Vernal Pools of Northeastern North America

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Abstract

Vernal pools of northeastern North America are small, seasonally flooded wetlands found in forested areas. They are defined by features such as length and timing of flooding and their biological community. Most reach their maximum depth and volume each spring and draw down during the summer. Their importance as habitat for some amphibians and invertebrates, and the unique adaptations of the fauna, make vernal pools of interest for conservation, education, and research.

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Introduction

Vernal pools of northeastern North America are small, seasonally flooded wetlands found in forested areas. They are commonly defined by a combination of habitat characteristics, especially hydroperiod (length and timing of flooding), and biological community, especially the presence of species adapted to temporary waters. In general, vernal pools flood annually, reaching their maximum depth and volume in early spring and becoming fully or partly drawn down during the growing season. Many vernal pools dry completely by early summer, but others remain flooded until early fall, and some dry only occasionally in drought years. The annual or periodic drawdown prevents the establishment of permanent fish populations, limits the distribution of many large invertebrate predators, and contributes to decomposition of detritus by aerobic and anaerobic bacteria and fungi. Reduced predation pressure and abundant, nutritious food support a wide variety of animal life adapted to surviving seasonal inundation and drawdown. In particular, vernal pools are important breeding and nursery habitats for certain amphibians as well as a suite of pool-dependent invertebrate species. Their small size, seasonality of flooding, and unique contributions to local and regional biodiversity make vernal pools of interest for conservation, scientific research, and education.

This chapter provides a brief overview of the major physical, chemical, biological, and ecological characteristics of vernal pools, considers some of the adaptations that allow pool animals to carry out their lives in these seasonally flooded habitats, and discusses key conservation issues. Many excellent books, papers, and reports are available for those who would like more details about the ecology of vernal pools touched on here – see, e.g., Wiggins et al. 1980; Williams 1987; Semlitsch 1998; Batzer and Sion 1999; Higgins and Merritt 1999; Schneider 1999; Biebighauser 2003; Colburn 2004; Gibbons et al. 2006; Calhoun and deMaynadier 2008; and others listed in the text and at the end of the chapter.

Landscape Distribution of Vernal Pools

Temporary waters occur worldwide. Whether they occur in southern Australia, eastern Africa, the countries bordering the Mediterranean sea, central California, North American prairies, holes scoured in sandstone in desert canyons, bottomland forests of southeastern United States, or northeastern North America, temporary pools share seasonality of flooding; year-to-year variability of hydrology, chemistry, and temperature; many similarities in their biological communities and in species’

Fig. 1 Haynes Brook vernal pool in Downeast, Maine, USA, at spring thaw (Photo credit: Aram Calhoun © Rights remain with the author)

adaptations to the seasonal presence and absence of water; and conservation challenges (Colburn 2004, 2008; Calhoun et al. 2014a, b).

Vernal pools as discussed in this chapter are found in forested regions of formerly glaciated eastern North America. These pools share commonalities in their biota, most notably in the suite of amphibian species that depend on them for reproduction and also in many of the common invertebrates. (Pools in grasslands, although similar to vernal pools as defined here, support a different suite of species.)

These pools may occur in any context where depressions in the ground fill with water between fall and spring and retain water until at least late spring or early summer (Colburn 2004; Calhoun and deMaynadier 2008). Vernal pools lie in discrete depressions in forested uplands (Fig. 1), exposed bedrock hollows on mountain ridges or rocky shores, former stream channels or flood-scoured areas in floodplains, low-elevation areas within larger forested wetlands, pits formed when trees blow down, interdunal swales, and borrow pits or other areas excavated by human activities. Vernal pools often occur in clusters, especially in glacial outwash where kettlehole depressions were produced by melting ice left by the departing continental ice sheet.

History of Pool Studies

In the first half of the twentieth century, naturalists and experimental biologists reported on the biological communities and conducted research on animals of temporary forest ponds. For example, our understanding of North American invertebrate biodiversity and of the biology and ecology of temporary ponds was greatly increased by community surveys by Shelford (1913) and Kenk (1949), who documented a great diversity of phyla, classes, orders, and species of invertebrates in Michigan pools. Experiments by Libbie Hyman (University of Chicago) in the 1920s on hydras, oligochaetes, and planarians from temporary waters added to early understanding of drought survival mechanisms and developmental processes. Multi-year surveys by Ralph Dexter (Kent State University) from the 1930s through the 1960s documented year-to-year variations in distributions of fairy shrimp and clam shrimp and chronicled the loss of pool habitats in the American Mid-West over time.

