ORIGINAL RESEARCH





Creating Temporary Pools as Wetland Mitigation: How Well Do They Function?

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Abstract Temporary forested pools are an important ecological resource throughout northern and eastern North America, yet they are often destroyed or degraded. Pool creation offers a potential mitigation solution, but long-term monitoring to assess the functioning of created pools is scarce. Furthermore, studies rarely integrate multiple, interacting levels of the pool ecosystem, including physical, chemical, and biological parameters. To address this knowledge gap, we compared the physical habitat, water chemistry, productivity, and community composition of macroinvertebrates and amphibians from 7year old created pools (n=7) to reference pools (n=6). Created pools were smaller in size, received more sunlight, had greater amounts of Lemna, Typha, and Phragmites, and were less likely to dry. Created pools had higher pH and conductivity, but algal biomass did not differ. Macroinvertebrate richness was similar across pools, but composition starkly differed. Amphibian species richness and composition was similar between created and reference pools; however, created pools had fewer focal pool-breeding amphibians, including the spotted salamander and wood frog. By assessing the entire pool ecosystem, we found that the ability of created pools to

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mimic the physical conditions and ecological functions of natural temporary pools is suspect.

Keywords Created wetlands · Pool-breeding amphibians · Macroinvertebrates · Temporary pools · Vernal pools · Wetland mitigation

Introduction

The continental United States has lost over half of its total wetlands since 1780 (Dahl 1990). Temporary freshwater pools (also called vernal pools, ephemeral or seasonal ponds, woodland pools) are particularly vulnerable because they are small, easy to destroy, and receive inadequate protection in most regions (Mahaney and Klemens 2002). The loss of temporary pools from the landscape is a critical concern for biodiversity because their ephemeral nature prevents populations of predatory fish from becoming established and enables predatorsensitive invertebrate and amphibian species to successfully reproduce (Semlitsch 2000; Calhoun et al. 2003; Paton 2005). Several taxa (e.g., wood frogs (Rana sylvatica = Lithobates sylvaticus), mole salamanders (family Ambystomidae)) that use temporary pools for breeding also rely on forested areas for the non-breeding season; thus, they are doubly threatened as upland forests surrounding breeding pools are degraded or destroyed (Semlitsch and Bodie 2003; Homan et al. 2004). Declines in temporary pool-breeding species, coupled with loss of temporary pools and surrounding upland forests, have become a concern in recent decades (Paton 2005; Windmiller et al. 2008).

To mitigate the loss of temporary pools from the landscape, pool creation or restoration is becoming more common (Lichko and Calhoun 2003; Calhoun et al. 2014). However, temporary pools are among the most difficult wetland systems



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to create, particularly with respect to hydroperiod (i.e., timing and length of inundation), which drives the recruitment and establishment of plant and animal communities in these systems (Zedler 2000; Calhoun et al. 2014). Monitoring of created temporary pools as part of mitigation requirements is variable and typically limited to short time periods (e.g., 2 to 3 years), which is inadequate to determine success (Mitsch and Wilson 1996; Lichko and Calhoun 2003). Furthermore, criteria for determining "success" are often inconsistent and ill-defined (Kihslinger 2008; Calhoun et al. 2014). Early research on evaluating the success of replicating wetland function in mitigation projects focused on hydrology, soils, and vegetation (Moore et al. 1999; Stolt et al. 2000; Campbell et al. 2002); more recent research has incorporated use of pools for supporting wildlife populations, especially amphibians (Brown et al. 2012; Denton and Richter 2013).

Although research into the success of temporary pool creation has begun to focus on broader aspects of wildlife habitat and amphibian production, studies have not comprehensively examined multiple levels of these ecosystems. As such, the current focus overlooks many physical, chemical, and biological properties, which interact to affect the functioning of pools. For instance, vegetation structure is critical to shaping pool ecosystems; yet, it is often not implicitly designed for or monitored in pool creation projects. Canopy cover over the pool basin can range from completely open to nearly entirely closed, which affects the in-pool vegetation structure. Opencanopy pools are often dominated by emergent vegetation, whereas closed-canopy pools typically have low emergent cover and fallen leaf litter dominates the pool basin (Skelly et al. 2002; Schiesari 2006). This vegetation structure can strongly influence water chemistry, with closed-canopy pools having lower water temperatures, dissolved oxygen, and pH (Werner and Glennemeier 1999; Skelly et al. 2002). Furthermore, vegetation structure can also influence biological parameters, including food quality (Werner and Glennemeier 1999; Skelly et al. 2002; Schiesari 2006) and species composition, abundance, and interactions (e.g., competition) (Skelly et al. 1999; Skelly et al. 2005; Werner et al. 2007). Yet, canopy cover is rarely assessed in pool restoration and creation. Additionally, while focal amphibians such as the wood frog and mole salamanders are often monitored in created wetlands, macroinvertebrate communities are less studied (but see Stanczak and Keiper 2004; Culler et al. 2014) despite their importance to nutrient cycling and food web dynamics (Batzer et al. 2005).

To address this gap in knowledge, we designed a study to more holistically assess how created temporary pools compare to a set of established, reference pools in terms of physical, chemical, and biological parameters. We compared a set of seven created pools (7 years post-construction) to six reference pools and evaluated physical habitat (e.g., hydrology, vegetation, leaf litter, canopy cover), water chemistry (e.g.,

temperature, nutrients), and biological parameters (algal biomass, macroinvertebrate and amphibian assemblages). We hypothesized that created pools would have altered hydrology (either shorter or longer hydroperiod) and a more open canopy than reference pools. We expected these physical differences would affect chemical properties, including reduced pool temperatures and fewer nutrients. Lastly, we hypothesized that physical and chemical differences would cascade to alter algal productivity and the composition of macroinvertebrates and amphibians.

Methods

Study System

In northern and eastern North America, temporary pools are widely distributed across forested landscapes with an estimated 1 to 15 pools km⁻² (Palik et al. 2003; Wu et al. 2014). Across this large region, pools share common traits including a small (<1 ha) size, shallow basin, isolation from permanent water bodies, seasonal drying, and common biological assemblages (Wiggins et al. 1980; Colburn 2004). While these characteristics do differ among pools and among different geographic areas, temporary woodland pools are classified as one distinctive habitat type throughout the glaciated northeast of North America (Colburn 2004).

