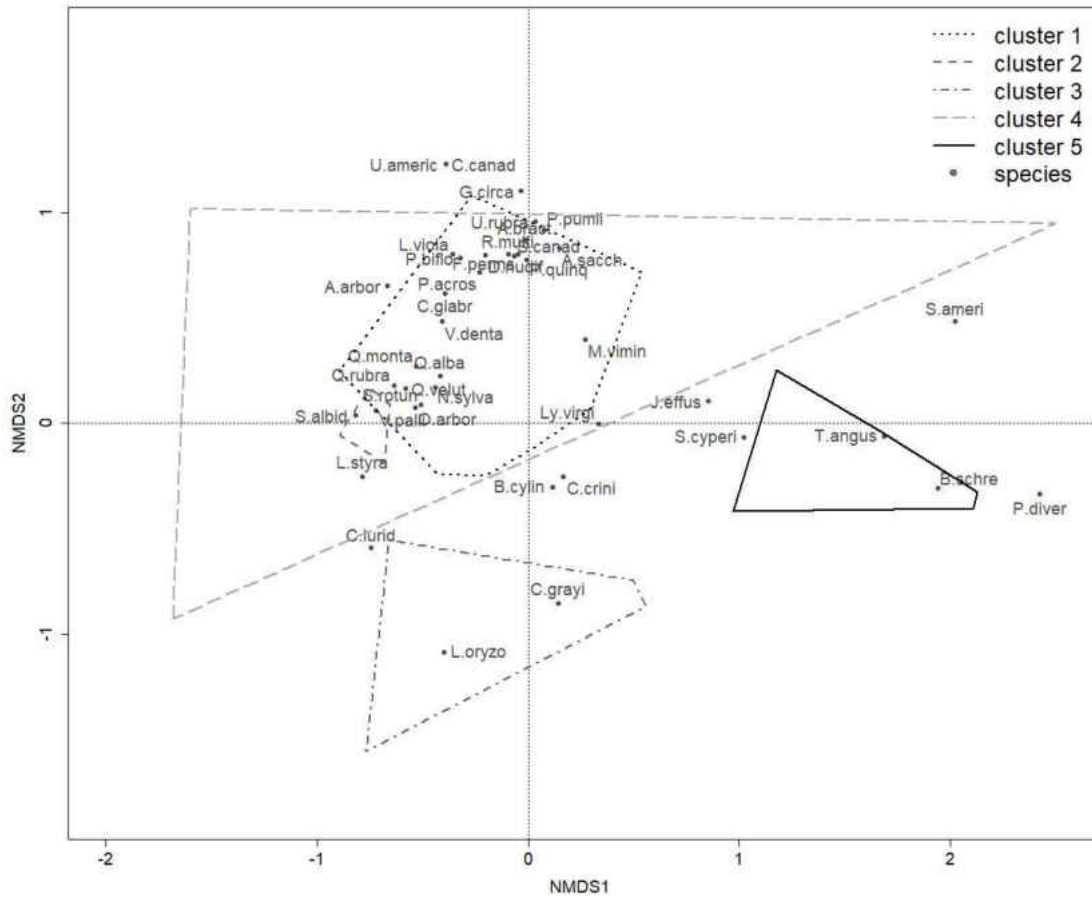


Figure 2-8. Plot of nonmetric multidimensional scaling (NMDS) species scores of plants at wetland vegetation survey plots at natural and constructed upland-embedded wetlands in the Daniel Boone National Forest. NMDS is based on a Bray-Curtis dissimilarity matrix of ordinally-transformed Braun-Blanquet cover/abundance scores. Species codes consist of the first letter of the genus and first 5 letters of the specific epithet. Hulls are based on hierarchical agglomerative cluster analysis, and indicate which plots clustered together. Stress = 0.13, dimensions = 2.

Table 2-10. Post-hoc Permutational Analysis of Variance (PERMANOVA) comparisons of plant communities at four different plot types. Plots were located at natural and constructed upland-embedded wetlands in the Daniel Boone National Forest. Plot types are defined as follows: nat.edge = edge of natural wetland, nat.mid = middle of natural, con.edge = edge of constructed, con.mid = middle of constructed. Significance (Bonferroni adjustment; $\alpha_{\text{adjusted}} = 0.008$) indicated by *.

pairs	F.Model	R ²	<i>p</i>
nat.edge vs nat.mid	9.02	0.265	0.001*
nat.edge vs con.edge	6.28	0.173	0.001*
nat.edge vs con.mid	12.65	0.355	0.001*
nat.mid vs con.edge	7.16	0.237	0.001*
nat.mid vs con.mid	5.42	0.253	0.001*
con.edge vs con.mid	6.37	0.233	0.001*

wetland construction event itself. Logging activity, vehicle traffic, canopy closure, and hydroperiod, which are closely tied to disturbance history, also affect plants to a lesser degree.

The main disturbance affecting constructed wetland plant communities in the DBNF is the aftermath of the construction event itself, which has often led to open canopy, permanent hydroperiod, and compacted soil at constructed wetland sites. It is possible that some permanent wetlands have been constructed in areas formerly occupied by natural ephemeral wetlands, thus disrupting the natural wetland plant communities that existed. Due to lack of records, I cannot determine the frequency of this type of occurrence; however, it is possible that future studies of hydrology, and wetland landscape placement could help clarify which, if any, constructed wetlands were built atop natural wetland sites.

Differences in canopy closure can affect plant richness and community composition (Anderson, Loucks, & Swain, 1969; Goldblum, 1997). In some systems,

open-canopy areas are associated with increased understory species richness (Goldblum, 1997), likely a result of increased light availability and increased precipitation throughfall in canopy openings (Anderson et al., 1969). However, Moore & Vankat (1986) found that canopy openings did not result in increased herbaceous richness. I think it is likely that the open canopy environment of constructed wetlands contributes to richness by increasing habitat heterogeneity, and that patches of differing light levels allow both shade-tolerant and shade-intolerant species to become established. However, further research would be needed to explore the effects of canopy closure on UEW understory richness.

The effects of canopy closure on species composition can be seen by examining the shade-tolerance of natural and constructed wetland indicator species. Natural wetland indicator species *Acer rubrum*, *Smilax rotundifolia*, *Nyssa sylvatica*, *Oxydendrum arboreum*, *Quercus rubra*, and *Carex grayi* are all at least moderately shade-tolerant (Burns & Honkala, 1990; Flora of North America Editorial Committee, 1993; Weakley, 2015). *Sassafras albidum* was the only shade-intolerant woody indicator species at the natural wetland sites. Constructed wetland indicators *Typha angustifolia* and *Brasena schreberi* require full or partial sunlight (Grace & Harrison, 1986; Les, 2017; USDA NRCS, 2006), and many of the other herbaceous species common to constructed sites, including *Lysimachia quadrifolia* (whorled yellow loosestrife), *Amphicarpaea bracteata* (American hogpeanut), and *Juncus effusus* (common rush) share these sunlight requirements and are usually found in openings or

forest edges and require direct or partial sunlight (Brockett & Cooperrider, 1983; Schively, 1897; USDA NRCS, 2002), making them more suited to open-canopy constructed wetlands than closed-canopy natural wetlands.

