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Physical wetland characteristics influence amphibian community composition differently in constructed wetlands and natural wetlands

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ABSTRACT

Wetlands provide critical habitat for a diverse group of organisms and provide important ecosystem services. Despite this, most natural wetlands have been lost to anthropogenic activities, and as a result, wetland construction is common mitigation practice. Therefore, examination of constructed wetland viability in replacing the function of lost wetlands is vital. Our primary objectives were to compare amphibian communities of shallow and deep constructed wetlands to natural wetlands and to identify which wetland characteristics affect species composition. All wetlands were hydrologically isolated and fishless; natural wetlands had an ephemeral hydrology, and constructed wetland hydrology varied from ephemeral to permanent. Overall, constructed wetlands did not sufficiently replicate natural wetlands with respect to the amphibian community. However, two of our constructed wetlands had a drying period and exhibited communities more similar to natural wetlands. Hydroperiod and canopy closure were indicators of amphibian community composition. Many species observed in natural wetlands were rare in shallow constructed and absent in deep constructed wetlands. Additionally, dominant predator species (primarily *Lithobates catesbeianus*, *Lithobates clamitans*, and *Notophthalmus viridescens*) associated with permanent water were more abundant in constructed wetlands. Water depth, pH, and emergent vegetation were lower in natural wetlands. These data influenced land managers to revise construction methods and to renovate deep constructed wetlands by creating gradual slopes, decreasing maximum depth to 20 cm or less, maintaining canopy cover, and decreasing soil compaction to attempt replication of natural wetland hydrology.

1. Introduction

Wetland loss is a global phenomenon; in fact, Myers (1997) suggests a worldwide wetland loss of 50% within the last century. In the United States, many states have lost a large percentage of historical wetlands. For example, Kentucky sustained a loss of 81% of its historic wetlands (512,332 ha) between 1780 and 1980, with much of this being attributable to conversion of wetlands for agriculture (Dahl 1990, 2000). Additionally, human alteration of wetland hydrology (e.g., deepening an ephemeral pool for cattle watering purposes) can change the natural community composition (Kingsford et al., 2004; Havel et al., 2005; Foti et al., 2012), which can be detrimental for species that have life-history traits specific to ephemeral wetlands (Kiesecker et al., 2001; Pechmann et al., 2001; Jenkins et al., 2005; Denton and Richter 2013; Calhoun et al., 2014). Habitat loss and alteration are two of the most important factors affecting persistence of amphibian communities in the US and worldwide (Becker et al., 2007; Gallant et al., 2007).

Because of the high rate of wetland loss over the last century, it has become routine to mitigate for these losses by constructing wetlands. Brown et al. (2012) synthesized the literature (37 peer-reviewed articles) on amphibian communities utilizing restored, newly constructed, and mitigated wetland sites. Presumably due to the lack of natural reference sites, only 16 of these studies on constructed wetlands used natural reference wetlands as a comparison. Most of the research observed differences in amphibian use of constructed and natural wetlands based primarily on wetland hydrology and presence of fish predators (Petranka et al., 2007). For example, Pechmann et al. (2001) found ephemeral natural wetlands had more salamander species present than permanent constructed wetlands. Additionally, Denton and Richter (2013) found constructed wetlands intended to be ephemeral were mostly permanent and did not support specialist amphibians of the

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ephemeral natural wetlands. These studies demonstrate the difficulty of replicating natural habitats when attempting to mitigate or create habitat for amphibians.

The composition and fitness of amphibian communities found within wetlands is influenced by multiple interacting factors including water quality (pH- Freda and Dunson 1986; Rowe et al., 1992; Grant and Licht 1993; Bunnell and Zampella 1999; McCoy and Harris 2003; salinity- Smith et al., 2007; Karraker et al., 2008; dissolved oxygen- McIntyre and McCollum 2000; Skelly et al., 2002; Schiesari 2006), hydroperiod (Snodgrass et al., 2000b; Eagan and Paton 2004; Baldwin et al., 2006; Ryan 2007), slope (Shulse et al., 2012), canopy closure (Skelly et al., 2002; Thurgate and Pechmann 2007; Denton and Richter 2013), aquatic vegetation (Eagan and Paton 2004; Shulse et al., 2010, 2012), predation (Werner 1986; Werner and McPeek 1994; Knutson et al., 2004; Petranka et al., 2007; Shulse et al., 2010, 2012), and competition (Werner et al., 1995; Shulse et al., 2012). Hydroperiod, in particular, has influential effects on multiple wetland characteristics and consequently species composition within wetland habitats (Wellborn et al., 1996; Korfel et al., 2010; reviewed in Calhoun et al., 2014). While wetlands with a long hydroperiod tend to have higher species richness (Babbitt et al., 2003), wetlands with a short hydroperiod tend to have less common, specialized species (Snodgrass et al., 2000b; Korfel et al., 2010). A short hydroperiod can be beneficial in excluding dominant amphibian predators (e.g. *Lithobates catesbeianus*, American bullfrogs) (Kiesecker et al., 2001), increasing water temperature, and influencing development and survival of larvae to metamorphosis (Rowe and Dunson 1995; Wellborn et al., 1996; Skelly et al., 2002). Thus, ephemeral wetlands with short hydroperiods are important for maintaining biological diversity (Snodgrass et al., 2000b; Calhoun et al., 2014). However, there is a risk of tadpole mortality during long periods of low precipitation within these temporary habitats (Rowe and Dunson 1995; Seigel et al., 2006).