Study Sites

The created pools are located adjacent to the Stewart International Airport in the rural towns of Newburgh and New Windsor, New York, USA. In 2006, as part of required mitigation, the New York State Department of Transportation (NYS DOT) constructed 12 temporary pools on this property. The created pools are located in a mixed deciduous-coniferous forest, north (n=2) and south (n=10) of the new airport access road. Five of the 12 created pools did not retain water for more than a few days at a time; therefore, our study includes only the seven remaining pools.

As no suitable reference pools were located within the immediate forest surrounding the created pools, we used a set of six reference pools located in Yale Myers Forest, a 3213-ha research forest in Tolland and Windham Counties, Connecticut, USA. While the reference and created pools were separated geographically (by ~150 km), forests were located in the same Eastern Broadleaf Forest ecoregion (McNab et al. 2005), with the same dominant ecotypes of Appalachian (Hemlock)-Northern Hardwood Forest and Northeastern Interior Dry-Mesic Forest (North Atlantic Landscape Conservation Cooperative 2014). Furthermore, both study sites represent mature, contiguous second-growth forest, with the only recent disturbance being construction of



the created pools (e.g., equipment access road to pool, removal of trees in created pool basins). The forest composition surrounding the pools was also similar, with oak (*Q. alba, Q. rubra, Q. velutina*) and maple (*Acer rubrum, A. saccharum*) present at both sites. Other dominant trees included slippery elm (*Ulmus rubra*), green ash (*Fraxinus pennsylvanica*), and shagbark hickory (*Carya ovata*) at the created sites, and eastern white pine (*Pinus strobus*) and Betulacea spp. at the reference sites. All study pools followed a similar seasonal wet-dry cycle where pools filled in the fall or winter and dried in the summer or early fall, with the exception of two of the created pools that contained water yearround.

Field Sampling

Physical Pool Basin and Vegetation General physical and vegetative characteristics of the pools were documented in mid-summer 2013. Vegetative cover of the pool was classified by: floating-leaved, submerged aquatic vegetation, emergent, shrub, or tree by rank percentage categories (0=0 %, 1=1– 10 %, 2 = 11 - 25 %, 3 = 26 - 50 %, 4 = 51 - 75 %, 5 = 76 - 60 %100 %). Rank percentage categories for Typha, Phragmites, and Lemna were also assigned. Substrate cover of the pool basin was classified by: leaf litter, sticks/logs, rock, or bare ground, using the same rank percentage categories. Canopy cover over the pools was determined pre- and post-leaf out in 2013 using hemispherical photographs (Halverson et al. 2003). Photographs were taken from the four cardinal directions and pool centers when pools were >300 m²; in smaller pools, one photograph from the pool center was taken. Incident light, measured as the global site factor (GSF), was calculated using Gap Light Analyzer in created pools (Simon Fraser University, Burnaby, British Columbia and Institute of Ecosystem Studies, Millbrook, New York, USA) or HemiView in reference pools (Delta-T Devices, Cambridge, UK). Maximum depth of the pools was measured biweekly through the sampling season (May–July) in 2013 and 2014. We measured leaf litter inputs to each pool in autumn of 2013. Litter traps (0.40 m diameter in created pools; 0.52 m diameter in reference pools) were built of wire cages covered with a fine mesh and were suspended above the water surface; three to four traps were deployed in each pool. Traps were installed prior to leaf off (late August/early September) and leaf litter was collected two to three times during the fall (with last collection late November/early December). Leaf litter was air-dried in paper bags, and weighed.

Algal Biomass Periphyton chlorophyll *a* was sampled biweekly from glass slides (Periphyton Sampler, Wildlife Supply Company, Yulee, Florida, USA). Glass slides were scraped, rinsed with water, and the resulting periphytonwater slurry was filtered onto pre-combusted Whatman GF/

F filters (Whatman, Brentford, UK) and frozen until analysis. Phytoplankton chlorophyll *a* was sampled from surface water reach samples biweekly. Water samples were pre-filtered through 150 μm mesh to remove most zooplankton and debris, filtered onto pre-combusted Whatman GF/F filters (Whatman, Brentford, UK), and frozen until analysis. Periphyton and phytoplankton chlorophyll *a* was measured using a fluorometer (TD-700 Fluorometer, Turner Designs, Sunnyvale, California, USA) following Environmental Protection Agency Method 445.0.

Water Chemistry and Temperature Total dissolved nitrogen (TDN), total dissolved phosphorus (TDP), and dissolved organic carbon (DOC) were measured monthly from surface water reach samples. Water was pre-filtered through 150 µm mesh to remove most zooplankton and debris, then filtered through pre-combusted Whatman GF/F filters (Whatman, Brentford, UK), and the filtrate was frozen until analysis. Concentrations of TDN and TDP were determined using a persulfate digestion and colorimetric standard methods (Clesceri et al. 1998) in conjunction with an autoanalyzer (Astoria2 Analyzer, Astoria- Pacific, Clackamas, Oregon, USA) following Environmental Protection Agency Method 365.4. Dissolved organic carbon was analyzed on a Shimadzu TOC 5000 auto-analyzer (Shimadzu Corporation, Kyoto, Japan).

Conductivity and pH were sampled bi-weekly (reference pools: Waterproof Multiparameter PCS Testr 35, Oakton Instruments, Vernon Hills, Illinois, USA; created pools: YSI Professional Plus Multiparameter, YSI Inc., Yellow Springs, OH, USA). Water temperatures were recorded every 30 min using HOBO pendant loggers (Onset Computer Corporation, Bourne, Massachusetts, USA) placed ten cm below the pool surface.

Amphibian and Macroinvertebrate Surveys Wood frog and spotted salamander (Ambystoma maculatum) egg masses were counted in each pool in 2013 and 2014. Dip-net surveys for amphibian larvae and macroinvertebrates were conducted biweekly from May–July (or until a pool was dry) in 2013 and 2014. This time period covers from around hatching until pool-breeding amphibian larvae reached metamorphosis. Dip-net sweeps through the substrate and water column were conducted throughout each pool; survey time was proportional to area of pool (range: 10–40 person minutes). Amphibian larvae were identified to species, counted in the field, and released on site. Any amphibian larvae not identifiable in the field were euthanized with tricaine methanesulfonate (MS-222) and preserved in 70 % ethyl alcohol for identification in the laboratory. Macroinvertebrates were preserved in 70 % ethyl alcohol and brought back to the laboratory for identification to family level. We restricted amphibian



community analyses of pools to those species that we documented breeding (i.e. eggs, larvae) at a given pool.