By determining indicator species, I do not mean to imply that any site with a natural wetland indicator species is a natural wetland, or that any site with a constructed wetland indicator species is a constructed wetland. All the indicator species I found can occur in both natural and constructed wetland types in different landscape settings throughout the eastern US, and indeed, several natural wetland indicator species are equally or more likely to be found in upland habitat than in a wetland. Rather, information regarding presence and cover of natural and constructed wetland indicator species at UEWs can be combined with other observations about the wetland habitat to aid in rapid assessment of wetland construction history. Due to the mixture of natural and constructed edge plots in cluster 1, indicator species found in wetland centers would be more useful for rapid assessment of construction history. Additional vegetation surveys during different times of year, at a greater number of sites, and in different Districts of the DBNF would be useful to gain a broader understanding of community differences and could be developed into a monitoring tool to assess post-construction succession and whether constructed UEWs are progressing toward a 'natural type' vegetative community.

With succession, canopy at some constructed wetlands may close over time. Although woody understory plants were more widespread at natural wetlands,

seedlings and saplings of many woody species were found at constructed sites. As these woody plants mature, they may influence an understory shift to more shade-tolerant and potentially more natural-type vegetation. However, compacted soil and thick understory growth of herbaceous species, such as *Microstegium vimineum*, can negatively impact forest regeneration and succession (Flory & Clay, 2010; Kozlowski, 1999). The trajectory of succession will vary from site to site, and in some cases will not progress toward natural conditions but rather toward any number of alternative states (Zedler & Callaway, 1999). Additionally, some constructed wetlands in the DBNF are in maintained forest openings and thus will not achieve closed canopy as long as the openings are managed.

Both natural and constructed wetlands have been affected by past logging activity and proximity to roads and trails. Like wetland construction, logging and road activity often result in soil compaction and loss of canopy closure, along with potential species introductions (Buckley et al., 2003; Forman & Alexander, 1998; Mortensen et al., 2009). Many constructed wetlands in the DBNF system have been built near active forest roads or in decommissioned logging roads, and some natural wetlands are also near forest roads and trails. Buckley et al. (2003) found that logging haul roads had greater understory richness and more nonnative species richness than both skid trails and undisturbed forest. Although I did not compare richness between constructed wetlands based on road association, this is an area for potential future research.

Although high plant species richness might sometimes indicate high-quality, undisturbed wetland habitat (Campbell, Cole, & Brooks, 2002; Stefanik & Mitsch, 2012), comparatively low species richness, such as what I found at natural UEWs, is not necessarily an indication of disturbed or degraded habitat (Flinn et al., 2008; Miller & Wardrop, 2006). The research of Balcombe et al. (2005) supports my findings of higher richness at constructed wetlands. In contrast to my results, Stefanik & Mitsch (2012), and Campbell et al. (2002) found higher vegetative richness at natural reference wetlands than constructed sites. However, the wetlands in these two latter studies differed greatly in classification, size, hydrology, and landscape placement from my study sites.

Hydroperiod, which is closely tied to construction history in the DBNF system, also affects species richness. Similar to my results, Little & Church (2018) found that permanent wetlands had higher species richness and greater herbaceous species richness than ephemeral wetlands in the same area. They also found that woody species represented a greater proportion of overall richness at ephemeral wetlands than at permanent wetlands (Little & Church, 2018). In natural settings where wetlands are connected to the local water table, presence of woody vegetation contributes to wetland drying through evapotranspiration (Klein, Berg, & Dial, 2005). However, information from the DBNF constructed wetland system suggests little water table connectivity due to soil compaction (Malzone, unpubl. data, 2017). Hydrologic variability has been found to increase vegetative richness, so in some cases ephemeral

wetlands may be expected to have greater species richness than permanent sites (Cronk & Fennessy, 2001). However, many constructed wetlands also have fluctuating water levels, which likely contributes to their richness. Because of the small number of constructed ephemeral/semipermanent wetlands ($n = 2$) in this study, and the lack of natural permanent wetlands, it is difficult to separate the effects of construction and hydroperiod.

Ecological conservatism and floristic quality are of concern at constructed wetlands. The significantly lower I' and \bar{C} of constructed wetlands is indicative of disturbance, which matches what is known about constructed ridge-top wetland history, and the observed patterns in community composition. Research has shown that vegetative structure and community composition of constructed and restored wetlands only recover to reference levels after many years (> 30), and sometimes fail to recover even after 100 years (Moreno-Mateos et al., 2012; Zedler & Callaway, 1999). Balcombe et al. (2005) found that plants with lower C values were characteristic of newly-constructed mitigation wetlands, while higher C values were associated with older mitigation sites. However, natural reference sites had higher C values than constructed sites of any age (Balcombe et al., 2005). Although seeding constructed and/or restored sites with native species helps establish native richness and diversity in the short-term, plant communities at constructed wetlands that have been seeded may regress to a more degraded, nonnative-rich composition after several years (Matthews & Spyreas, 2010; Reinartz & Warne, 1993). Lower ecological conservatism

and floristic quality at constructed sites indicates that although constructed wetlands in the DBNF provide habitat for vegetative species, this habitat is not of similar condition to natural reference sites (Balcombe et al., 2005; Stefanik & Mitsch, 2012).

Zedler & Kercher (2004) posit that small-watershed wetlands that are primarily rainwater- and groundwater-fed, such as my ridge-top study sites, tend to have high native species richness and low numbers of invasive plants due to low nutrient concentrations. However, disturbance increases susceptibility to invasion (Zedler & Kercher, 2004). Wetland construction events are sources of disturbance that often result in soil compaction, permanent hydroperiod, and open canopy (Biebighauser, 2003; Denton & Richter, 2013; Drayer & Richter, 2016). Roads and trails also serve as corridors for introduction of invasive species (Forman & Alexander, 1998). Although paved roads pose the greatest invasion risk (Gelbard & Belnap, 2003; Joly et al., 2011), invasive species such as *M. vimineum* commonly occur in logging roads, trails, utility rights-of-way, and other lightly-trafficked corridors (Cole & Weltzin, 2004; Redman, 1995). From the significantly greater nonnative richness and significantly lower I' values at constructed study sites, it is clear that invasive species are of concern at constructed UEWs, and indeed at wetlands in general (Zedler & Kercher, 2004). Invasive species are controllable, but invulnerable areas require regular monitoring and treatment (DeMeester & deB. Richter, 2010). Few, if any, constructed UEWs in the DBNF are currently monitored or managed to control invasive species.

My findings support other research which found no significant difference in proportion of richness represented by each WIS group between natural and constructed sites (Balcombe et al., 2005; Hartzell et al., 2007). Due to the depth and permanent hydroperiod of most constructed wetlands, it was surprising that constructed upland-embedded sites did not have a greater proportion of obligate and facultative wetland species. One possible explanation for this is that soil compaction and lack of hydrological connectivity around constructed wetlands (Malzone, unpubl. data, 2017), as well as a narrow zone of transition between wetland and upland habitat, resulted in artificially high prevalence of FACU and UPL species in study plots at these sites, balancing out the presence of OBL and FACW plants.