Wetland design for non-game wildlife, specifically amphibians, is a burgeoning field of study (Petranka et al., 2007; Biebighauser, 2011; Shulse et al., 2012; Denton and Richter 2013; Calhoun et al., 2014). Wetland building for game species (e.g. deer, turkey, etc.) has a long tradition in wildlife management (Leopold 1987). Historically, these wetlands functioned as "all-purpose" permanent water sources (often stocked with fish) with wide variability in design; usually consisting of deep, steep-sided wetlands constructed by deepening an existing wetland or constructing a large clay-based groundwater dam (Biebighauser, 2007, 2011). Conversely, sensitive amphibian species tend to thrive in complex habitats with shallow littoral zones for basking and predator avoidance (Porej and Hetherington 2005; Shulse et al., 2012; Denton and Richter 2013), woody debris and emergent vegetation for egg attachment (Shulse et al., 2010, 2012), and have species dependent tree canopy specifications (Skelly et al., 2002; Thurgate and Pechmann 2007; Denton and Richter 2013). Previous research on constructed wetlands as amphibian habitat has frequently addressed species richness or presence as an indicator of success (Knutson et al., 2004; Balcombe et al., 2005; Canals et al., 2011; Bellakhal et al., 2014) rather than focusing on replication of natural amphibian community structure as a gauge of success.

There were two primary objectives of this research: (1) to examine whether or not constructed wetlands foster amphibian community composition comparable to amphibian communities occupying natural ephemeral wetlands and (2) to determine what wetland characteristics affect species composition. In particular, this study focused on wetland characteristics with potential management implications including dimensions, depth, hydroperiod, canopy closure, aquatic vegetation, and water chemistry. Identification and quantification of specific characteristics that differ between natural and constructed wetlands are important information for land managers for improvement of current constructed habitats and for success of future amphibian enhancement projects.

2. Material and methods

2.1. Study sites

Wetlands have been constructed by the U.S. Forest Service in the Daniel Boone National Forest (DBNF), Kentucky, USA for over 50 years, with hundreds constructed since 1988 for the purpose of wildlife habitat enhancement (T. Biebighauser, pers. comm.). The wetlands used as study sites for this project consisted of ridge-top constructed and natural wetlands located within the Cumberland Ranger District of the DBNF in the Western Allegheny Plateau ecoregion (Woods et al., 2002). All of the study wetlands were hydrologically isolated ephemeral, semi-permanent, or permanent fishless wetlands located on ridge tops. We selected 14 study wetlands including 5 natural ephemeral (all known to exist), 5 shallow (2 ephemeral, 3 permanent) constructed wetlands (minimum depth <20 cm), and 4 permanent deep constructed wetlands (minimum depth >20 cm) for sampling in 2010 (Fig. 1) based on preliminary data on water depths (see Drayer, 2011). The study wetlands ranged in size from a surface area of 44.6–1415.6 m^2 (median = 351.9 m^2).

2.2. Sampling: amphibians

During the spring and summer 2010, we surveyed each wetland for amphibians in two-day increments in consecutive one-month intervals for a total of four sampling periods. Sampling commenced in May and ended in August. Each amphibian wetland survey included a perimeter visual encounter survey, aural survey, aquatic minnow trapping, and dipnetting (Crump and Scott 1994; Scott and Woodward 1994). Visual and aural encounter surveys started upon arrival at the wetland and consisted of walking the perimeter of the wetland while recording adults, juveniles, larvae, and egg masses observed. We deployed three collapsible mesh minnow traps along the perimeter of each wetland and distributed them evenly among heterogeneous habitat types. As the ephemeral wetlands decreased in size, we decreased the number of traps we placed in them. The traps were checked for amphibians within 24 h, and all species were recorded. Before dipnetting, a compass was used to separate the wetland into quadrants following the cardinal directions, north, south, east, and west from the geographic center of the wetland. For each 1400 m^2 (surface area), 20 one-meter dipnet sweeps (split evenly between the four sections) were performed. The number of dipnet sweeps was scaled up or down based on the estimated size of the wetland during each sampling. All habitat types (e.g., emergent vegetation, floating vegetation, and open water) were sampled evenly.