Statistical Analysis To compare physical habitat characteristics that were measured once over the study, we used t-tests to test for significant differences between created and reference pools. To assess differences in water chemistry, water temperature, and algal biomass that were measured multiple times in a season and across years, we created linear mixed-effects models in R (R Version 3.1.2, R Core Team) using the "lme4" package (Bates et al. 2014). Each model tested the fixed effects of pool type (created or reference), day of the year, and their interaction, and included individual pool name as a random effect to account for temporal pseudoreplication. Models were run for each year (2013 and 2014) separately. For created pools, we also conducted a t-test to assess differences in conductivity levels between pools near (<100 m) and far (>170 m) from the access road. For temperature, daily average temperatures were used from each pool.

To assess differences in macroinvertebrate and amphibian communities, we conducted t-tests for taxon richness between created and reference pools. We then conducted a cluster analvsis using Jaccard similarity index using the "vegan" package in R (Oksanen et al. 2010, R Development Core Team 2010) for macroinvertebrate families and amphibian species. Nonmetric Multidimensional Scaling (NMDS) was used with the "vegan" package in R to observe clustering of macroinvertebrate families by pool type. We used "envfit" in the "vegan" package to fit scaled environmental variables to the NMDS to observe correlations and directionality. To avoid problems with collinearity (variable inflation factor >5), the following environmental variables were included: pool surface area, permanence, light at leaf-out, leaf litter inputs, floating Lemna cover, emergent Typha cover, emergent Phragmites cover, mean phytoplankton biomass, mean periphyton biomass, mean TDP, mean DOC, mean pH, mean temperature, and mean depth. Only variables significant at $\alpha \le 0.10$ were retained.

To test for differences in the abundance of focal temporary pool taxa (wood frogs and spotted salamanders) between created and reference pools, we used t-tests on egg mass numbers (standardized by pool area) and larval counts from dip-net

Table 1 Summary of physical habitat characteristics between the created (n=7) and reference pools (n=6). Values are means and standard error

Variable	Created	Reference	<i>t</i> -value	df	<i>p</i> -value
Surface Area (m ²)	326 (85.7)	588 (78.5)	-2.25	11	0.046
Maximum Depth (m)	62.0 (7.9)	69.7 (8.1)	-0.68	10.8	0.511
Area / Depth	5.9 (2.0)	9.1 (1.4)	-1.30	10.3	0.224
Leaf litter inputs (dry g m ⁻²)	210.0 (45.7)	217.6 (10.8)	-0.16	6.7	0.878
Canopy off (GSF)	56.8 (2.1)	37.2 (3.6)	4.74	8.1	0.001
Canopy on (GSF)	27.1 (1.9)	22.1 (2.5)	1.58	9.7	0.147

Statistically significant values are in bold

surveys (standardized by person minutes). Larval counts were averaged from sampling rounds after amphibians had hatched, but before metamorphosis (May – June for wood frogs; June – July 17 for spotted salamanders).

Results

Physical Habitat Characteristics Created pools were significantly smaller $(326\pm86~\text{m}^2)$ than reference pools (588 $\pm79~\text{m}^2$; Table 1). Created and reference pools did not differ in depth, area to depth ratio, or areal inputs of leaf litter (Table 1). Before leaf out, created pools received significantly more light than reference pools (Table 1). The trend was similar, but not significant, once leaves emerged on the trees (Table 1). Across the 2-year study, five of the seven created pools exhibited seasonal drying whereas all six reference pools dried.

Substrate type was similar among created and reference pools: the substrate was predominantly leaf litter, with some woody debris, and low amounts of rock and bare substrate (Table 2). Submerged aquatic plant and shrub cover were low and did not differ between created and reference pools (Table 2). Created pools had significantly more floating duckweed (*Lemna* sp.) than reference pools (Table 2). Additionally, while total emergent vegetation cover was similar among created and reference pools, the species differed. Both cattail (*Typha latifolia* and *Typha angustifolia x latifolia*) and common reed (*Phragmites australis*) cover were greater in created pools than reference pools, where neither species occurred (Table 2).

Water Chemistry and Temperature There were no differences in TDN between created and reference pools in 2013; however, TDN increased more dramatically over time and was greater in reference compared to created pools in 2014 (Table 3, Appendix 1). For TDP, there was an interaction between pool type and day of the year (Table 3, Appendix 1). In 2013, TDP increased seasonally in reference pools and decreased in created pools. In 2014, TDP increased in both pools, but the increase was greater in reference pools. Dissolved organic carbon increased seasonally in both pool



Table 2 Summary of substrate and vegetation for the created (n=7) and reference pools (n=6). Values are means, ranked from 0 to 5 (see text)

Category	Habitat	Created	Reference	<i>t</i> -value	df	<i>p</i> -value
Substrate	Leaf	4.71	4.33	1.00	7.91	0.347
	Wood	1.86	1.17	1.82	8.63	0.103
	Rock	0.14	0.00	1.00	6.00	0.356
	Bare	0.14	0.67	-0.77	5.46	0.474
Vegetation	Floating-leaved duckweed	2.57	0.17	2.80	6.47	0.029
Submerged aquation	Submerged aquatic	0.86	0.67	0.40	10.95	0.697
	Emergent	3.14	2.17	1.25	9.60	0.241
	Shrub	0.14	0.50	-0.96	6.73	0.368
Emergent	Cattail (Typha)	2.00	0.00	2.37	6.00	0.055
C	Common reed (Phragmites)	1.57	0.00	4.26	6.00	0.005
	Loosestrife	0.29	0.00	1.55	6.00	0.17

Statistically significant values are in bold

types in 2014, but the increase was greater in reference pools (Table 3, Appendix 1). Conductivity and pH were all higher in created compared to reference pools in both years (Table 3,

Appendix 1). Created pools closer (<100 m; n=3) to the main airport access road had average conductivity levels twice as high as created pools farther (>170 m; n=4) from the road

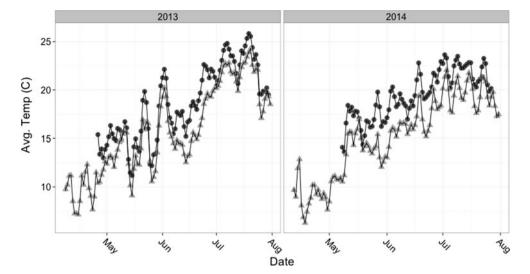
Table 3 Linear mixed effects models evaluating the effect of pool type (reference or created) and day of year on water chemistry and algal biomass. Models include pool as a random effect