Conservation implications

It is clear that natural ephemeral UEWs have different plant communities than constructed permanent UEWs. The data also suggest that vegetation of constructed ephemeral UEWs also differs from that of natural ephemeral UEWs. However, constructed ephemeral wetlands are rare in the DBNF, so this speculation is based on information from a single site. Natural UEWs are characterized by ephemeral hydroperiod, high canopy closure, and relative lack of anthropogenic disturbance. Constructed UEWs are characterized by permanent hydroperiod, low canopy closure, and anthropogenic impacts including permanent hydroperiod and soil compaction. These different characteristics have resulted in natural wetlands having higher quality, more ecologically conservative vegetation than constructed wetlands. Although

wetland species found at UEWs also exist at other wetland types, UEWs provide habitat for these species on xeric and mesic ridge-tops where they would otherwise not survive.

It is important to continue to expand our understanding of natural wetland communities and the effects of anthropogenic management practices on those communities. With continuing anthropogenic habitat loss and fragmentation, conservation of natural wetlands and mitigation of wetland loss become increasingly important. Constructed wetlands have been shown to differ from natural wetlands in terms of vegetation (Balcombe et al., 2005; Zedler & Callaway, 1999), amphibian habitat (Calhoun et al., 2014; Denton & Richter, 2013; Drayer & Richter, 2016; Gamble & Mitsch, 2009; Kross & Richter, 2016; Vasconcelos & Calhoun, 2006), and hydrogeology (Malzone, unpubl. data). Natural wetlands are an important reference both when planning wetland construction projects and when assessing the quality and ecological function of constructed and restored wetlands. Richness should be evaluated alongside measures of floristic quality and ecological conservatism such as the Adjusted Floristic Quality Assessment Index (I') and mean coefficient of conservatism (\bar{C}) to gain a more complete picture of habitat condition and disturbance history. To adequately address conservation needs, I recommend that constructed wetlands should match the ecological function of natural reference sites. Natural wetlands, with the plants, amphibians, and other organisms they support, should be valued and protected.

Introduction

Management and additional research are recommended in the upland-embedded wetland (UEW) system in the Daniel Boone National Forest. Management will serve to improve habitat at constructed UEWs, and research will fill knowledge gaps regarding amphibian and plant communities at both natural and constructed wetlands. Constructed UEWs currently do not provide similar ecological structure and function to natural UEWs in the District. Constructed UEWs host populations of newts and green frogs that are both historically-absent from the ridge-top environment and detrimental to ephemeral-wetland obligate amphibian species. Additionally, UEWs have been constructed in extraordinarily high density in many areas. In locations of highest wetland density, there are more than 10 times the number of constructed wetlands as natural wetlands per square mile (Fedders, pers. obs., 2018).

Research should address amphibian and plant communities at natural and constructed UEWs throughout all districts of the DBNF, as well as wetland hydrology and geology. Goals include the following: A.) continue amphibian research to advance our knowledge of target species such as marbled salamanders and to gain a more complete understanding of amphibian communities in other districts of the DBNF. B.) Address effects of hydroperiod, canopy closure, logging roads, invasive species, and other complex factors on plant communities and ecological succession at constructed UEWs. C.) Study hydrogeologic factors including soil compaction, hydraulic

conductivity, surface water-groundwater connectivity, and soil characteristics. D.)

Detect and map undocumented constructed wetland sites to inform on-the-ground management and restoration projects.

Land managers should seek to improve UEW habitat for native plants and ephemeral-wetland obligate amphibians. Management goals include the following: A.) Conserve and protect existing natural upland-embedded wetlands. B.) Identify wetlands that are candidates for restoration/removal by examining existing records and continuing to survey ridge-tops. C.) Reduce the overall density of constructed upland-embedded wetlands to more closely resemble the density of naturally-occurring wetlands and alter a subset of the remaining constructed wetlands to achieve ephemeral to semipermanent hydroperiod. D.) Monitor restored sites regularly to track amphibian and plant community trajectories and determine if conservation goals are being met.

Research

Amphibians

We have gained a solid foundation of data concerning amphibian community composition in the Cumberland District UEW system, and to a lesser extent in the London District (cite all previous research papers here). Still, information gaps remain. Previous research has raised questions regarding marbled salamanders (*Ambystoma opacum*), and whether constructed wetlands serve as population sinks for this species

in a similar way to wood frogs. Further research is needed to examine marbled salamander breeding, reproductive behavior, and survival at natural and constructed wetlands. Research should include studies of oviposition site selection, clutch size, parental behavior, and offspring survival at each life stage from egg to adult. This will help to determine whether constructed wetlands serve as population sinks for marbled salamanders, and also illuminate life history information that will help inform management and conservation decisions to benefit this species.

Other districts of the DBNF also have many constructed wetlands, albeit at lower density than in the Cumberland District. Research in the London District (McTaggart, 2016) indicates that overall patterns of amphibian community composition and hydroperiod interactions are similar to the Cumberland District, with a few notable exceptions. Natural wetlands in the London District are larger and have longer hydroperiods than those in the Cumberland. Also, instances of wood frog coexistence with newts and green frogs are more common in the London District than the Cumberland. This is likely due to lower constructed wetland density, which leads to lower overall newt and green frog abundance and decreased predation pressure. Future research can address wetlands in the Stearns and Redbird districts, and determine whether patterns of amphibian presence and abundance are similar to those of the Cumberland or London districts. This will also aid in continuing to understand the effects of wetland density on abundance of newts and green frogs.

Plants

The results of plant surveys at UEWs in the DBNF (Chapter 2) suggest complex effects of multiple factors on plant communities in terms of overall richness, nonnative species occurrence, ecological conservatism, floristic quality, and floristic structure. These factors include active and decommissioned forest roads, forest edges and clearings, soil compaction, and canopy closure at both natural and constructed wetlands. Future research could address these topics individually or comprehensively to delineate effects of biotic and abiotic features at both local and landscape scales.

Wetland sites should be surveyed at intervals to determine successional trajectories of plant communities. Although this is of interest at all UEWs, succession is of particular importance at constructed wetland sites. Research has shown that plant communities at many constructed wetlands do not progress to resemble reference communities, but rather towards any number of alternative postdisturbance states (Moreno-Mateos et al., 2012, Zedler & Callaway, 1999). In the DBNF system, plant communities at constructed UEWs are at risk of monoculture takeover due to cattail, as well as encroaching nonnative species such as Japanese siltgrass (*Microstegium vimineum*). There is also the concern that even at constructed wetlands with high richness, the floristic structure and function are not equivalent to that of natural reference wetlands.

Wetland detection and mapping

In order to inform management decisions, it is important to have a full understanding of wetland locations in order to address questions of constructed wetland density, landscape connectivity, wetland condition, and species composition. Current National Wetland Inventory data for Kentucky is often inaccurate, and does not account for many small depressional wetlands including ridge-top wetlands. Other methods are necessary to locate, map, and ground-truth small UEWs in Kentucky.