Starting in the 1970s there was a great increase in scientific and conservation interest in vernal pools (Pough and Wilson 1976; Pierce 1993). This was fueled in part by new awareness of worldwide declines in amphibian populations and evidence that atmospheric deposition ("acid rain") had detrimental effects on the development of amphibian embryos in some temporary ponds in the Northeast as well as by broader concerns about the loss of local and regional biodiversity. These concerns led to applied and theoretical research focusing on conservation, especially in relation to vernal-pool-specialist amphibians (Shoop 1974). They also contributed to broader studies of vernal pool biological community composition and dynamics. During the same period, scientific curiosity about species' adaptive strategies for survival under variable disturbance regimes and about vernal pools and their inhabitants as possible aquatic models conforming to theories of island biogeography, r and K selection, and metapopulation dynamics spawned a host of research studies. Such research continued to add to theoretical understanding of vernal pools and to support conservation efforts directed toward protecting local and regional biodiversity.

Size, Depth, and Water Quality of Vernal Pools

Overall, vernal pools are highly heterogeneous (for more details see especially reviews in Colburn 2004; Calhoun and deMaynadier 2008).

Pool size and depth – Most pools are small. More than two thirds of those reported in the literature cover fewer than 0.05 ha when flooded. Fewer than one percent exceed 1.5 ha, and 6 ha is the largest reported pool area. Vernal pools also are usually shallow. The median depth of a large number of pools is 1 m, and the range is 16–300 cm. Potential implications of pool surface area for the biological community include shading by canopy trees – lower for large pools unless they are shallow enough to have trees growing within the pool basin; leaf litter inputs; depth; mixing of the water; hydroperiod (timing and duration of flooding); and extent and heterogeneity of habitat.

Water quality – Water chemistry in vernal pools covers a wide range and varies with water sources, bedrock, soils, surrounding plant community, and land use in the watershed. Reported value ranges include: pH 3.6–10.2; alkalinity 0–960; specific conductance 10–375 uS/cm; sulfate 0.5–12 mg/l; calcium 1–47 mg/l; chloride

0.1–3.0 mg/l; color 0–356 f (Vermont Wetlands Bioassessment Program 2003; Batzer et al. 2004; Colburn 2004).

Depending on a pool's size, depth, canopy cover, and water color, the water temperature may undergo dramatic diurnal fluctuations, and there may be strong thermal gradients from the surface to the bottom. These can influence the rate of embryonic development of amphibian and invertebrate eggs; affect metabolism and growth of pool animals; and, in the case of high water temperatures, reduce the amount of dissolved oxygen that the water can hold (less oxygen is available in warm water than cold).

The source of water feeding a pool can influence water temperature and chemistry. Runoff carries sediments, organic detritus, and dissolved materials transported by snowmelt and storm runoff from the watershed. Groundwater is likely to provide more constant thermal and chemical water quality than precipitation and runoff.

Hydrology

Water sources – Whether a pool is fed solely by precipitation and runoff and dries in response to evaporation from the pool surface and uptake of water by adjacent trees or if the pool is in contact with the water table and fluctuates additionally with groundwater may substantially affect the timing and duration of flooding or hydroperiod (Sobczak 1999; Sobczak et al. 2003; Leibowitz and Brooks 2008).

Hydrologic continuum for vernal pool hydroperiods – The timing and duration of flooding in vernal pools span a broad temporal continuum (Schneider 1999; Colburn 2004; Leibowitz and Brooks 2008). Highly ephemeral pools that fill following heavy rainstorms and dry within days or a couple of weeks do not remain flooded long enough to support vernal-pool-dependent species. Among pools that do support characteristic species and communities, those at the dry end of the continuum fill in spring, remain inundated for several months, and dry by early summer. Longer hydroperiod pools fill in spring but retain water through summer and sometimes into early fall. Many pools typically start to fill in fall, reach their maximum volume and depth in spring, and dry by early summer. The seasonally flooding pools that have the longest hydroperiods fill in fall and retain water through most of the following summer, with only a few weeks of drawdown in late summer before they fill again. There are also some functional vernal pools that are semi-permanently flooded, drying only during periods of drought. A particular pool may have a characteristic pattern of filling and drying over many years, but in any given year a pool may lie on the wetter or drier end of the continuum, depending on local patterns of precipitation and temperature.