	2013			2014		
	SS	F	P	SS	F	Р
Total dissolved nitrogen ((ln)			,		
Type × Julian day	0.53	1.56	0.22	0.53	12.27	0.002
Pool type	0.74	2.18	0.15	0.43	10.03	0.004
Julian day	0.05	0.01	0.90	1.59	36.66	< 0.001
Total dissolved phosphor	us (ln)					
Type × Julian day	1.93	7.47	0.01	2.33	12.33	0.002
Pool type	2.33	9.03	0.005	2.05	10.85	0.003
Julian day	0.10	0.38	0.54	5.34	28.30	< 0.001
Dissolved organic carbon						
Type × Julian day				0.42	7.14	0.01
Pool type				0.19	3.30	0.08
Julian day				1.47	25.20	< 0.001
рН						
Type × Julian day	0.72	4.11	0.05	0.08	1.93	0.17
Pool type	1.80	10.28	0.002	0.93	23.01	< 0.001
Julian day	0.35	2.00	0.16	0.09	2.13	0.15
Conductivity						
Type × Julian day	3.16	38.40	< 0.001	0.09	0.15	0.70
Pool type	4.90	59.55	< 0.001	0.32	5.50	0.02
Julian day	2.36	28.67	< 0.001	0.57	9.74	0.002
Temperature						
Type × Julian day	2.2	0.41	0.52	179.7	63.21	< 0.001
Pool type	36.1	6.58	0.01	277.9	97.76	< 0.001
Julian day	15200.6	2769.3	< 0.001	6350.6	2233.8	< 0.001
Periphyton Chlorophyll a						
Type × Julian day	5.77	7.43	0.01	1.69	2.52	0.12
Pool type	3.28	4.22	0.04	1.17	1.74	0.19
Julian day	34.85	44.83	< 0.001	38.31	57.18	< 0.001
Phytoplankton Chlorophy	ıll a					
Type × Julian day	0.02	0.01	0.91	3.22	1.99	0.16
Pool type	0.01	0.01	0.92	4.45	2.75	0.10
Julian day	0.47	0.32	0.57	11.91	7.37	0.008

Statistically significant values are in bold



Fig. 1 Mean daily temperatures for created (*black circles*) and reference (*gray triangles*) pools in 2013 and 2014



(near: $181.18 \pm 58.52 \,\mu\text{S cm}^{-1}$, far: $95.13 \pm 15.04 \,\mu\text{S cm}^{-1}$, t-test, t=2.90, df=5, p=0.02). Mean daily temperatures increased seasonally in the pools, and created pools were significantly warmer than reference sites (Table 3, Fig. 1).

Algal Biomass Periphyton chlorophyll *a* increased seasonally in both years, and was higher in reference pools in 2013 but not 2014 (Table 3, Appendix 1). Phytoplankton chlorophyll *a* did not differ across time or among reference and created pools in 2013. In 2014, phytoplankton chlorophyll *a* increased seasonally but there were no differences among reference and created pools (Table 3, Appendix 1).

Macroinvertebrate Assemblages We identified 39 macroinvertebrate families across the 13 pools. Five families occurred in all 13 pools and 12 families were common, occurring in over two thirds of both reference and created sites (Table 4). There were six additional families common only to created pools and five families common only to reference pools (Table 4). Of these, three families were exclusive to created pools and three were exclusive to reference pools (Table 4). Overall family richness did not differ significantly between created and reference pools, although it was slightly higher in created pools (reference: 18.33, created: 20.43, t-test, t=1.23, p=0.25). While richness did not differ, community assemblages clustered by pool type (Fig. 2).

Macroinvertebrate families clustered between reference and created pools (stress=0.09, linear fit R^2 =0.96). The environmental variables that best fit the NMDS were pH (r^2 =0.59, p=0.01), water temperature (r^2 =0.69, p=0.002), *Phragmites* cover (r^2 =0.47, p=0.04), *Lemna* cover (r^2 =0.52, p=0.02), and light at leaf-on (r^2 =0.37, p=0.10) (Fig. 3).

Amphibian Assemblages We found larvae from seven amphibian species across the 13 pools. Species richness did not

differ between reference and created pools (reference: 4.83 species, created: 4.29 species, t-test, t=-0.66, p=0.52). Amphibian species occupancy did not cluster by reference or created pools, indicating that assemblages were similar across pool types (Fig. 4).

The two focal species, spotted salamanders and wood frogs, were found in all six reference pools each year, but were not found across all created sites. We found wood frogs in five and six of the seven created pools in 2013 and 2014, respectively. Spotted salamanders were found in three and four of the seven created pools in 2013 and 2014, respectively. There were significantly more spotted salamander egg masses per unit area in reference compared to created pools (Table 5).

Table 4 Common macroinvertebrate families (found in >66 % of pools) that are shared between created and reference pools or common only in created or reference pools

Shared common families	Common in created pools	Common in reference pools
Aeshnidae	Belostomatidae	Asellidae
Chaoboridae a	Coenagrionidae	Chirocephalidae c
Chironomidae ^a	Crangonyctidae b	Corydalidae
Corixidae	Haliplidae	Gyrinidae ^c
Culicidae	Hydrophilidae b	Phryganeidae ^c
Dytiscidae ^a	Physidae ^b	
Gerridae ^a		
Lestidae		
Libellulidae		
Limnephilidae		
Notonectidae a		
Sphaeriidae		

^a Denotes families found in all 13 pools



^b Denotes families found exclusively in created pools

^c Denotes families found exclusively in reference pools

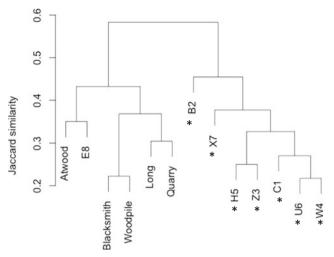


Fig. 2 Cluster diagram for macroinvertebrate families found across the 13 study pools. *Asterisks* indicate created pools

There were also significantly more wood frog egg masses per unit area in reference pools compared to created pools in 2014. A similar, but not significant pattern, was seen for wood frog egg masses in 2013 (Table 5). In our dip-net surveys, we caught significantly more larval spotted salamanders and wood frogs per person minute in reference compared to created pools in both 2013 and 2014 (Table 5).

Discussion

We found that created pools differed from reference pools in several key physical, chemical, and biological characteristics, calling into question the ability of created pools to functionally match reference pools.