Light detection and ranging (LiDAR) imagery can be used to identify small depressions on ridge-tops that have the potential to hold water. Constructed wetland depressions have been shown to stand out in LiDAR imagery and often have distinct characteristics including steep sides and high, flat-topped dams (Figure 3-1). Natural

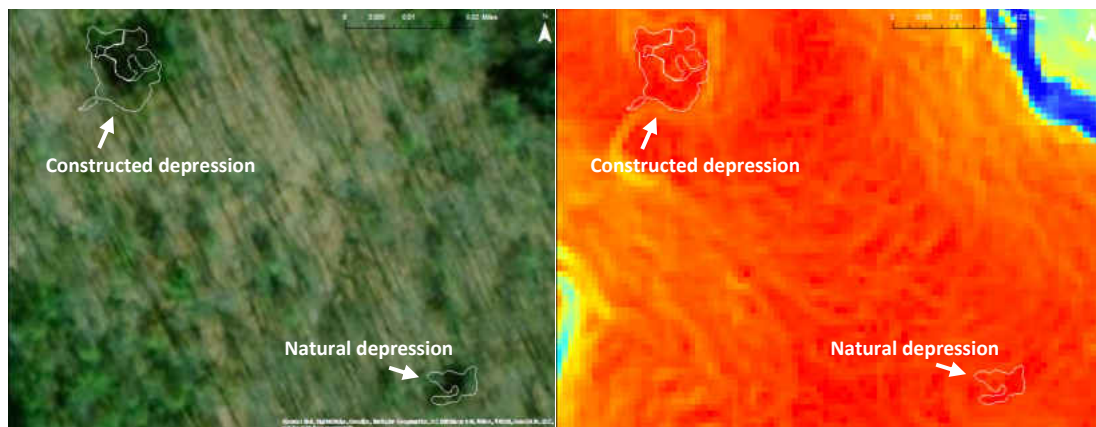


Figure 3-1. Constructed and natural wetland depressions in the Cumberland District of the Daniel Boone National Forest (DBNF) are visible in aerial imagery (A) and LiDAR (B). Most constructed wetlands have steeper littoral zones. In this imagery, low slope pixels are red, and high slope pixels are blue, with moderate slope pixels orange, yellow, and green.

depressions are not as visually apparent in LiDAR imagery, but are still detectable using GIS software or hand-digitization (Watson et al., unpubl. data, 2018). After potential wetland depressions are identified, each site should be visited to determine wetland presence. If a wetland is present, preliminary surveys should record wetland size, habitat features, estimates of hydroperiod, natural/constructed type, and amphibian species presence.

Hydrogeology

Hydroperiod has been shown to play the primary role in amphibian community composition at UEWs, and hydroperiod also affects plant assemblages. Constructed wetland hydroperiod is influenced by wetland characteristics including substrate compaction and depression depth. Natural wetland hydroperiod is influenced by water table fluctuations in perched aquifers, surface water- ground water interactions, and evapotranspiration rates (Malzone, unpubl. data, 2018). By continuing to study hydrogeological wetland features, we can gain a better understanding of the drivers of hydroperiod at both natural and constructed sites. This will better inform wetland construction and restoration projects in the future and allow land managers to better construct wetlands that emulate natural conditions and to alter constructed wetlands to achieve natural hydrological regimes. Greater knowledge of hydroperiod will also become increasingly important as hydrological regimes shift in response to climate change (Brooks, 2009; Greenberg et al., 2015).

Management

Conservation

The first goal of management should be conservation. Natural wetlands should be protected wherever possible. Although constructed wetlands can provide important habitat for amphibians and other fauna and flora (Brand & Snodgrass, 2010), many constructed wetlands are not successful in emulating the ecological function of natural wetlands (Calhoun et al., 2014; Denton & Richter, 2013; Drayer & Richter, 2016; Kross & Richter, 2016; McTaggart, 2016; Pechmann et al., 2001; Vasconcelos & Calhoun, 2006). Wetland construction and restoration are crucial steps to slow amphibian declines, but these processes must be done correctly to avoid introducing novel habitat types and historically-absent species. If wetlands are to be constructed, land managers should consider the ecological requirements of the desired target species (Brown et al., 2012).

Identifying candidate wetlands

Identifying wetlands that are candidates for restoration and removal is an important first step in management. Wetlands that are candidates for removal may include very deep sites, constructed sites with high percent cover of invasive species such as cattails, constructed sites in areas of highest wetland density, and constructed wetlands that have been built very close to natural wetlands. Wetlands that are candidates for restoration include constructed wetlands that host populations of wood frogs and marbled salamander larvae; constructed wetlands with natural-type

characteristics such as shallow depth, variable microtopography, high canopy closure, and upland habitat connectivity; and altered natural basins where hydroperiod has been disrupted by anthropogenic disturbance.

Reduction of wetland density and alteration of constructed wetlands

It is important to reduce overall constructed UEW density to achieve landscape structure that is similar to natural UEWs. Maximum constructed wetland density (~18 constructed wetlands/mi²) in the Cumberland District of the DBNF is more than ten times that of maximum natural wetland density (~1 natural wetland/mi²). Reduction of constructed UEW density to more closely resemble the density of naturally-occurring wetlands is recommended.

A subset of constructed wetlands should also be altered with the aim of inducing ephemeral hydroperiod. Experimentation and adaptive management will be necessary to determine the best methods to achieve this condition. Candidate methods could include decompacting soils, planting native trees to draw down water levels through evapotranspiration, and altering dams to make wetlands shallower. Planting trees and woody shrubs will also increase canopy closure, which improves habitat for amphibians and may help control invasive species such as *Microstegium vimineum* (Japanese stiltgrass) (Cole & Weltzin, 2004). Prudent experimentation and adaptive management should be implemented to identify the best methods of altering or removing permanent constructed wetlands.

Long-term monitoring

Long-term monitoring is an important part of habitat alteration and restoration projects. Monitoring for at least six years is recommended to determine amphibian colonization and reproduction success (Vasconcelos & Calhoun, 2006; Calhoun et al., 2014). Plant communities tend to take even longer to recover after wetland construction or significant disturbance (Moreno-Mateos et al., 2012; Zedler & Callaway, 1999). Long term amphibian monitoring in the UEW system should encompass counts of wood frog egg masses, presence and abundance of ephemeral-wetland obligate amphibian larvae, and presence and abundance of adult eastern newts and larval green frogs prior to and post-alteration. Vegetation monitoring should document, at minimum, canopy closure and presence/cover of invasive species. Periodic surveys for plant richness and understory species cover could take place to track community development, floristic quality, and ecological conservatism over time. Wetland depth and hydroperiod should also be tracked to determine whether water is present in adequate depth and length of time to allow successful amphibian breeding, hatching, and metamorphosis.

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APPENDICES

Appendix A: Amphibian Models

Appendix A: Amphibian Models

Table A-1. Candidate models for multiple linear regression and logistic regression modeling of amphibian CPUE. T = water temperature, cond = specific conductivity, DO = % saturation dissolved O₂, ORP = oxidation-reduction potential, dep. = maximum wetland depth, slope = average slope of littoral zone, type = type of wetland (natural, RS [random-selection] constructed, TS [targeted-selection] constructed), CWD = coarse woody debris volume, can. = canopy closure, # var = number of variables in that model. ψ Depth and littoral slope were correlated ($r > 0.80$) and were not included simultaneously in any models.

model name	Variables										# var
	T	cond	DO	ORP	pH	dep.	slope	type	CWD	can.	
DO	.	.	x	1
slope	x	.	.	.	1
depth	x	1
type	x	.	.	1
canopy ^ψ	x	1
pH	x	1
ORP	.	.	.	x	1
T	x	1
cond	.	x	1
CWD ^ψ	x	.	1
depth, type	x	.	x	.	.	2
slope, type	x	x	.	.	2
T, cond	x	x	2
pH, depth	x	x	2
ORP, T	x	.	.	x	2
ORP, DO	.	.	x	x	2
DO, pH	.	.	x	.	x	2
cond, depth	.	x	.	.	.	x	2
T, slope	x	x	.	.	.	2
water quality	.	x	x	.	x	3
water characteristics	.	x	x	x	x	4
water quality, depth	.	x	x	.	x	x	4
water quality, slope	.	x	x	.	x	.	x	.	.	.	4
cond, type, pH, depth	.	.	.	x	x	.	x	.	.	.	4
water quality, slope, type	.	x	x	.	x	.	x	x	.	.	5