2.3. Sampling: physical wetland characteristics

To understand which factors within natural and constructed wetlands potentially affect amphibian community composition, the following variables were measured (at each wetland): wetland size, percent aquatic vegetation, water quality, depth at one meter from shoreline, maximum water depth, minimum water depth, and canopy closure. All variables were measured each sampling period except for percent canopy closure. Percent canopy closure was measured at maximum leaf-out and was estimated with a spherical densiometer at each of the four cardinal directions (from the geographic center of the wetland) along the perimeter and one point directly above the geometric center of each wetland. A meter stick was affixed in the deepest part of the wetland to record maximum and minimum depth measurements. Minimum depth refers

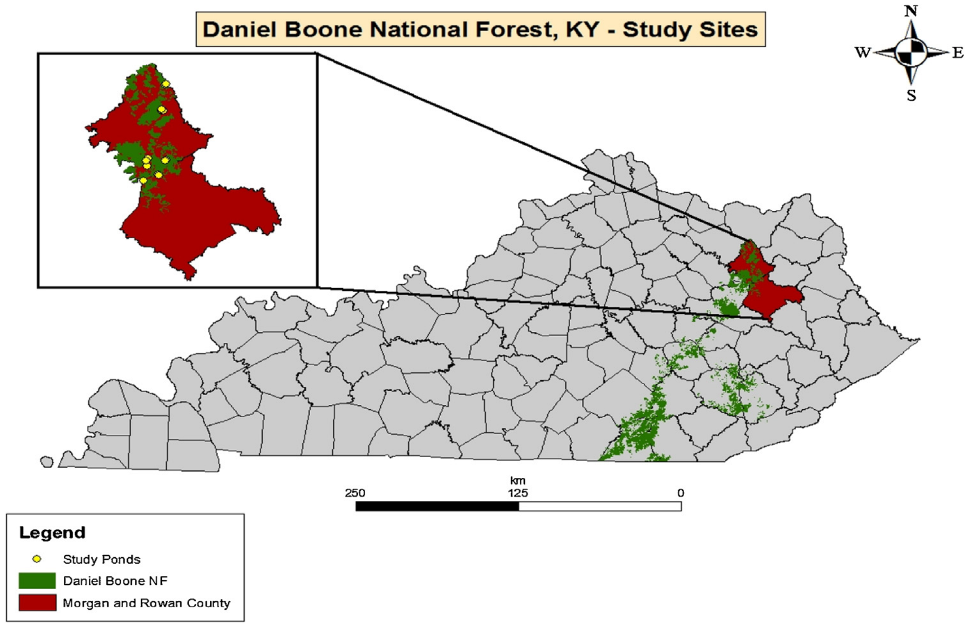

Fig. 1. Map of 2010 study sites in Daniel Boone National Forest, KY. Sites are located on ridgetops in Rowan and Morgan Counties in eastern Kentucky.

to the lowest depth recorded for the wetland for the entire sampling season. Additionally, we measured water depth at one meter from shoreline (littoral depth) at each cardinal direction point. A 1-m^2 plot was placed on the edge of the wetland at each cardinal direction point and extended into the wetland one meter. In each plot, we visually estimated percent vegetation cover and made note of specific vegetation types (cattails, sedges, etc.). Conductivity (μmhos), pH, and dissolved oxygen (% saturation) were taken one meter out from the wetland edge in each of the cardinal directions with a YSI 556 multi-parameter water quality meter (Yellow Springs Instruments; Yellow Springs, OH). In addition, we categorized each wetland by hydroperiod, permanent or ephemeral. In order for a wetland to be categorized as ephemeral, it had to dry down completely.

2.4. Data analyses: amphibians

To understand the pattern of amphibian communities present within the sampled wetland types, presence-absence data from a comprehensive species list (trap, dipnet, aural, and visual encounter data) and a breeding species list (larvae only) were entered into Quantitative Analysis in Ecology (QUANTAN; Brower et al., 1997). The QUANTAN program calculated measures of similarity for the entire community and for the breeding community, including Jaccard's and Sorensen's coefficients, Shannon Wiener Diversity Indices ($H = -\text{sum}(P_i \ln[P_i])$), and Shannon Wiener Evenness ($[E = H/\ln(S)]$, where S = species richness). Dipnet data were standardized by catch-per-unit-effort (CPUE) and used for abundance-based analyses. Amphibian abundance data (CPUE) and all habitat variables for constructed and natural wetlands were examined using redundancy analysis (RDA) in R Version 2.12.1 (R Development Core Team, Vienna, Austria) with package VEGAN (Oksanen et al., 2011). Normality assumptions were met using Hellinger transformation of species data prior to the RDA procedure (Legendre and Gallagher 2001). Permutation tests using the "anova.cca" command in Program R were used to examine significance of individual habitat parameters and axes used in RDA plots (Oksanen et al., 2011). Amphibian community composition differences among wetland types were evaluated with a permutational multivariate analysis of variance using a distance matrix and 10,000 permutations with the ADONIS function in R. The distance measure selected was the Bray-Curtis Similarity Index because of its success in approximating ecological distance (Bray and Curtis 1957; Faith et al., 1987). Sequential Bonferroni corrected p-values were used for pairwise comparisons.

2.5. Data analyses: physical wetland characteristics

Physical wetland variables were analyzed with a one-way ANOVA followed by Tukey post-hoc multiple comparisons to compare the variables with equal variances between natural and both constructed wetland types, including canopy cover, maximum depth, emergent vegetation, depth at one meter from shoreline, dissolved oxygen, pH, and wetland size. The other variable, conductivity, was analyzed with a Welch's t-test.