Physical Habitat Characteristics Created pools differed from reference pools in terms of hydroperiod and canopy

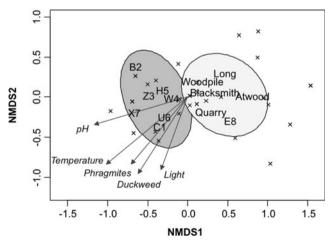


Fig. 3 NMDS analysis of macroinvertebrate family distributions. Created pools circle together in the *dark gray circle*; reference pools cluster together in the *light gray circle*

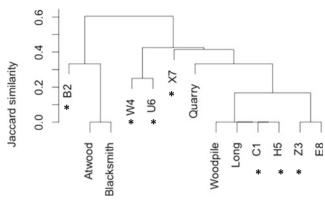


Fig. 4 Cluster diagram for amphibian species found across the 13 study pools. *Asterisks* indicate created pools

cover, both of which influence the abiotic and biotic characteristics of pools. Nine of the 12 (75 %) created pools had a hydroperiod either too short or too long to successfully mimic the seasonal drying of temporary pools. Specifically, five pools dried before amphibian breeding occurred and on the opposite extreme, two pools held water year-round. Hydroperiod affects community composition, with permanent pools often hosting different assemblages of plants (Colburn 2004; Cutko and Rawinski 2008), macroinvertebrates (Collinson et al. 1995; Tarr et al. 2005), and amphibians (Snodgrass et al. 2000; Pechmann et al. 2001).

The created pools also had a more open canopy than reference pools. More open-canopy pools receive higher levels of incident light and have warmer temperatures, which was observed here and in other created pools (Fig. 1, Korfel et al. 2010). Because both created and reference pools were located in mature second-growth forests, we attribute the more open canopy in created pools to disturbance associated with their creation (e.g., removal of trees to create the pool basins). The physical habitat differences between created and reference pools could cascade to differences in water chemistry, species composition, and species performance.

Vegetation The composition of floating-leaved and emergent vegetation differed between reference and created pools (Table 2). *Lemna* sp. (duckweed) was present in five of the seven created pools, covering over 50 % of the surface area in three of those pools. In contrast, *Lemna* sp. was documented in only one reference pool, where it covered less than 10 % of the surface area. Floating mats of *Lemna* can shade underlying waters and decrease algal biomass (Parr et al. 2002) as well as remove nitrogen and phosphorous from the water column (Culley et al. 1981; Cedergreen and Madsen 2013), which could reduce nutrient availability in created pools.

Created pools, but not reference pools, were colonized by both *Typha* spp. (4 of 7 pools) and *Phragmites australis* (6 of 7 pools), species not typically seen in temporary pools (Colburn 2004). Both *Typha* and *Phragmites* are aggressive colonizers



Table 5 Mean (±SE) number of egg masses (m⁻²) and larvae caught (per person minute) of wood frogs and spotted salamanders in created and reference pools

	2013			2014		
	Created	Reference	P	Created	Reference	P
Spotted salamander egg masses	0.02 (0.01)	0.34 (0.08)	0.008	0.003 (0.002)	0.34 (0.09)	0.017
Wood frog egg masses	0.11 (0.07)	0.27 (0.04)	0.098	0.04 (0.02)	0.38 (0.08)	0.007
Spotted salamander larvae	0.26 (0.11)	5.9 (0.85)	< 0.001	0.87 (0.48)	8.55 (1.46)	< 0.001
Wood frog larvae	27.00 (14.27)	84.28 (16.36)	0.01	16.8 (8.00)	125.2 (25.45)	0.001

Statistically significant values are in bold

that can transform wetlands by modifying pool structure through creating dense stands that exclude other species (Chambers et al. 1999; Olson et al. 2009), reducing pool hydroperiod through increased evapotransporation (Herbst and Kappen 1999), and altering biogeochemical processes (Meyerson et al. 1999).

Water Chemistry The higher conductivity and pH in created pools compared to reference pools (Table 3) could be due to different underlying geology, hydrology, soils, or land use between reference and created pools (Freda and Dunson 1985; Colburn 2004). For instance, roadside runoff of deicing agents can increase conductivity (Karraker et al. 2008; Brady 2012), which may explain why created pools closer to the main access road to Stewart International Airport had average conductivity levels twice as high as the other four created pools. It is also possible that created sites were more influenced by groundwater as opposed to precipitation in the reference sites, which can elevate conductivity and pH (Palik et al. 2001; Colburn 2004; Brooks 2005). Alternatively, conductivity and pH can be affected by the soils (Freda and Dunson 1985), which were disturbed in created pools during construction. The exposed mineral soils may have increased pH and conductivity as opposed to the organic sediments accumulated in the reference pools. Overall, while interesting, these differences in conductivity and pH are unlikely to be dramatic enough to affect pool fauna (Sadinski and Dunson 1992; Karraker et al. 2008).

The seasonal increases in TDN, TDP, and DOC in both created and reference pools were potentially due to pool drying concentrating nutrients in the remaining water (Holgerson 2015). Reference pools demonstrated greater seasonal increases, potentially because they dried faster, had greater leaf litter decomposition rates (Williams 2006), or had increased nutrient recycling due to higher densities of focal amphibians (Capps et al. 2015).

Algal Biomass Periphyton and phytoplankton biomass tended to increase seasonally, likely due to increased temperatures. We found it curious that while created pools were warmer and received more sunlight, algal biomass was similar to reference pools. This suggests that light may not limit algal

production, contrasting the assumption that canopy closure reduces primary production in forested pools (Skelly et al. 2002; Schiesari 2006). Alternatively, *Lemna* and emergent vegetation in the created pools could have reduced algal biomass or differential grazing pressure could have obscured trends in biomass production between created and reference pools.

Macroinvertebrate Assemblages Macroinvertebrate assemblages differed starkly between created and reference pools. Macroinvertebrate diversity can be driven by several factors, including canopy openness (Palik et al. 2001; Batzer et al. 2004; Batzer et al. 2005; Plenzer and Michaels 2015), hydroperiod (Brooks 2000; Batzer et al. 2004), depth (Batzer et al. 2000), and leaf litter inputs (Batzer et al. 2004; Batzer et al. 2005; Batzer and Palik 2007). However, the relationship between macroinvertebrate richness and environmental conditions is often weak in temporary pools, suggesting the macroinvertebrate community is composed of habitat generalists (Batzer et al. 2004; Hanson et al. 2009). Our results indicate that while temporary pools may have a core set of habitat generalists (they shared 20 families, 12 of which were common), many invertebrates were more specialized. For instance, there were ten and nine families that were exclusively found in reference and created pools, respectively (3 of which were common).