Table A-1 continued

model name	<i>Variables</i>										# var
	T	cond	DO	ORP	pH	dep.	slope	type	CWD	can.	
water quality, depth, type	.	x	x	.	x	x	.	x	.	.	5
“global” lacking depth ψ	x	x	x	x	x	.	x	x	.	.	7
“global” lacking slope ^ψ	x	x	x	x	x	x	.	x	.	.	7

Appendix B: Vegetation Table

Appendix B Vegetation Table

Table B-1. Species presence at natural and constructed wetland sites in the Cumberland District of the Daniel Boone National Forest. Family, scientific name, species author, function group (FG), coefficient of conservatism (C), and wetland indicator status (WIS) are indicated. Functional group symbols: W = woody, P = perennial forb, A = annual forb, B = biennial forb, G = graminoid, F = fern. Wetland indicator status symbols: OBL = obligate wetland species, FACW =

species	family	FG	native	WIS	C	DG ₁ ^φ	DC ₂ ^φ	DC ₃ ^φ	DC ₄ ^φ	3-10	3-08	3-03	3-02	JRC	JRN ^φ	HEC	HEN ^φ	BPP	BPN ^φ	ELC	ELN ^φ	GLC	GLN ^φ	977C	977N ^φ	
<i>Acer rubrum</i> L.	Sapindaceae	W	Y	FAC	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Acer saccharum</i> Marshall	Sapindaceae	W	Y	FACU	5	1	.	1	1
<i>Actaea racemosa</i> L.	Ranunculaceae	PF	Y	FACU	7	1
<i>Ageratina altissima</i> (L.) R.M. King & H. Rob.	Asteraceae	PF	Y	UPL	3	1	.	.	1
<i>Agrimonia parviflora</i> Aiton	Rosaceae	PF	Y	FACW	2	1
<i>Agrimonia pubescens</i> Wallr.	Rosaceae	PF	Y	NA	5	1
<i>Agrostis perennans</i> (Walter) Tuck.	Poaceae	G	Y	FACU	6	1	1
<i>Alisma subcordatum</i> Raf.	Alismataceae	PF	Y	OBL	2	1
<i>Ambrosia artemisiifolia</i> L.	Asteraceae	AF	Y	FACU	0	1
<i>Amelanchier arborea</i> (F. Michx.) Fernald	Rosaceae	W	Y	FAC	5	1	1	1	1	1	1	1	.	.	1	1	1	1	1	1	1	1	1	1	1	1
<i>Amphicarpa bracteata</i> (L.) Fald	Fabaceae	A/PF	Y	FAC	4	1	1	1	1	1
<i>Andropogon virginicus</i> L.	Poaceae	G	Y	FACU	2

Table B-1 (continued)

species	family	FG	native	WIS	C	DC6 ^φ	DC5 ^φ	DC4 ^φ	DC2 ^φ	3-10	3-08	3-03	3-02	JRC	JRN ^φ	HEC	HEN ^φ	BPP	BPN ^φ	ELC	ELN ^φ	GLC	GLN ^φ	977C	977N ^φ	
<i>Apios americana</i> Medik.	Fabaceae	PF	Y	FACW	3	1
<i>Apocynum cannabinum</i> L.	Apocynaceae	PF	Y	FACU	1	.	1	.	.	.	1
<i>Aralia spinosa</i> L.	Araliaceae	W	Y	FAC	5	1	1	1
<i>Asimina triloba</i> (L.) Dunal	Annonaceae	W	Y	FAC	6	.	1	1
<i>Athyrium filix-femina</i> (L.) Roth	Dryopteridaceae	F	Y	FAC	5	1
<i>Aureolaria laevigata</i> (Raf.) Raf.	Scrophulariaceae	PF	Y	UPL	8	1
<i>Betula alleghaniensis</i> Britton	Betulaceae	W	Y	FAC	7	1
<i>Betula lenta</i> L.	Betulaceae	W	Y	FACU	7
<i>Betula nigra</i> L.	Betulaceae	W	Y	FACW	9	1
<i>Bidens polylepis</i> S. F. Blake	Asteraceae	AF	Y	UPL	*	1
<i>Bidens</i> sp. L.	Asteraceae	NA	Y	NA	NA	.	.	.	1	1	1	1	.	1	.	1	.	1	.	1	1	1	1	1	1	1
<i>Boehmeria cylindrica</i> (L.) Sw.	Urticaceae	PF	Y	FACW	4	.	.	1	1	.	.	1	1	.	.	1	.	1	1	1	1	1	1	1	1	1
<i>Brachyelytrum erectum</i> (Schreb.) P. Beauv.	Poaceae	G	Y	FACU	5	1	1	1
<i>Brasenia schreberi</i> J.F.Gmel.	Cabombaceae	PF	Y	OBL	7	1	1	.	.	.	1	.	1	.	1	1	1
<i>Carex abscondita</i> Mack.	Cyperaceae	G	Y	FACW	U	1	1

Table B-1 (continued)

species	family	FG	native	WIS	C	DC6 ^φ	DC5 ^φ	DC4 ^φ	DC2 ^φ	3-10	3-08	3-03	3-02	JRC	JRN ^φ	HEC	HEN ^φ	BPP	BPN ^φ	ELC	ELN ^φ	GLC	GLN ^φ	977C	977N ^φ	
<i>Carex albolutescens</i> Schwein.	Cyperaceae	G	Y	FACW	7
<i>Carex crinita</i> Lam.	Cyperaceae	G	Y	FAC	7
<i>Carex digitalis</i> Willd.	Cyperaceae	G	Y	UPL	4
<i>Carex festuacea</i> Schkuhr.	Cyperaceae	G	Y	FAC	7	.	.	.	1
<i>Carex frankii</i> Kunth	Cyperaceae	G	Y	OBL	2
<i>Carex grayi</i> J. Carey	Cyperaceae	G	Y	FACW	5	.	.	1	1	1
<i>Carex laxiculmis</i> Schwein.	Cyperaceae	G	Y	UPL	3
<i>Carex lurida</i> Wahlenb.	Cyperaceae	G	Y	OBL	3
<i>Carex squarrosa</i> L.	Cyperaceae	G	Y	FACW	4	1	1
<i>Carex swanii</i> (Fald) Mack.	Cyperaceae	G	Y	FACU	4	.	.	1	.	.	1	1	1	1
<i>Carex tribuloides</i> Wahlenb.	Cyperaceae	G	Y	FACW	4	1
<i>Carex typhina</i> Michx.	Cyperaceae	G	Y	FACW	5	1
<i>Carex vulpinoidea</i> Michx.	Cyperaceae	G	Y	OBL	1	1
<i>Carpinus caroliniana</i> Walter	Betulaceae	W	Y	FAC	5
<i>Carya glabra</i> (Mill.) Sweet	Juglandaceae	W	Y	FACU	5	.	1	1	.	1	.	1	1	1