Effects of hydroperiod on pool biota – Different species of pool animals are distributed across this hydrologic continuum, depending on the timing of flooding and the duration of inundation. Hydroperiod has been identified as a primary factor influencing which species can survive in a given vernal pool (Karraker and Gibbs 2009; Wiggins 1973). Hydroperiod may act both directly, with short flooding durations preventing the establishment of species that lack drought-resisting adaptations, and indirectly, with long hydroperiods allowing for greater overall species richness but excluding predation-sensitive species.

Wiggins et al. (1980) conducted a comprehensive survey of the biota from a series of pools in Ontario with differing flooding durations and evaluated the various species' adaptations for survival in the absence of water. They concluded that "vernal temporary pools," which they defined as filling in spring and drying by early summer, support species with well-developed strategies for avoiding desiccation during the long period in which the pool is without water. In contrast, they observed that species from pools with longer hydroperiods, such as "autumnal vernal pools" that fill in fall and dry by early summer, support species that can only withstand shorter periods of drying. "Permanent pools" support species that lack adaptations for withstanding drawdown. These species sometimes include predatory fish as well as invertebrate predators that can prevent successful development by vernal-pool-dependent species.

Subsequent research on a larger population of vernal pools throughout the glaciated northeast has shown that hydrologic conditions in vernal pools cover a broader continuum than discussed by Wiggins et al. (1980). Long-hydroperiod pools may provide animals with longer periods for growth and development, allowing amphibian larvae to reach larger sizes before metamorphosis, or providing invertebrates such as snails or fingernail clams with multiple opportunities to reproduce in a year (see discussions of life cycles in Colburn 2004).

During multi-year flooded periods, semi-permanent pools may support vertebrate predators including bullfrog *Lithobates catesbeiana* and green frog *L. clamitans* tadpoles (which need to overwinter before transforming the following year into frogs) (Vasconcelos and Calhoun 2006) and red-spotted newts *Notophthalmus viridescens*. Also commonly in these pools are large invertebrate predators including some dragonfly nymphs, various water bugs, and water beetle larvae. These predators can prevent most vernal-pool specialists from successfully completing their development. Such predators may be present continuously in semi-permanent pools during multi-year flooded periods, but when they are eliminated periodically by drawdown during low-water years, dormant eggs and cysts of short-hydroperiod vernal-pool species, such as fairy shrimp, may hatch and, released from predation pressure, successfully grow and reproduce. Dan Schneider (1999) has shown that hydroperiod acts as a "filter" controlling the distribution of predators whose presence limits the successful development of some species that appear to be restricted to short-hydroperiod pools but that can survive long-hydroperiod conditions in the absence of predation.

In permanent pools, predaceous fish may become established, and in their absence the presence of amphibian and invertebrate predators can limit the successful growth and development of vernal-pool-dependent amphibians and invertebrates.

Vernal Pools as Wetlands

Vernal pools fall within several categories of wetlands as defined by the US Fish and Wildlife Service (Cowardin et al. 1979) or by the Hydrogeomorphic (HGM) method (U.S. Natural Resources Conservation Service 2008). Some vernal pools support wetland vegetation and are underlain by hydric soils. Hydrophytes may be absent from pools with dense canopy cover, in deep depressions, and/or with long hydroperiods that prevent the establishment of emergent plants. Pools that occur on bedrock or with short annual hydroperiods may not be underlain by typical hydric soils.

Plant Communities

Northeastern vernal pools share many features with seasonal forest pools farther south, and with temporary waters in nonforested regions, but they are different in their general lack of unique plant communities and endemic plant species. If vegetated, they support plant species that are common in other nearby wetlands (Colburn 2004; Cutko and Rawinski 2008). As mentioned above, vernal pools in northeastern North America are of particular conservation interest because of their fauna, especially pool-dependent amphibians and crustaceans, and invertebrate species that are restricted to short-hydroperiod pools.