Canopy openness, and consequently, temperature, may have driven differences in species composition. Notably, all seven of the warmer and sunnier created pools had physid snails and hydrophilid beetles, which tend to use wetlands with more light (Palik et al. 2001; Batzer et al. 2004; Binckley and Resetarits 2007). All seven created pools also had crangonyctid amphipods, whereas none of the reference sites did. Amphipods are thought to be more common in southern wetlands (Batzer et al. 2005; Batzer and Ruhí 2013); however, our results suggest that habitat factors (perhaps light or temperature) may mediate their presence in northern wetlands as well. It is also notable that the fairy shrimp (*Eubranchipus vernalis*; Family: Chirocephalidae), an indicator species for temporary pools (Weaver 1943), were present in five of the six reference wetlands, but were absent from all of the created sites. It is possible that *E. vernalis* was



absent from the created pools due to limitations in colonization or environmental conditions.

It is worth noting that the geographic distance (~150 km) between reference and created sites could result in different species assemblages, which is a limitation of our study. However, pools with relatively similar geography in the same ecoregion tend to have similar macroinvertebrate assemblages assuming similar habitat and hydrology (Batzer and Ruhí 2013). To evaluate the magnitude to which macroinvertebrate assemblages differed among reference and created pools, we conducted a cluster analysis to compare our 13 sites to a global meta-analysis of macroinvertebrate communities from 447 wetlands worldwide (Batzer and Ruhí 2013). We found that the six reference sites clustered together, the seven created sites also clustered together, and that our 13 study ponds collectively clustered together within a group of 20 pools (Appendix 2). Because the study ponds were similar when compared on a global scale, the differences we observed were likely driven by different physical and chemical characteristics of the pools (as opposed to geographic differences). It would be productive for future studies to evaluate macroinvertebrate community assemblies between nearby reference and created pools, as well as evaluate how any differences cascade to affect functional traits or food web structure.

Amphibian Assemblages While amphibian species assemblages were similar across reference and created sites, created pools had fewer numbers of key temporary pool species: the wood frog and spotted salamander. Since these species were present across both reference and created pools, habitat quality, as opposed to colonization, likely limited their densities and/or survival. We hypothesize that canopy cover, vegetation type, and predation could all influence the success of wood frogs and spotted salamanders in created pools.

Open-canopy pools tend to foster higher diversity of amphibian species, whereas closed-canopy pools are dominated by high densities of fewer species, such as the wood frog and spotted salamander (Skelly et al. 1999; Werner and Glennemeier 1999). The mechanisms driving this pattern are not well understood, but poorer quality and quantity of algal food resources are believed to reduce species diversity in closed-canopy pools (Skelly et al. 2002; Schiesari 2006; Schiesari et al. 2009), although anoxia (Wassersug and Seibert 1975), earlier pool drying, or predation may also be contributing factors (Werner et al. 2007). As we found no clear differences in algal biomass between created and reference pools, algal food resources did not likely limit amphibian performance. It is possible, however, that the composition or quality of algae or plant detritus differed among sites and reduced or altered food resources for wood frogs and spotted salamanders.

While inputs of terrestrial leaf litter were similar among created and reference pools, created pools had dense stands of *P. australis* and *Typha* spp., which add to the detrital pool and alters physical habitat structure. Detritus quality is associated with amphibian performance: litter with higher carbon:nutrient ratios can reduce larval amphibian survival, growth, and development (Maerz et al. 2010; Cohen et al. 2012). *Phragmites* has relatively low C:nutrient ratios and may provide high quality detritus for amphibians; however, *Typha* has much higher C:nutrient ratios and can reduce amphibian performance (Maerz et al. 2010). It is possible that *P. australis* and/or *Typha* altered detrital quality and habitat structure in created pools, with possible effects on the amphibian communities.

In addition to canopy cover and emergent vegetation, differences in predation risk could affect wood frog and spotted salamander densities. Predatory amphibians were found in longer-hydroperiod wetlands; specifically, the two permanent created pools and one of the reference pools had second-year larval green frogs (Rana clamitans = Lithobates clamitans), which can prey voraciously on wood frog egg masses and limit reproductive success (Vasconcelos and Calhoun 2006). Predatory macroinvertebrate richness and abundance also increase with increasing hydroperiod (Babbitt et al. 2003; Werner et al. 2007) and incident light (Werner et al. 2007), indicating that created pools may have higher densities of macroinvertebrate predators. While our analysis only looks at family occurrences, we found predatory Belostomatidae and Nepidae more often in created pools (although predatory Dytiscidae and Notonectidae were found across all study pools). It is possible that amphibians occupying created pools were exposed to greater risk of predation, which warrants further study.

Conclusion Creating temporary pools to mitigate for destruction is common across northern and eastern North America. Yet the recipe for successfully creating temporary pools is far from complete, and our results have several important implications for improving pool construction. First, canopy cover and forest connectivity need to be considered during pool creation as they affect pool temperatures, food resources, and species occupancy. Secondly, we need to improve our ability to design pools with intermittent hydroperiods, which likely requires more research to better predict pool hydrology. Lastly, monitoring of created pools should be long-term (>3 years) and assess the physical, chemical, and biological parameters of pools and their interactions. While our study may be limited by the geographic distance among reference and created pools (~150 km), we believe the key findings of our study are broadly applicable to the temporary pools of glaciated northeastern North America. Furthermore, our findings provide clear directions for future studies to address the mechanisms underlying our observed patterns. Unraveling the causal mechanisms behind these trends will advance our knowledge and potential success in conserving these



important resources. Overall, given our current knowledge, the ability of created pools to replicate the physical, chemical, and biological characteristics of reference pools is questionable.