Table B-1 (continued)

species	family	FG	native	WIS	C	DC6 [‡]	DC5 [‡]	DC4 [‡]	DC2 [‡]	3-10	3-08	3-03	3-02	JRC	JRN [‡]	HEC	HEN [‡]	BPP	BPN [‡]	ELC	ELN [‡]	GLC	GLN [‡]	977C	977N [‡]	
<i>Carya tomentosa</i> (Poir.) Nutt.	Juglandaceae	W	Y	UPL	6		1	1	1	1	1	1	1			1		1		1	1					
<i>Castanea dentata</i> (Marshall) Borkh.	Fagaceae	W	Y	UPL	6	1																				
<i>Cephalanthus occidentalis</i> L.	Rubiaceae	W	Y	OBL	6		1														1					
<i>Cercis canadensis</i> L.	Fabaceae	W	Y	FACU	3		1	1	1																	
<i>Chamaecrista fasciculata</i> (Michx.) Greene	Fabaceae	AF	Y	FACU	3			1																		
<i>Chamaecrista nictitans</i> (L.) Moench	Fabaceae	AF/PF	Y	FACU	4																	1				
<i>Chysanthemum leucanthemum</i> L.	Asteraceae	PF	N	UPL	*				1																	
<i>Cinna arundinacea</i> L.	Poaceae	G	Y	FACW	5																		1			
<i>Conoclinium coelestinum</i> (L.) DC.	Asteraceae	PF	Y	FAC	3				1					1												
<i>Cornus florida</i> L.	Cornaceae	W	Y	FACU	5				1																	
<i>Cornus foemina</i> Mill.	Cornaceae	W	Y	FACW	7		1		1														1	1	1	1
<i>Coronilla varia</i> L.	Fabaceae	PF	Y	NA	*																					
<i>Cryptotaenia canadensis</i> (L.) DC.	Apiaceae	PF	Y	FAC	3								1													
<i>Cypripedium acaule</i> Aiton	Orchidaceae	PF	Y	FACU	8	1																				
<i>Danthonia spicata</i> (L.) P. Beauv.	Poaceae	G	Y	UPL	4																					1
<i>Daucus carota</i> L.	Apiaceae	BF	N	UPL	*																					
<i>Desmodium glutinosum</i> (Muhl. ex Willd.) Alph. Wood	Fabaceae	PF	Y	UPL	5				1																	1

Table B-1 (continued)

species	family	FG	native	WIS	C	DC6 ^φ	DC5 ^φ	DC4 ^φ	DC2 ^φ	3-10	3-08	3-03	3-02	JRC	JRN ^φ	HEC	HEN ^φ	BPP	BPN ^φ	ELC	ELN ^φ	GLC	GLN ^φ	977C	977N ^φ	
<i>Desmodium nudiflorum</i> (L.) DC.	Fabaceae	PF	Y	UPL	5	1	.	1	.	1	.	.	.	1
<i>Desmodium paniculatum</i> (L.) DC.	Fabaceae	PF	Y	FACU	3	1	1	.	1	.	1	.	1	.	1	.	1
<i>Desmodium rotundifolium</i> DC.	Fabaceae	PF	Y	UPL	6	1	.	1
<i>Dichanthelium boscii</i> (Poir.) Gould & C.A. Clark	Poaceae	G	Y	UPL	6	1	1
<i>Dichanthelium clandestinum</i> (L.) Gould	Poaceae	G	Y	FAC	2	1	.	.	1	1
<i>Dichanthelium dichotomum</i> (L.) Gould	Poaceae	G	Y	FAC	0	1	.	1	.	1	.	1	.	1	.	1	.	1	1	1	1	1
<i>Dichanthelium latifolium</i> (L.) Gould & C.A. Clark	Poaceae	G	Y	FACU	4	1	1	1	.	1	.	1	1	.	.	.
<i>Dichanthelium laxiflorum</i> (Lam.) Gould	Poaceae	G	Y	FACU	7	1
<i>Dichanthelium malacophyllum</i> (Nash) Gould	Poaceae	G	Y	UPL	10	1
<i>Dichanthelium polyanthes</i> (Schult.) Mohlenbr.	Poaceae	G	Y	FACU	3	1
<i>Dichanthelium sphaerocarpon</i> (Elliot) Gould	Poaceae	G	Y	FACU	4	1	1	.	.	.	1
<i>Dioscorea villosa</i> L.	Dioscoreaceae	PF	Y	FAC	4	1	1	1	.	1	.	1	1	1	1	1
<i>Diospyros virginiana</i> L.	Ebenaceae	W	Y	FAC	4	1
<i>Doellingeria infirma</i> (Michx.) Nees	Asteraceae	PF	Y	UPL	8	1

Table B-1 (continued)

species	family	FG	native	WIS	C	DC6 ^φ	DC5 ^φ	DC4 ^φ	DC2 ^φ	3-10	3-08	3-03	3-02	JRC	JRN ^φ	HEC	HEN ^φ	BPP	BPN ^φ	ELC	ELN ^φ	GLC	GLN ^φ	977C	977N ^φ	
<i>Echinochloa crus-galli</i> (L.) P. Beauv.	Poaceae	G	N	FAC	*								1													
<i>Echinochloa muricata</i> (P. Beauv.)	Poaceae	G	Y	FACW	2						1							1								
<i>Eleocharis ovata</i> (Roth) Roem. & Schult.	Cyperaceae	G	Y	OBL	9						1									1						
<i>Elephantopus carolinianus</i> Raeusch.	Asteraceae	PF	Y	FACU	4						1	1	1							1						
<i>Erechtites hieracifolia</i> (L.) Raf.	Asteraceae	AF	Y	FACU	2	1																				
<i>Erigeron strigosus</i> Muhl. ex Willd	Asteraceae	AF	Y	FACU	1																					1
<i>Eurybia divaricata</i> (L.) G.L. Nesom	Asteraceae	PF	Y	UPL	5				1	1				1												1
<i>Euthamia graminifolia</i> (L.) Nutt. ex Cass	Asteraceae	PF	Y	FAC	2						1															1
<i>Eupatorium fistulosum</i> (Barratt)	Asteraceae	PF	Y	FACW	6																					1
<i>Fagus grandifolia</i> Ehrh.	Fagaceae	W	Y	FACU	7	1											1	1								
<i>Fraxinus pennsylvanica</i> Marshall	Oleaceae	W	Y	FACW	3	1					1	1	1				1	1								1
<i>Galium circaezans</i> Michx.	Rubiaceae	PF	Y	UPL	4						1															
<i>Galium pilosum</i> Aiton	Rubiaceae	PF	Y	UPL	4						1															
<i>Galium tinctorium</i> (L.)	Rubiaceae	PF	Y	OBL	4																					1
<i>Galium triflorum</i> Michx.	Rubiaceae	PF	Y	FACU	4						1															1