Detritus and In-Pool Photosynthesis

Occurring as they do in forested contexts, vernal pools receive substantial inputs of fallen leaves each autumn (Fig. 2). Leaf decomposition, nutrient cycling, and the conversion of cellulose into digestible carbohydrates and glycoproteins by aerobic and anaerobic decomposer fungi and bacteria provide abundant food for vernal pool shredders and collector-gatherer feeders and may contribute importantly to forest biogeochemistry (Bärlocher et al. 1978; Capps et al. 2014). Food quality affects the distribution and development of aquatic animals, and caddisfly larvae given choices of detritus from permanent vs. intermittently flooded habitat preferred and grew better with the vernal pool detritus (Richardson and Mackay 1984). Depending on their size and location, vernal pools may receive little or substantial amounts of

Fig. 2 (**a**) Southern New England vernal pool embedded in an oak forest at spring thaw and (**b**) drying down exposing the detritus layer of fallen leaves and woody material (Photo credit: Kevin J. Ryan © Rights remain with the author)

sunlight, and in-pool photosynthesis may be extensive or very limited. The availability of algae vs. detritus is one of many important variables affecting the relative success of different amphibian species in vernal pools (Skelly et al. 2002).

Amphibians in Vernal Pools

The importance of vernal pools for many amphibian species is central to much of the interest in these small wetlands. Amphibians are important components of local and regional biodiversity, and they are also important agents of energy exchange between forests and vernal pools and between pools and upland forests. Vernal pools are optimal breeding habitats for wood frogs *Lithobates sylvaticus* and mole salamanders in the genus *Ambystoma*, including the spotted salamander *A. maculatum*, marbled salamander *A. opacum*, small-mouthed salamander *A. tremblayi*, Eastern tiger salamander *A. tigrinum tigrinum*, and members of the Jefferson-blue-spotted salamander complex (*A. jeffersonianum* and *A. laterale*) – whose closely related species have interbred to form a variety of triploid and tetraploid unisexual hydrids (Brodman 2005). Other amphibians that often breed in vernal pools – usually at the longer-hydroperiod end of the continuum – and also breed widely in other aquatic habitats include American and Fowlers toads (*Anaxyrus* (formerly *Bufo*) *americanus* and *A. fowleri*), spring peepers *Pseudacris crucifer*, gray treefrogs (*Hyla versicolor* and *H. chrysoscelis*), and, west of the Appalachians, chorus frogs *Pseudacris* spp. Spadefoot toads *Scaphiopus holbrookii* breed most commonly in pools that fall along the ephemeral end on the continuum and often retain water for too short a time to support typical vernal pool species assemblages, but they also breed in vernal pools in some locations.

The life cycles of vernal-pool amphibians are tailored to maximize the likelihood of young successfully maturing and emerging from pools before drying (see reviews in Colburn 2004; Semlitsch and Skelly 2008). When water is first available in early spring, cold water temperatures, the possibility of a late freeze, and limited food availability pose challenges for early breeding, but the chance of a pool drying before young have completed development places limitations on how late breeding can occur, especially in shorter-hydroperiod pools. Wood frogs (Fig. 3), spring peepers, and mole salamanders typically move to vernal pools in early spring, often while snow is still on the ground and ice may be present on the pool surface. (An exception is the marbled salamander, which moves to dry pool depressions in autumn and lays its eggs on the damp or dry ground; the eggs start to develop when the pool floods.) The adult wood frogs and salamanders spend relatively few days in the pools, mating and depositing eggs, before migrating back into the upland forests where they spend most of their lives. Pools are warming rapidly in early spring, and food becomes increasingly available during the period when embryos are developing, so that tadpoles and salamander larvae find abundant food resources upon hatching (in a few weeks for wood frogs, more than a month for salamanders). Rapid development of eggs and larvae, especially in wood frogs, which often breed in shorter-hydroperiod pools than mole salamanders, maximizes the likelihood that

Fig. 3 Wood frogs spend the majority of the year in the forest away from their breeding pools. Their brown color, dark mask, and striped legs help them blend into the forest floor (Photo credit: Kristine Hoffmann © Rights remain with the author)

juveniles will be ready to leave before the pool dries. Early pool drying often results in high proportions of wood frog tadpoles failing to complete development. In the salamanders, both egg and larval development are slower than in wood frogs. After larvae reach a minimum size threshold for transformation, they may remain in pools for a period of time if conditions remain favorable for growth, as size at metamorphosis affects reproductive fitness. After juveniles leave the pools, they disperse into the upland where they will feed on invertebrates until they reach maturity. In a subsequent spring, most pool amphibians return to their larval pools when ready to breed.