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References

- Babbitt KJ, Baber MJ, Tarr TL (2003) Patterns of larval amphibian distribution along a wetland hydroperiod gradient. Canadian Journal of Zoology 81:1539–1552
- Bates D, Maechler M, Bolker B, Walker S (2014) Lme4: linear mixed effects models using Eigen and S4. R package version 1.0-7
- Batzer DP, Palik BJ (2007) Variable response by aquatic invertebrates to experimental manipulations of leaf litter input into seasonal woodland ponds. Fundamental and Applied Limnology/Archiv für Hydrobiologie 168:155–162
- Batzer DP, Ruhí A (2013) Is there a core set of organisms that structure macroinvertebrate assemblages in freshwater wetlands? Freshwater Biology 58:1647–1659
- Batzer DP, Jackson CR, Mosner M (2000) Influences of riparian logging on plants and invertebrates in small, depressional wetlands of Georgia, U.S.A. Hydrobiologia 441:123–132
- Batzer DP, Palik BJ, Buech R (2004) Relationships between environmental characteristics and macroinvertebrate communities in seasonal woodland pools of Minnesota. Journal of the North American Benthological Society 23:50–68
- Batzer DP, Dietz-Brantley SE, Taylor BE, DeBiase AE (2005) Evaluating regional differences in macroinvertebrate communities from forested depressional wetlands across eastern and central North America. Journal of the North American Benthological Society 24:403–414
- Binckley CA, Resetarits WJ Jr (2007) Effects of forest canopy on habitat selection in treefrogs and aquatic insects: implications for communities and metacommunities. Oecologia 153:951–958
- Brady SP (2012) Road to evolution? Local adaptation to road adjacency in an amphibian (Ambystoma maculatum). Scientific Reports 2:235
- Brooks RT (2000) Annual and seasonal variation and the effects of hydroperiod on benthic macroinvertebrates of seasonal forest ("vernal") ponds in central Massachusetts, USA. Wetlands 20:707–715
- Brooks RT (2005) A review of basin morphology and pool hydrology of isolated ponded wetlands: implications for seasonal forest pools of the northeastern United States. Wetlands Ecology and Management 13:225–348
- Brown DJ, Street GM, Nairn RW, Forstner MRJ (2012) A place to call home: amphibian use of created and restored wetlands. International Journal of Ecology 2012:1–11

- Calhoun AJK, Walls TE, Stockwell SS, McCollough M (2003) Evaluating vernal pools as a basis for conservation strategies: a Maine case study. Wetlands 23:70–81
- Calhoun AJK, Arrigoni J, Brooks RP, Hunter ML Jr, Richter SC (2014) Creating successful vernal pools: a literature review and advice for practitioners. Wetlands 34:1027–1038
- Campbell DA, Cole CA, Brooks RP (2002) A comparison of created and natural wetlands in Pennsylvania, USA. Wetlands Ecology and Management 10:41–49
- Capps KA, Berven KA, Tiegs SD (2015) Modelling nutrient transport and transformation by pool-breeding amphibians in forested landscapes using a 21-year dataset. Freshwater Biology 60:500–511
- Cedergreen N, Madsen TV (2013) Nitrogen uptake by the floating macrophyte *Lemna minor*. New Phytologist 155:285–292
- Chambers RM, Meyerson LA, Saltonstall K (1999) Expansion of Phragmites australisinto tidal wetlands of North America. Aquatic Botany 64:261–273
- Clesceri LS, Greenberg AE, Eaton AD (eds) (1998) Standard methods for the examination of water and waste water. American Public Health Association, Washington, DC
- Cohen JS, Maerz JC, Blossey B (2012) Traits, not origin, explain impacts of plants on larval amphibians. Ecological Applications 22:218–228
- Colburn EA (2004) Vernal pools: natural history and conservation. McDonald and Woodward Publishing Company, Blacksburg
- Collinson NH, Biggs J, Corfield A, Hodson MJ, Walker D, Whitfield M, Williams PJ (1995) Temporary and permanent ponds: an assessment of the effects of drying out on the conservation value of aquatic macroinvertebrate communities. Biological Conservation 74:125–133
- Culler LE, Smith RF, Lamp WO (2014) Weak relationships between environmental factors and invertebrate communities in constructed wetlands. Wetlands 34:351–361
- Culley DD Jr, Rejmankova E, Kvet J, Frye JB (1981) Production, chemical quality, and use of duckweed (Lemnaceae) in aquaculture, waste management, and animal feeds. Journal of the World Mariculture Society 12:27–49
- Cutko A, Rawinski TJ (2008) Flora of northeastern vernal pools. In: Calhoun AJK, deMaynadier PG (eds) Science and conservation of vernal pools in northeastern North America. CRC Press, Boca Raton, pp 71–104
- Dahl TE (1990) Wetlands losses in the United States, 1780s to 1980s.
 Report to the Congress, No. PB-91-169284/XAB. National Wetlands Inventory, St. Petersburg, Florida
- Denton RD, Richter SC (2013) Amphibian communities in natural and constructed ridge top wetlands with implications for wetland construction. Journal of Wildlife Management 77:886–896
- Freda J, Dunson WA (1985) The effect of acidic precipitation on amphibian breeding in temporary ponds in Pennsylvania. US Fish and Wildlife Service, Eastern Energy and Land Use Team, Biological Report 80 (40.22)
- Halverson MA, Skelly DK, Kiesecker JM, Freidenburg LK (2003) Forest mediated light regime linked to amphibian distribution and performance. Oecologia 134:360–364
- Hanson MA, Bowe SE, Ossman FG, Fieberg J, Butler MG, Koch R (2009) Influences of forest harvest and environmental gradients on aquatic invertebrate communities of seasonal ponds. Wetlands 29: 884–895
- Herbst M, Kappen L (1999) The ratio of transpiration versus evaporation in a reed belt as influenced by weather conditions. Aquatic Botany 63:113–125
- Holgerson MA (2015) Drivers of carbon dioxide and methane supersaturation in small, temporary ponds. Biogeochemistry 124:305–318
- Homan RN, Windmiller BS, Reed JM (2004) Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. Ecological Applications 14:1547–1553