Table B-1 (continued)

species	family	FG	native	WIS	C	DC6 ^φ	DC5 ^φ	DC4 ^φ	DC2 ^φ	3-10	3-08	3-03	3-02	JRC	JRN ^φ	HEC	HEN ^φ	BPP	BPN ^φ	ELC	ELN ^φ	GLC	GLN ^φ	977C	977N ^φ	
<i>Gaultheria procumbens</i> L.	Ericaceae	W	Y	FACU	5										1											
<i>Gaylussacia baccata</i> (Wangenh.) K. Koch	Ericaceae	W	Y	FACU	6	1																				
<i>Geum virginianum</i> L.	Rosaceae	PF	Y	FAC	3								1													
<i>Glyceria septentrionalis</i> Hitchc.	Poaceae	G	Y	OBL	6																					1
<i>Glyceria striata</i> (Lam.) Hitchc.	Poaceae	G	Y	OBL	2																					
<i>Hamamelis virginiana</i> L.	Hamamelidaceae	W	Y	FACU	5																					
<i>Houstonia purpurea</i> L.	Rubiaceae	PF	Y	UPL	5								1													1
<i>Hypericum mutilum</i> L.	Clusiaceae	AF/PF	Y	FACW	3																					
<i>Hypericum stragulum</i> W. P. Adams & N. Robson	Clusiaceae	W	Y	UPL	6										1											
<i>Ilex verticillata</i> (L.) A. Gray	Aquafoliaceae	W	Y	FACW	6																					
<i>Impatiens capensis</i> Meerb.	Balsaminiaceae	AF	Y	FACW	2																					
<i>Iris cristata</i> Soland. ex Aiton	Iridaceae	PF	Y	UPL	5																					1
<i>Juncus acuminatus</i> Michx.	Juncaceae	G	Y	OBL	4																					
<i>Juncus coriaceous</i> Mack.	Juncaceae	G	Y	FACW	6																					
<i>Juncus effusus</i> L.	Juncaceae	G	Y	FACW	1								1													

Table B-1 (continued)

species	family	FG	native	WIS	C	DC6 [†]	DC5 [†]	DC4 [†]	DC2 [†]	3-10	3-08	3-03	JRC	JRN [†]	HEC	HEN [†]	BPP	BPN [†]	ELC	ELN [†]	GLC	GLN [†]	977C	977N [†]	
<i>Juniperus virginiana</i> L.	Cupressaceae	W	Y	FACU	3	1
<i>Kalmia latifolia</i> L.	Ericaceae	W	Y	FACU	7	.	.	1	1
<i>Leersia oryzoides</i> (L.) Sw.	Poaceae	G	Y	OBL	1	1	1	1	1	.	.	1	1	.	.	1	.	.	.
<i>Leersia virginica</i> Willd.	Poaceae	G	Y	FACW	4	1	.	1	1	1	1	1
<i>Lespedeza intermedia</i> (S. Watson) Britton	Fabaceae	PF	Y	UPL	3	1
<i>Lespedeza hirta</i> (L.) Hornem.	Fabaceae	PF	Y	UPL	5	1	.	1	1	.	.	.
<i>Lespedeza procumbens</i> Michx.	Fabaceae	PF	Y	UPL	5	1
<i>Lespedeza violaceae</i> (L.) Pers.	Fabaceae	PF	Y	UPL	4	1	1	.	.	.
<i>Lespedeza virginica</i> (L.) Britton	Fabaceae	PF	Y	UPL	3	1	.	.	.
<i>Lindera benzoin</i> (L.) Blume	Lauraceae	W	Y	FAC	5	.	.	1	1	.	.	1	1	1	.	.
<i>Liquidambar styraciflua</i> L.	Altingiaceae	W	Y	FAC	6	.	.	.	1	.	1
<i>Liriodendron tulipifera</i> L.	Magnoliaceae	W	Y	FACU	6	.	.	.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Lobelia inflata</i> L.	Campanulaceae	AF	Y	FACU	1
<i>Lobelia puberula</i> Michx.	Campanulaceae	PF	Y	FACW	5	1

Table B-1 (continued)

species	family	FG	native	WIS	C	DC6 [‡]	DC5 [‡]	DC4 [‡]	DC2 [‡]	3-10	3-08	3-03	3-02	JRC	JRN [‡]	HEC	HEN [‡]	BPP	BPN [‡]	ELC	ELN [‡]	GLC	GLN [‡]	977C	977N [‡]	
<i>Lobelia siphilitica</i> L.	Campanulaceae	PF	Y	FACW	3	1
<i>Lobelia spicata</i> Lam.	Campanulaceae	PF	Y	FAC	5	1
<i>Lonicera japonica</i> Thunb.	Caprifoliaceae	PF	N	FAC	*	1	1
<i>Ludwigia alternifolia</i> L.	Onagraceae	PF	Y	FACW	3	1	1	1
<i>Ludwigia palustris</i> (L.) Elliott	Onagraceae	PF	Y	OBL	3
<i>Lycopus virginicus</i> L.	Lamiaceae	PF	Y	OBL	3	1	1	1
<i>Lysimachia lanceolata</i> Walter	Primulaceae	PF	Y	FAC	6	1
<i>Lysimachia quadrifolia</i> L.	Primulaceae	PF	Y	FACW	5	1	1	1
<i>Magnolia acuminata</i> (L.) L.	Magnoliaceae	W	Y	FACU	7
<i>Magnolia tripetala</i> L.	Magnoliaceae	W	Y	FACU	8	1
<i>Maianthemum racemosum</i> (L.) Link	Convallariaceae	PF	Y	FACU	4	1	1
<i>Microstegium vimineum</i> (Trin.) A. Camus	Poaceae	G	N	FAC	*	1	1	1	1
<i>Mitchella repens</i> L.	Rubiaceae	PF	Y	FACU	5	1	1
<i>Monarda clinopodia</i> L.	Lamiaceae	PF	Y	FAC	4
<i>Nyssa sylvatica</i> Marshall	Nyssaceae	W	Y	FAC	7	1	1	1	1	.	1	.	1	.	1	1	1	1	1	1	.	1	1	1	1	1

Table B-1 (continued)

species	family	FG	native	WIS	C	DC6 [‡]	DC5 [‡]	DC4 [‡]	DC2 [‡]	3-10	3-08	3-03	3-02	JRC	JRN [‡]	HEC	HEN [‡]	BPP	BPN [‡]	ELC	ELN [‡]	GLC	GLN [‡]	977C	977N [‡]	
<i>Onoclea sensibilis</i> L.	Dryopteridaceae	F	Y	FACW	2
<i>Oxydendrum arboreum</i> (L.) DC.	Ericaceae	W	Y	UPL	7	1	1	1	.	.	1	.	.	1	1	1	1	.	1	.	.	1	1	1	1	.
<i>Panicum anceps</i> Michx.	Poaceae	G	Y	FAC	3	1	1	.	1	.	1
<i>Parthenocissus quinquefolia</i> (L.) Planch.	Vitaceae	PF	Y	FACU	2	1	1	1	1	1	1	1	1	.	1	.	1	1	1	1	1	1
<i>Pilea pumila</i> (L.) A. Gray	Urticaceae	AF	Y	FACW	2	1	.	1	1
<i>Pinus strobus</i> L.	Pinaceae	W	Y	FACU	*	1
<i>Pinus virginiana</i> Mill.	Pinaceae	W	Y	UPL	3	1	1	1	.	.	1	.	1	.	1
<i>Plantago major</i> L.	Plantagaceae	PF	N	FACU	*
<i>Platanus occidentalis</i> L.	Platanaceae	W	Y	FACW	7	1	.	1
<i>Podophyllum peltatum</i> L.	Berberidaceae	PF	Y	FACU	4
<i>Polygonatum biflorum</i> (Walter) Elliott	Convallariaceae	PF	Y	FACU	4	1	1	1	1	1
<i>Polygonum caespitosum</i> Blume	Polygonaceae	AF	N	FACU	*	1
<i>Polygonum punctatum</i> Elliott	Polygonaceae	AF	Y	OBL	6	1
<i>Polystichum acrostichoides</i> (Michx.) Schott	Dryopteridaceae	F	Y	FACU	3	1	.	1	1	.	.	1	1	1	1	1	1