3. Results

3.1. Amphibian community composition

Of the 16 potential pond-breeding amphibian species present within the sampling region, 14 were observed during the sampling season [Exceptions: *Lithobates sphenocephalus* (southern leopard frog) and *Acris crepitans* (northern cricket frog)]. Natural wetlands and shallow constructed wetlands both had 13 species using them, whereas the deep constructed wetlands were used by nine species. When all survey types were combined, species composition varied widely between wetland types. Shallow constructed wetland communities had greater similarity to natural wetlands compared to deep constructed wetlands (Table 1a). Five species, *Scaphiopus holbrookii* (eastern spadefoot), *Pseudacris brachyphona* (mountain chorus frog), *Ambystoma opacum* (marbled salamander), *L. sylvaticus* (wood frog), and *Anaxyrus* spp. (American and Fowler's toads), were exclusively found in natural and shallow constructed wetlands but not deep constructed wetlands, while *L. catesbeianus* and *L. palustris* (pickerel frog) were only observed in constructed wetland types. The two constructed wetland types were weakly similar in amphibian community composition. When breeding success, as indicated by larval presence, was considered, the similarity between natural and shallow constructed wetlands weakens and

Table 1
Similarity and diversity indices for amphibian presence/absence data. Natural wetlands (N), shallow constructed (D < 20 = minimum depth less than 20 cm), and deep constructed (D > 20 = minimum depth greater than 20 cm). (a) Whole community similarity measures (adults, juveniles, and larvae), (b) Similarity measures based on breeding as indicated by larvae only, (c) Shannon-Wiener Diversity (H) and Evenness (E) measures based on larvae and newt adults.

a. Similarity: Whole Community (Adults, Juveniles, and Larvae)

Wetland Comparisons	Jaccard's Coefficient	Sorensen's Coefficient
N/D < 20	0.93	0.96
N/D > 20	0.62	0.76
D < 20/D > 20	0.57	0.73

b. Similarity: Breeding (Larvae Only)

Wetland Comparisons	Jaccard's Coefficient	Sorensen's Coefficient
N/D < 20	0.58	0.74
N/D > 20	0.36	0.53
D < 20/D > 20	0.64	0.78

c. Diversity: Shannon-Wiener Diversity (H) and Evenness (E) (Larvae/Newt Adults)

Wetland Type	H	E
Natural	0.58	0.28
D < 20	1.89	0.79
D > 20	1.69	0.87

Table 2
Physical wetland characteristics statistics summary table for 2010. Asterisks indicate statistical significance.

Physical Wetland Characteristics	Statistical Test	Test Statistic	df	p-value
Maximum Depth (cm)	One-Way ANOVA	F = 6.125	2	0.016*
% Canopy Closure	One-Way ANOVA	F = 2.937	2	0.095
% Emergent Vegetation	One-Way ANOVA	F = 4.569	2	0.036*
Depth at 1 m from Shoreline (cm)	One-Way ANOVA	F = 6.552	2	0.013*
pH	One-Way ANOVA	F = 18.839	2	<0.001*
% Dissolved Oxygen	One-Way ANOVA	F = 1.103	2	0.366
Conductivity (μS/cm)	Welch's *t*-test	t = 1.969	2	0.217
Wetland Size (m^2)	One-Way ANOVA	F = 2.063	2	0.173

* Asterisks indicate statistical significance.

the similarity between the constructed wetland types is stronger (Table 1b). Species diversity and evenness were lower for natural wetlands when compared to both types of constructed wetlands (Table 1c).

Individual species abundances varied across wetland types and had four patterns: (1) similar abundance in natural and shallow constructed wetlands (*L. sylvaticus*), (2) more abundant in constructed wetland types than natural (*P. crucifer*, *A. jeffersonianum*, *A. maculatum*), (3) only found in constructed (*Lithobates clamitans*, *L. catesbeianus*, *N. viridescens*, and *An.* spp.), (4) similar abundance in all wetland types (*H. chrysoscelis*). Conversely, *A. opacum*, *P. brachyphona*, and *Hemidactylium scutatum* (four-toed salamander), were observed more often in naturals, but had lower abundances (Fig. 2).

The RDA accounted for 68.5% of the total variation in amphibian community and habitat data, and the RDA model was significantly different from random ($F_8 = 4.54$, $p = 0.001$; Fig. 3). RDA1 and RDA2 axes accounted for 47.5% and 19.9% of the explained variation, respectively. Significant vector terms include hydroperiod ($F_1 = 13.89$, $p = 0.001$), canopy closure ($F_1 = 5.68$, $p = 0.001$), conductivity ($F_1 = 4.33$, $p = 0.002$), percent emergent vegetation ($F_1 = 3.84$, $p = 0.011$), dissolved oxygen ($F_1 = 2.62$, $p = 0.032$), and wetland size ($F_1 = 3.20$, $p = 0.02$). The ADONIS procedure revealed significant differences among wetland types in amphibian community composition (global $R^2 = 0.267$, $p = 0.038$), in which natural wetlands were significantly different from deep constructed wetlands ($F_1 = 3.57$, $p = 0.031$). Shallow constructed wetlands were not significantly different from deep constructed wetlands ($F_1 = 1.54$, $p = 0.162$) or natural wetlands ($F_1 = 1.28$, $p = 0.204$).