Unlike the wood frogs and mole salamanders, toads and gray treefrogs start to breed later in the spring, and they tend to remain in pools for weeks at a time, the males trilling to attract mates and the females moving into pools to deposit eggs over longer periods of time and later into the spring. These animals breed in vernal pools with longer hydroperiods and also in permanent waters.

Spadefoot toads spend much of their lives burrowed into sandy soil, moving to the surface to feed on wet nights. They emerge during torrential rainstorms from spring to fall. Migrating to shallow pools, the males call with a loud, honking noise during thunderstorms, lightening reflecting off of their inflated throat pouches, and attracting females. Breeding is fast, eggs develop within days in the short-lived rainwater pools, tadpoles feed on a host of small organisms in the water, and metamorphosis is complete in just a few weeks.

Invertebrates in Vernal Pools

More than 400 species of invertebrates have been identified from northeastern vernal pools (see Wiggins et al. 1980; Williams 1987, 2006; Colburn 2004; Colburn et al. 2008). Among the most characteristic vernal pool taxa are branchiopod crustaceans including fairy shrimp *Eubranchipus* spp., clam shrimp *Lynceus brachyurus*, and cladocerans (water fleas, especially Daphniidae and Chydoridae) and water beetles (especially species of predaceous diving beetles, Dytiscidae). A host of other kinds of aquatic insects as well as aquatic earthworms, leeches, molluscs, flatworms, and even hydras also occur in vernal pools.

Invertebrates in relation to hydroperiod and seasonality – This diversity is spread across the hydrologic continuum. Long-hydroperiod pools tend to be more species-rich than short-hydroperiod pools, but the species composition is different (Schneider 1999; Brooks 2000). Collectively, the richness of species within a cluster of vernal pools with a range of hydroperiods and other habitat characteristics is greater than the number of species in the most species-rich pool, reflecting the importance of pool heterogeneity for local and regional biodiversity. A range of hydroperiods, from very short to long, is necessary to allow for the greatest richness of vernal pool invertebrate species in a particular location or region.

The composition of the aquatic invertebrate community changes as the season progresses. Early in spring one commonly finds fairy shrimp, copepods, water fleas, planarians, caddisfly larvae, mosquito and phantom midge larvae, some beetle adults that overwinter in the pool sediment, and certain dytiscid beetle larvae – known popularly as “water tigers” because of their massive, sharp jaws and their aggressive predation on fairy shrimp, tadpoles, and other pool residents. Snails and fingernail clams may be present in pools where water is not excessively acidic. As the water warms, planarians, mosquitoes, and fairy shrimp disappear; clam shrimp and different water fleas may become abundant; caddisflies pupate and fly away as brown, moth-like adults; and migratory insects including adult water beetles such as *Agabus* spp., water boatmen (Corixidae), backswimmers (Notonectidae), and other water bugs (Hemiptera, Heteroptera) fly in from permanent waters where they overwintered. In longer hydroperiod pools, especially those with some aquatic vegetation, damselfly and dragonfly nymphs may become abundant in late spring and summer, emerging progressively to feed on insects above the pool and in the adjacent forest.

Many vernal pool invertebrates are widely distributed, but other species vary with pool characteristics such as hydroperiod, forest cover, water chemistry, land use, and vegetation (Schneider 1999; Vermont Wetlands Bioassessment Program 2003).

Invertebrate life histories – As with the amphibians, the life histories of vernal pool invertebrates allow survival and reproduction in an aquatic habitat that is periodically without water, and they may also provide for dispersal to new habitats. These life cycles include strategies for withstanding pool drying within the pool basin or for escaping drying in some way. Some animals, such as planarians, form cysts that resist drying in the sediment; others including snails and fingernail clams withdraw into their shells and aestivate during drawdown; and crustaceans and many insects have eggs that lie dormant in the dry pool sediment and hatch after flooding. Post-flooding hatching may occur immediately upon water appearing in the pool, or it may be subject to other conditions such as specific water temperatures, a period of prior exposure to cold, or oxygen concentrations in the water. Some invertebrates follow the amphibian strategy of breeding and maturing in vernal pools but migrating elsewhere (often to permanent waters) as adults.