Table B-1 (continued)

species	family	FG	native	WIS	C	DC6 [‡]	DC5 [‡]	DC4 [‡]	DC2 [‡]	3-10	3-08	3-03	3-02	JRC	JRN [‡]	HEC	HEN [‡]	BPP	BPN [‡]	ELC	ELN [‡]	GLC	GLN [‡]	977C	977N [‡]	
<i>Populus grandidentata</i> Michx.	Salicaceae	W	Y	FACU	2
<i>Potamogeton diversifolius</i> Raf.	Potamogetonaceae	PF	Y	OBL	5	1	1
<i>Potamogeton nodosus</i> Poir.	Potamogetonaceae	PF	Y	OBL	3	1
<i>Potentilla canadensis</i> L.	Rosaceae	PF	Y	UPL	3	1	1	1	1	1
<i>Prenanthes serpentaria</i> Pursh	Asteraceae	PF	Y	UPL	5	1	.	.	.	1	1	1
<i>Prunus</i> sp. L.	Rosaceae	NA	Y	NA	NA	1
<i>Pycnanthemum</i> sp. Michx.	Lamiaceae	NA	Y	NA	NA	1
<i>Quercus alba</i> L.	Fagaceae	W	Y	FACU	6	.	1	.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Quercus montana</i> Willd.	Fagaceae	W	Y	UPL	7	1	1	1	1	1	1	.	.	1	1	1	1	1	1	1	1	1	1	1	1	.
<i>Quercus rubra</i> L.	Fagaceae	W	Y	FACU	6	1	1	1	1	1	.	.	.	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Quercus stellata</i> Wangenh.	Fagaceae	W	Y	UPL	7	1
<i>Quercus velutina</i> Lam.	Fagaceae	W	Y	UPL	7	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Robinia pseudoacacia</i> L.	Fagaceae	W	Y	FACU	0	1	1
<i>Rosa carolina</i> L.	Rosaceae	W	Y	UPL	4	1
<i>Rosa multiflora</i> Thunb.	Rosaceae	W	N	FACU	*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table B-1 (continued)

species	family	FG	native	WIS	C	DC6 [‡]	DC5 [‡]	DC4 [‡]	DC2 [‡]	3-10	3-08	3-03	3-02	JRC	JRN [‡]	HEC	HEN [‡]	BPP	BPN [‡]	ELC	ELN [‡]	GLC	GLN [‡]	977C	977N [‡]	
<i>Rubus</i> sp. L.	Rosaceae	W	Y	NA	NA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Salix nigra</i> Marshall	Salicaceae	W	Y	OBL	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Sambucus canadensis</i> (L.) R. Bolli	Caprifoliaceae	W	Y	FACW	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Sanicula canadensis</i> L.	Apiaceae	PF	Y	UPL	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Sassafras albidum</i> (Nutt.) Nees	Lauraceae	W	Y	FACU	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Scirpus atrovirens</i> Willd.	Cyperaceae	G	Y	OBL	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Scirpus cyperinus</i> (L.) Kunth	Cyperaceae	G	Y	FACW	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Scirpus georgianus</i> R. M. Harper	Cyperaceae	G	Y	OBL	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Scirpus pendulus</i> Muhl. ex Elliott	Cyperaceae	G	Y	OBL	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Scirpus polyphyllus</i> Vahl	Cyperaceae	G	Y	OBL	6	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Silphium terebinthinaceum</i> Jacq.	Asteraceae	PF	Y	FACU	8	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Sisyrinchium angustifolium</i> Mill.	Iridaceae	PF	Y	FACW	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Smilax rotundifolia</i> L.	Smilacaceae	W	Y	FAC	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Solanum carolinense</i> L.	Solanaceae	PF	Y	FACU	*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table B-1 (continued)

species	family	FG	native	WIS	C	DC6 [†]	DC5 [†]	DC4 [†]	DC2 [†]	3-10	3-08	3-03	3-02	JRC	JRN [†]	HEC	HEN [†]	BPP	BPN [†]	ELC	ELN [†]	GLC	GLN [†]	977C	977N [†]		
<i>Solidago canadensis</i> L.	Asteraceae	PF	Y	FACU	1	1	
<i>Solidago gigantea</i> Aiton	Asteraceae	PF	Y	FACW	3	1	
<i>Solidago nemoralis</i> Aiton	Asteraceae	PF	Y	UPL	2	1	1	
<i>Solidago</i> sp. L.	Asteraceae	NA	Y	NA	NA	1	1	
<i>Sorghastrum nutans</i> (L.) Nash	Poaceae	G	Y	FACU	5	1	
<i>Sparganium americanum</i> Nutt.	Typhaceae	G	Y	OBL	6	1	.	.	1	.	1	
<i>Symphoricarpos orbiculatus</i> Moench	Caprifoliaceae	W	Y	UPL	3	1	
<i>Thelypteris noveboracensis</i> (L.) Nieuwl.	Thelypteridaceae	F	Y	FAC	4	1	.	1	
<i>Toxicodendron radicans</i> (L.) Kuntze	Anacardiaceae	PF	Y	FAC	1	.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Trifolium campestre</i> Schreb.	Fabaceae	AF	N	UPL	*	1	
<i>Tripsacum dactyloides</i> (L.) L.	Poaceae	G	Y	FACW	5	1	
<i>Typha angustifolia</i> L.	Typhaceae	G	N	OBL	*	1	1	1	.	.	1	
<i>Ulmus americana</i> L.	Ulmaceae	W	Y	FACW	2	1	.	1	
<i>Ulmus rubra</i> Muhl.	Ulmaceae	W	Y	FAC	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Uvularia perfoliata</i> L.	Uvulariaceae	PF	Y	FACU	5	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	

Table B-1 (continued)

species	family	FG	native	WIS	C	DC6 [†]	DC5 [†]	DC4 [†]	DC2 [†]	3-10	3-08	3-03	3-02	JRC	JRN [†]	HEC	HEN [†]	BPP	BPN [†]	ELC	ELN [†]	GLC	GLN [†]	977C	977N [†]	
<i>Vaccinium pallidum</i> Aiton	Ericaceae	W	Y	UPL	6	1	1	1	1	1	1	1	1	1	1	1	1					1	1	1	1	.
<i>Vernonia gigantea</i> (Walter) Trel.	Asteraceae	PF	Y	FAC	2	1	1	1	1
<i>Viburnum acerifolium</i> L.	Adoxaceae	W	Y	UPL	6	1	1	1	1	1	.
<i>Viburnum dentatum</i> L.	Adoxaceae	W	Y	FAC	2	1	1	1	1	1	1
<i>Viola</i> sp. L.	Violaceae	NA	Y	NA	NA	1	.	.	.	1	1
<i>Vitis vulpina</i> L.	Vitaceae	W	Y	FAC	3	.	1	.	.	1	.	1	1	1	.	1	1	1	1	1	1	