3.2. Physical wetland characteristics

Four wetland characteristics were significantly different among wetland types: maximum wetland depth, percent emergent vegetation, wetland depth at one meter from shoreline, and pH; whereas canopy closure (although much higher in natural wetlands), dissolved oxygen, conductivity, and wetland size were not statistically different among wetland types (Table 2).

Based on post-hoc pairwise comparisons, natural wetlands were significantly lower than deep constructed wetlands in terms of percent emergent vegetation and wetland depth at one meter from shoreline (Table 3, Fig. 4).

Natural wetlands were significantly lower in pH compared to shallow and deep constructed wetlands, and as expected, deep constructed wetlands had a greater wetland depth than shallow constructed and natural wetlands (Table 3, Fig. 4).

4. Discussion

Deep constructed wetlands in our study system do not sufficiently replicate natural, ephemeral pond-breeding amphibian habitat. As a group, shallow constructed wetlands had the same species richness as natural wetlands; however, breeding success in these wetlands was lower when compared to natural wetlands. Individually, two of our shallow constructed wetlands show promise as they had physical wetland characteristics that mimicked the natural wetlands more closely, most importantly a drying cycle. Although these wetlands were built primarily for game wildlife management, understanding the effects on non-target species (e.g., amphibians) is imperative. This approach to ecosystem management has not benefited the natural amphibian community as a whole, and it appears that deep and some shallow constructed wetlands are detrimental to many species of the historic natural community. Overall, amphibian community composition was influenced most strongly by hydroperiod. Most of the constructed wetlands do not have a drying cycle or closed

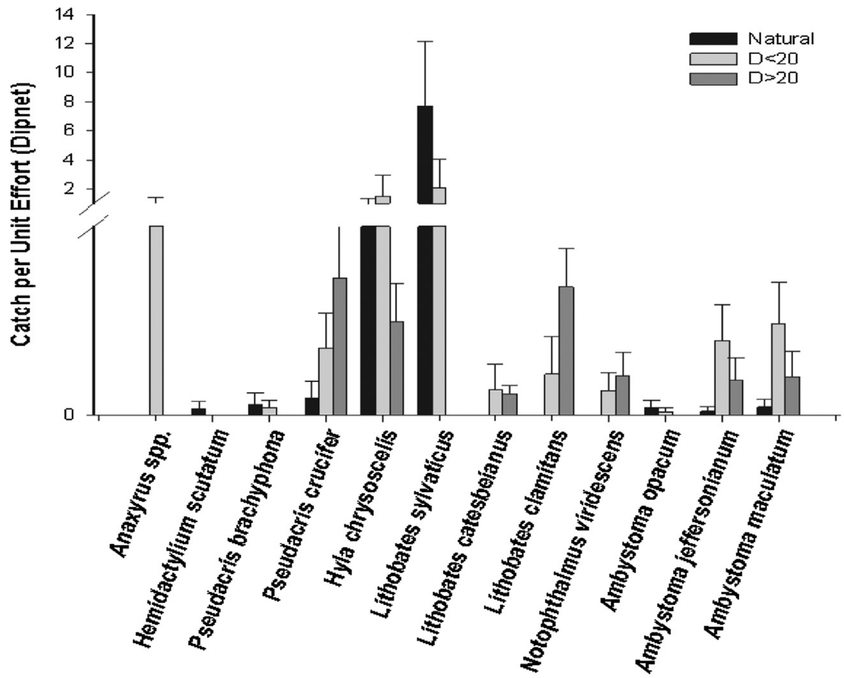

Fig. 2. Amphibian mean species abundances ± standard error (dipnet catch per unit effort; CPUE) for May–August 2010 by wetland type: natural, shallow constructed (D < 20 = minimum depth less than 20 cm), and deep constructed (D > 20 = minimum depth greater than 20 cm).

Table 3
Tukey pairwise comparison summary table for 2010 physical wetland characteristics. Natural wetlands (Natural), shallow constructed (minimum depth less than 20 cm), and deep constructed (minimum depth greater than 20 cm).

Physical Wetland Characteristics	Wetland TypePairwise Comparison	MeanDifference ±SE	q	df	p-value
Maximum	Natural–Deep	−34.0 ± 11.4	−2.97	2	0.032
Depth	Shallow–Deep	−36.5 ± 11.4	−3.19	2	0.022
% Emergent Vegetation	Natural–Deep	−23.6 ± 7.8	−3.02	2	0.029
Depth at 1 m from Shoreline	Natural–Deep	−9.0 ± 2.5	−3.62	2	0.010
pH	Natural–Shallow	−1.4 ± 0.2	−6.11	2	<0.001
	Natural–Deep	−0.8 ± 0.2	−3.48	2	0.013

canopy, contrary to natural wetlands in this system. Permanent wetlands create suitable source habitat for populations of dominant amphibian predators with long larval periods (i.e. *L. catesbeianus*, *L. clamitans*) or an aquatic adult stage (i.e. *N. viridescens*) that would otherwise be absent or in low abundance in this ridge-top ecosystem. As a result, amphibian communities found within the constructed wetlands were dominated by these permanent pond-breeding amphibians. Additionally, these permanent environments and these three species have higher potential to be reservoirs for disease (Gahl et al., 2009; Gray et al., 2009; Greenspan et al., 2012), and we documented a high prevalence of ranavirus in some of the permanent constructed wetlands in this study (Richter et al., 2013).