Invertebrates also have several different mechanisms for maximizing the likelihood that offspring will survive pool conditions and reach maturity. Some species produce very large numbers of eggs; even if most die, there is a chance that a few will survive to complete development. Others produce small numbers of large eggs; having access to large stores of resources helps improve an individual offspring's chances of survival. Closely related species may use alternative strategies – examples are seen in crustaceans such as copepods and in molluscs such as fingernail clams (see Wiggins et al 1980; and reviews in Colburn 2004 and Colburn et al. 2008).

Fairy shrimp are among the most classic vernal-pool-dependent animals. They (and many other pool crustaceans) have eggs that resist drying and can remain in the pool sediment for many years. When the eggs hatch, tiny shrimps emerge (seemingly by magic – hence "fairy shrimp") and can be seen swimming on their backs in vernal pools in early spring, synchronously waving a dozen feathery legs and filtering fine particles and microorganisms from the water for food. After the shrimps mature and mate, eggs fall from the females' egg pouches onto the pool bottom, and the adults die, long before salamanders and most insect predators are active in the pools. Before the eggs can hatch, they need to experience drying, chilling, and reflooding. In a semi-permanent pool, there may be no fairy shrimp for many years without drawdown and then, after a dry year when the pool bottom becomes exposed to desiccation and winter cold, fairy shrimp will appear when the pool refloods in spring. Not all eggs will hatch the first or the second – or even the third time they experience these conditions; some will remain in the sediment and hatch another time. This "bet-hedging" strategy protects the population against catastrophic losses if the pool should dry early, before the shrimp mature and mate.

Agabus is a large genus of predaceous diving beetles with several species in vernal pools. Larvae hatch from eggs in the sediment in early spring. Some weeks later, adults fly in from permanent waters where they overwintered. They mate and females leave eggs on the pool bottom. Those eggs will not hatch until the following spring. The larvae will hatch, feed, grow, pupate, and emerge as adults which disperse to permanent water when the pool dries, flying back to vernal pools the following spring to start the cycle over again. It thus takes two full years for a complete life cycle, and it includes not only the pool but also a permanent water body plus food resources in both habitats.

Water mites have even more complex life cycles. Eggs hatch into parasitic larvae that attach to discrete locations on particular species of adult insects and feed on the adult's blood as the insect flies around the pool looking for food or mates (as might be the case for a dragonfly adult) or it is carried by the adult host (such as a water beetle or water bug) to a permanent lake or pond for the winter (where it remains attached to its host) and is then returned to the original pool or dispersed to another when the adult migrates to pools the following spring. The fed larva drops into the pool and transforms into a nymph, which is a predator on the eggs of small crustaceans or of mosquito or other fly larvae. The nymph then transforms into an adult which is also predatory on the same species as the nymph. Adults mate, lay eggs, and the cycle starts over again.

Conservation of Vernal Pools

Because vernal pools are important at both pool-level (i.e., breeding habitat for specialized biotic communities) and landscape scales (e.g., genetic, hydrologic and biogeochemical reservoirs, and resting and foraging habitat for water bugs and beetles, birds, mammals, and non-pool-dependent herptiles) and because pools vary in flooding regime, geomorphic setting, and environmental quality, conservation approaches must be tailored to specific desired outcomes. Conservation strategies are further limited because these small, ephemeral wetlands largely occur on private properties. Additionally, vernal pools are hard to identify remotely (often, more than 33% are missed in pre-identification exercises), they often function as clusters of pools, and their functions depend on linkages with other pools, wetlands, and uplands (Mushet et al. 2015). We provide short guidance on conserving pool functions at the pool or species-specific scale and at the landscape scale while encouraging managers to employ all these approaches. Useful sources of additional information include Semlitsch (2002), review papers in Calhoun and deMaynadier (2008), Calhoun et al. (2014a, b), Rains et al. 2016; Cohen et al. (2016) and papers cited below.