- Karraker N, Gibbs JP, Vonesh JR (2008) Impacts of road deicing salt on the demography of vernal pool-breeding amphibians. Ecological Applications 18:724–734
- Kihslinger RL (2008) Success of wetland mitigation projects. National Wetlands Newsletter 30:14–16
- Korfel CA, Mitsch WJ, Hetherington TE, Mack JJ (2010) Hydrology, physiochemistry, and amphibians in natural and created vernal pool wetlands. Restoration Ecology 18:843–854
- Lichko LE, Calhoun AJK (2003) An evaluation of vernal pool creation projects in New England: project documentation from 1991-2000. Environmental Management 32:141–151
- Maerz JC, Cohen JS, Blossey B (2010) Does detritus quality predict the effect of native and non-native plants on the performance of larval amphibians? Freshwater Biology 55:1694–1704
- Mahaney WS, Klemens MW (2002) Vernal pool conservation policy: the federal, state, and local context. In: Calhoun AJK, deMaynadier PG (eds) Science and conservation of vernal pools in northeastern North America. CRC Press, Boca Raton, pp 193–212
- McNab WH, Cleland DT, Feeouf JA, Keys JE, Nowacki GJ, Carpenter CA et al (2005) Description of ecological subregions: sections of the conterminous United States [CD-Rom]. Department of Agriculture, Forest Service, Washington, DC
- Meyerson LA, Chambers RM, Vogt KA (1999) The effects of *Phragmites* removal on nutrient pools in a freshwater tidal marsh ecosystem. Biological Invasions 1:129–136
- Mitsch WJ, Wilson RF (1996) Improving the success of wetland creation and restoration with know-how, time, and self-design. Ecological Applications 6:77–83
- Moore HH, Niering WA, Marsicano LJ, Dowdell M (1999) Vegetation change in created emergent wetlands (1988-1996) in Connecticut (USA). Wetlands Ecology and Management 7:177–191
- North Atlantic Landscape Conservation Cooperative (2014) Northeast Ecological Systems (2014 Update), Ecosystem Type. http://nalcc.databasin.org/datasets/85caf35ebb80411eb3c42fe0aaeeaeef. Accessed 30 Dec 2015
- Oksanen J et al (2010) Vegan: community ecology package. R package version 1.17-4. Available at http://CRAN.R-project.org/package=vegan
- Olson A, Paul J, Freeland JR (2009) Habitat preferences of cattail species and hybrids (*Typha* spp.) in eastern Canada. Aquatic Botany 91:67–70
- Palik B, Batzer DP, Buech R, Nichols D, Cease K, Egeland L, Streblow DE (2001) Seasonal pond characteristics across a chronosequence of adjacent forest ages in northern Minnesota, USA. Wetlands 21:532– 542
- Palik BJ, Buech R, Egeland L (2003) Using an ecological land hierarchy to predict seasonal-wetland abundance in upland forests. Ecological Applications 13:1153–1163
- Parr LB, Perkins RG, Mason CF (2002) Reduction in photosynthetic efficiency of *Cladophora glomerata*, induced by overlying canopies of *Lemna* spp. Water Research 36:1735–1742
- Paton PWC (2005) A review of vertebrate community composition in seasonal forest pools of the northeastern United States. Wetlands Ecology and Management 13:235–246
- Pechmann JHK, Estes RA, Scott DE, Gibbons JW (2001) Amphibian colonization and use of ponds created for trial mitigation of wetland loss. Wetlands 21:93–111
- Plenzer MA, Michaels HJ (2015) Terrestrial habitat quality impacts macroinvertebrate diversity in temporary wetlands. Wetlands 35:1093–1103
- R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

- Sadinski WJ, Dunson WA (1992) A multilevel study of effects of low pH on amphibians in temporary ponds. Journal of Herpetology 26:413–422
- Schiesari L (2006) Pond canopy cover: a resource gradient for anuran larvae. Freshwater Biology 51:412–423
- Schiesari L, Werner EE, Kling GW (2009) Carnivory and resource-based niche differentiation in anuran larvae: implications for food web and experimental ecology. Freshwater Biology 54:572–586
- Semlitsch RD (2000) Principles for management for aquatic-breeding amphibians. Journal of Wildlife Management 64:615–631
- Semlitsch RD, Bodie JR (2003) Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17:1219–1228
- Skelly DK, Werner EE, Cortwright SA (1999) Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80:2326– 2337
- Skelly DK, Freidenburg LK, Kiesecker JM (2002) Forest canopy and the performance of larval amphibians. Ecology 83:983–992
- Skelly DK, Halverson MA, Freidenburg LK, Urban MC (2005) Canopy closure and amphibian diversity in forested wetlands. Wetlands Ecology and Management 13:261–268
- Snodgrass JW, Komoroski MJ, Bryan AL Jr, Burger J (2000) Relationships among isolated wetland size, hydroperiod, and amphibian species richness: implications for wetland regulations. Conservation Biology 14:414–419
- Stanczak M, Keiper JB (2004) Benthic invertebrates in adjacent created and natural wetlands in northeastern Ohio, USA. Wetlands 24:212– 218
- Stolt MH, Genthner MH, Daniels WL, Groover VA, Nagle S, Haering KC (2000) Comparison of soil and other environmental conditions in constructed and adjacent palustrine reference wetlands. Wetlands 20:671–683
- Tarr TL, Baber MJ, Babbitt KJ (2005) Macroinvertebrate community structure across a wetland hydroperiod gradient in southern New Hampshire, USA. Wetlands Ecology and Management 13:321–334
- Vasconcelos D, Calhoun AJK (2006) Monitoring created seasonal pools for functional success: a six-year case study of amphibian responses, Sears Island, Maine, USA. Wetlands 26:992–1003
- Wassersug RJ, Seibert EA (1975) Behavioral responses of amphibian larvae to variation in dissolved oxygen. Copeia 1975:86–103
- Weaver CR (1943) Observations on the life of cycle of the fairy shrimp Eubranchipus vernalis. Ecology 24:500–502
- Werner EE, Glennemeier KS (1999) Influence of forest canopy cover on the breeding pond distributions of several amphibian species. Copeia 1999:1–12
- Werner EE, Skelly DK, Relyea RA, Yurewicz KL (2007) Amphibian species richness across environmental gradients. Oikos 116:1697–1712
- Wiggins GB, Mackay RJ, Smith IM (1980) Evolutionary and ecological strategies of animals in annual temporary pools. Archiv für Hydrobiologie, Supplement 58:97–206
- Williams DD (2006) The biology of temporary waters. Oxford University Press, New York
- Windmiller BS, Homan RN, Regosin JV, Willitts LA, Wells DL, Reed JM (2008) Breeding amphibian population declines following loss of upland forest habitat around vernal pools in Massachusetts, USA. In: Mitchell JC, Jung RE, Bartholomew B (eds) Urban herpetology. Herpetol Conserv 3:41–51
- Wu Q, Lane C, Liu H (2014) An effective method for detecting potential woodland vernal pools using high-resolution LiDAR data and aerial imagery. Remote Sensing 6:11444–11467
- Zedler JB (2000) Progress in wetland restoration ecology. Trends in Ecology & Evolution 15:402–407