In previous studies, hydroperiod gradients have been linked to amphibian community composition and species richness (Wellborn et al., 1996; Snodgrass et al., 2000a, 2000b; Korfel et al., 2010; Semlitsch et al., 2015). Snodgrass et al. (2000a) summarized the general models of predicted lentic community structure as follows: (1) a species richness curve will have a peak in intermediate hydroperiod wetlands, (2) large predator presence (i.e. fish) will be correlated with lower species richness in wetlands with longer hydroperiods, and (3) community structure will be driven by differences in life-history characteristics. These patterns were generally supported for our study wetlands with two exceptions. First, contrary to the first model, our study reveals two species richness peaks (for natural ephemeral wetlands and shallow constructed wetlands) and a species richness decrease for deep constructed wetlands. Second, while we did observe a reduction in species richness in deep wetlands, fish were not the primary predator associated with this decrease. In our study, dominant amphibian species (*L. catesbeianus*, *L. clamitans*, and *N. viridescens*) were the primary predators in these habitats. The third model was supported by our study because we found distinct breaks in the community structure based on life-history characteristics.

Key information can be gathered about the natural wetlands we studied by considering the life history traits of the most abundant species present within them. These traits allow species to flourish within these less predictable habitats. For example, *L. sylvaticus*, the most abundant natural wetland species, is adapted to these habitats in that adults arrive early to breed at wetlands in February and March when the wetlands typically fill, and their larval period is short relative to other species of *Lithobates* (Redmer and Trauth 2005). This irregular flux in hydrology of the wetlands reduces the amount of vertebrate and invertebrate predators for these specialized species (Wellborn et al., 1996). Permanent wetlands also have a particular set of species that thrive in the habitat they provide. Top amphibian predators, *L. clamitans*, *N. viridescens and L. catesbeianus*, observed in our constructed wetlands are opportunistic foragers and regularly depredate other amphibian species living within their habitats (Werner et al., 1995; Kats and Ferrer 2003; Vasconcelos and Calhoun 2006; Kross and Richter 2016). In the natural wetlands, larvae of these predatory species were absent and juveniles and adults were rare because the length of their larval periods exceed the hydroperiod of natural ephemerals in our study region (Casper and Hendricks 2005; Pauley and Lannoo

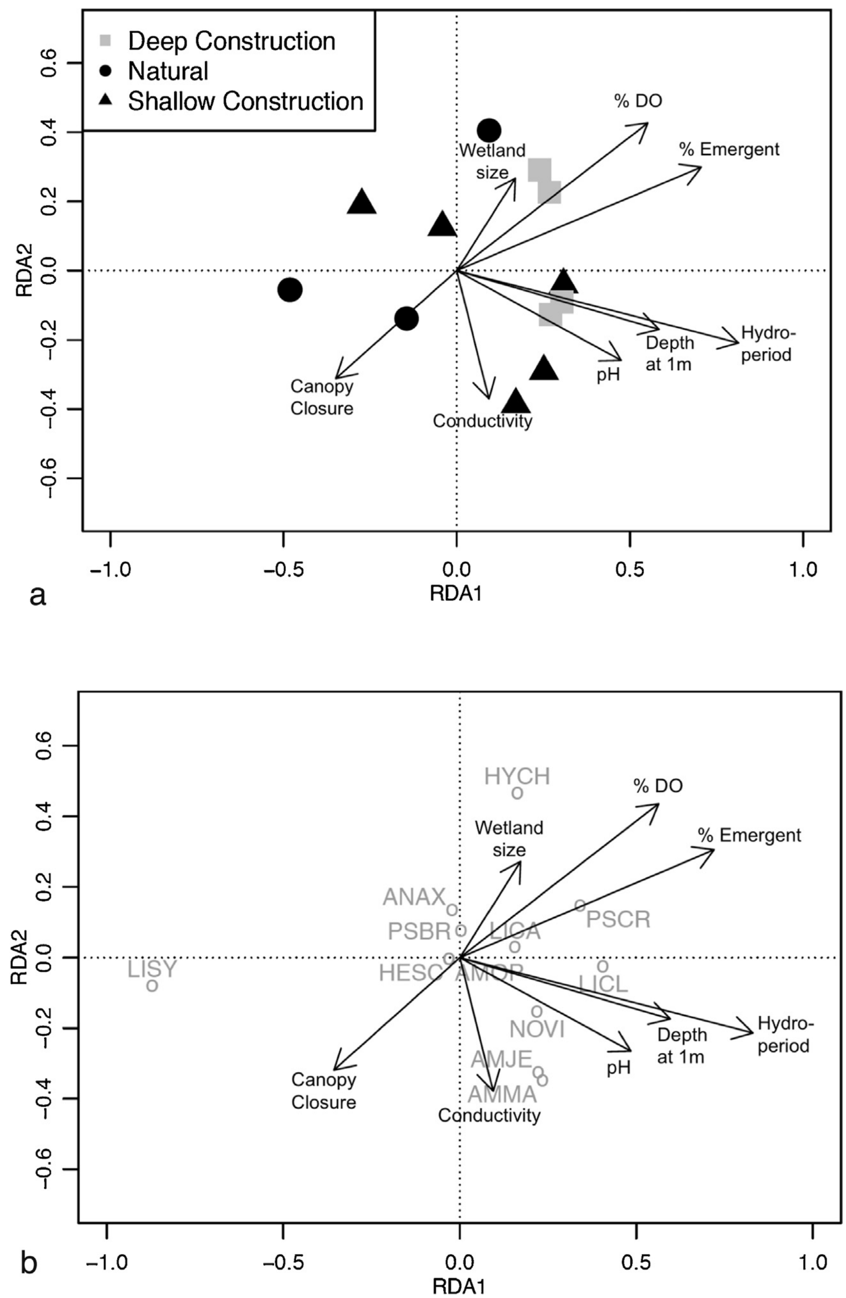

Fig. 3. Triplots from redundancy analysis (RDA) depicting (A) wetlands by type and (B) species abundance based on capture per unit effort of amphibians in the Daniel Boone National Forest, Kentucky. The proportion of variance in the data explained by the RDA was 68.5%; axes 1 and 2 accounted for 47.5% and 19.9% of that total, respectively. Species abbreviations represent the first two letters of the genus followed by the first two letters of the specific epithet. All wetlands were included in the analysis, but some natural wetlands markers overlap because of similarity in characteristics and amphibians.

2005; Hunsinger and Lannoo 2005). We found that species diversity and evenness varied greatly between natural ephemeral wetlands and constructed wetlands. The increase in diversity and evenness in the constructed habitats is a result of the aforementioned top amphibian predators, which are absent in the natural wetlands. The low evenness index for the natural wetlands is explained by the high abundance of *L. sylvaticus* larvae, especially compared to other species.

Several species were more common in the constructed wetlands, regardless of construction depth type. These species span a range of different breeding strategies and life-history traits. *Pseudacris crucifer* and *L. palustris* do not have long larval periods like *N. viridescens* and *L. catesbeianus*, but they prefer areas with large amounts of emergent fringe vegetation (Butterfield et al., 2005; Redmer 2005). While constructed permanent habitats might be considered population sinks for some ephemeral pond-breeding specialists (i.e. *L. sylvaticus* and *A. opacum*), other adaptable species such as *A. maculatum* might benefit from an extended larval period and subsequent larger body size at metamorphosis associated with increased wetland longevity (Rowe and Dunson 1995). This might explain a higher frequency of *A. maculatum* and *A. jeffersonianum* in constructed wetlands that do not seasonally dry. However, Rowe and Dunson (1995) stated the individual fitness advantage of a larger body size was only observed for *A. maculatum* and not *A. jeffersonianum*. Additionally, fitness advantage may only be conveyed to a minority of the hatchlings due to depredation within these permanent wetlands, thus allowing for a lower survival rate

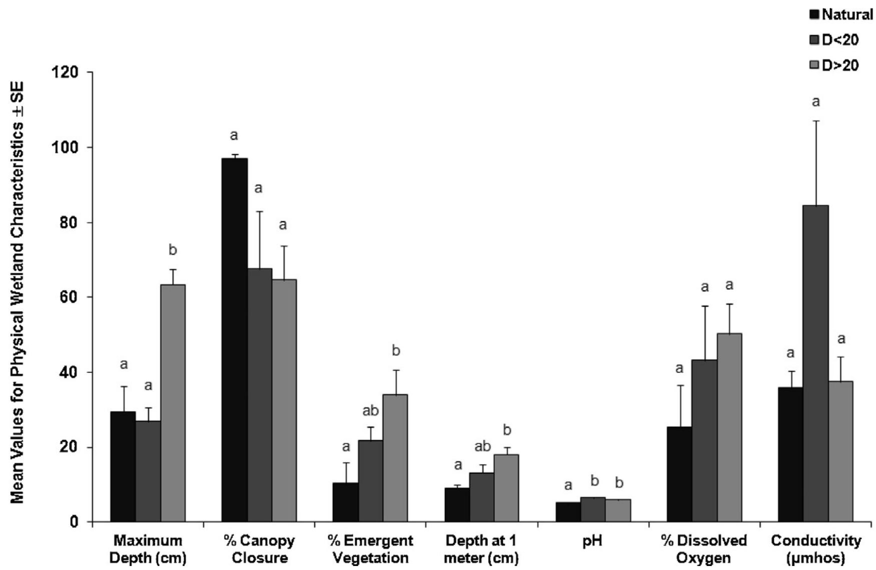

Fig. 4. Mean values for wetland characteristics ± standard error by wetland type: natural, shallow constructed (D < 20 = minimum depth less than 20 cm), and deep constructed (D > 20 = minimum depth greater than 20 cm) for 2010. Different letters above bars indicate statistical significance between groups and shared letters indicate lack of statistical significance between groups.

to metamorphosis and a higher survival post metamorphosis (Kats and Ferrer 2003; Cabrera-Guzman et al., 2013).

Canopy closure can have a significant impact on wetland chemistry and processes ultimately influencing larval growth rates and interspecies interactions (Harkey and Semlitsch 1988; McIntyre and McCollum 2000; Skelly et al., 2002; Schiesari 2006). During construction of wetlands, trees are often removed and soils are compacted by heavy equipment, which reduces canopy cover and limits tree colonization (Biebighauser, 2011). Our results indicated lower canopy closure at our constructed wetland sites compared to natural sites. While not statically significant (due to variation in constructed wetland sites), this difference is biologically significant as evidenced by our RDA amphibian community analysis. Certain species may benefit from open-canopy wetlands (e.g., *L. sevosus*, dusky gopher frogs; Thurgate and Pechmann 2007); however, the natural pool-breeding species in our study are adapted to and obligates of closed-canopy wetlands (Calhoun et al., 2014). Other wetland physical characteristics (maximum wetland depth, emergent vegetation, littoral zone depth, and pH) differed between constructed and natural wetlands studied, illuminating the importance of physical wetland structure and chemistry in shaping suitable amphibian habitats. The species richness data from this project corroborates Porej and Hetherington (2005) findings of higher species richness at wetlands with shallow littoral zones. The occurrence of shallower depths at the edge of the wetland may provide basking areas for developing tadpoles and predator avoidance habitat, specifically for interspecific predator-prey interactions (Porej and Hetherington 2005). A closed canopy likely decreases the type of emergent vegetation observed at the constructed wetlands (cattails) and allows for more natural emergent sedges and rushes to colonize successfully.

Similar to natural wetlands further south on the Cumberland Plateau and in the Pinelands of New Jersey, pH at our natural wetland sites was found to be significantly lower than constructed wetlands (Freda and Dunson 1986; Bunnell and Zampella 1999; Colburn 2004) because of the presence of tannins, acidic soils, and geology (Colburn 2004). Even though the natural wetlands we studied have naturally low pH (4.8–5.5), which can have detrimental lethal and sub-lethal effects on embryos and larvae of some amphibian species (Rowe et al., 1992), the most abundant species in the natural wetlands studied, *L. sylvaticus,* has a high tolerance to low pH levels (3.5–4.0, lethal pH level; 3.5–4.5, critical pH level) (Grant and Licht 1993). Low pH levels found naturally in the wetlands we studied may serve as an advantage for pH-tolerant species such as *L. sylvaticus.* The impacts of differences in the above mentioned wetland characteristics, in most cases, are not immediately apparent; therefore, when intending to replicate natural amphibian habitats, care must be taken to monitor and resolve differences in wetland structure and water quality.

5. Conclusions and management implications

Using wetland creation as a mitigation option should be a last resort (Calhoun et al., 2014). However, the continued loss of natural, hydrologically isolated wetlands, which are not currently under Federal jurisdiction, increases the need for replacement with constructed wetlands in particular geographic areas. When necessary, it is imperative for land managers to construct wetlands that provide the best surrogate habitat for hydrologically isolated wetland-dependent species. Land managers that construct wetlands for mitigation and habitat enhancement should consider historical wetland hydrology (i.e. ephemeral, semi-permanent, or permanent) and canopy closure while focusing efforts on creating the most natural habitats possible. To provide the best replacement habitat, our data suggest attention must be given to characteristics of a wetland ecosystem including: wetland depth (maximum and littoral), hydrology (permanent, semi-permanent, or ephemeral), canopy closure, vegetation structure, and water quality. For example, when constructing wetlands on ridge tops in this region of DBNF, land managers should attempt to replicate the natural wetland communities present in the landscape by creating isolated wetlands with an annual drying cycle, shallow littoral zones, and a closed canopy. Limiting tree mortality and reducing compaction of soils at the construction site should facilitate a closed canopy and soil percolation important for an annual drying cycle.

Proximity of construction to nearest natural wetland should be considered. When feasible, isolated depression wetlands should be created in proximity to naturally occurring wetlands of the same type to foster rapid colonization by desired species and potential establishment of connected populations across the landscape (Petranka et al., 2007; Calhoun et al., 2014). However, our study demonstrates how this proximity can have negative effects if the constructed wetlands provide habitat for species not native to the ecosystem. Non-permanent hydrology is the most difficult parameter to replicate, so to ensure success, land managers must include post-construction monitoring (with natural wetland comparisons), and when constructed wetlands fail to meet management goals, renovation or removal of wetlands might be required (Calhoun et al., 2014).

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