Conservation of individual pools or species – Pool-scale conservation tools are limited to regulatory protection for a subset of exemplary pools or pools associated with rivers or lakes (this varies by state; Mahaney and Klemens 2008) and to voluntary best management practices (e.g., Calhoun and deMaynadier 2004; Calhoun and Klemens 2002). If regulated vernal pools are degraded or destroyed, mitigation may include pool creation or restoration. Restoring or creating pool habitat often fails, particularly for pool-breeding amphibians and invertebrates, due to an inability to recreate hydrology (Calhoun et al. 2014a). With the exception of regions where pool losses are very high, pool creation should be a last resort and coupled with pool preservation (Kross and Richter 2016).

Conserving habitat for individual species requires knowledge of breeding and post-breeding behaviors which varies among species and with regional context (Semlitsch et al. 2009). The biphasic life histories of vernal-pool amphibians make the adjacent terrestrial habitat an integral part of conserving pool functions (Semlitsch 2002). Similarly, the seasonal use of permanent waters by many insects of vernal pools means that a pool alone is not sufficient to meet these species' life history requirements (Colburn 2004). Although pool-breeding amphibians disperse and migrate 100s of meters between breeding pools and upland habitat (Rittenhouse and Semlitsch 2007), national and state regulations on vernal pools regulate activities within at most 10–80 m from the pool's edge (Mahaney and Klemens 2008). Stricter regulations may apply if state-listed species are documented. Within regulatory constraints, managers should work to develop mitigation or protection strategies that incorporate as much ecologically relevant habitat as possible for target species. For example, the configuration may be in the form of corridors linking and incorporating relevant habitat rather than neat circles around the pool (Baldwin et al. 2006). Given the challenge of providing meaningful post-breeding habitat for amphibians and other pool ecosystem services, we highly recommend conservation strategies that couple pool-specific conservation with broader landscape approaches.

Landscape-scale approaches to pool conservation – Because pools do not exist as isolated wetland depressions but rather as vital biological, physicochemical, and ecological integrators in a terrestrial matrix (McLaughlin et al. 2014; Cohen et al. 2016) and because many vernal pool species' life cycles extend beyond pool basins, conserving "vernal poolscapes" – complexes of vernal pools and other aquatic habitats plus associated uplands – is a preferred conservation approach. Landscape-scale conservation allows for the protection of pools spanning an array of hydrogeomorphic settings (ones that support short-to-long hydroregimes in different physical settings) that conserve a range of biogeochemical and water quality functions and support diverse biota (Mitchell et al. 2007; Marton et al. 2015). This approach also buffers changes in pool functions against changes in climate.

Landscape approaches can use stakeholder-driven energy and expertise and can be developed at scales ranging from local, low-cost, voluntary programs using citizen scientists (Jansujwicz and Calhoun 2010, 2013) to more resource-intensive regional inventory and assessments associated with research, consulting projects, or government initiatives (Lathrop et al. 2005). Development of citizen science programs is an effective strategy to develop municipal or regional pool conservation plans (Morgan and Calhoun 2014; www.vernalpools.me) and web-based reporting of vernal pools as citizens encounter them (Carpenter et al. 2011); this provides an evolving database of resources that would be too expensive for government agencies or NGOs to inventory comprehensively.

Costs of conservation at landscape scales call for collaborative approaches. For example, an incentivized approach for vernal pools in New England is being developed through collaboration among federal, state, and local governments, ecologists, the development community, land trusts, and environmental nongovernmental organizations to provide an alternative mitigation tool for vernal pools agreed upon by all parties. This tool is a local *in lieu* fee program where developers may impact wetlands in municipal growth zones in return for a fee collected to incentivize local landowners to conserve exemplary vernal pools and post-breeding habitat in municipal rural zones (Special Area Management Plan for Vernal Pools in US Army Corps of Engineers Region 1; see Levesque et al. 2016). Vernal poolscapes in this program will be targeted through partnerships with local land trusts or other conservation organizations. This innovative approach improves federal regulations by tailoring conservation of vernal pools to local needs that support both conservation and economic development. In this case discontent with the top-down "stick" of government regulations that assume one-size-fits-all served as momentum for creativity (Calhoun et al. 2014b). This type of management approach that recognizes the spatial distribution of benefits and costs and full extent of conservation costs is more likely to navigate this challenge successfully (Sunding and Terhorst 2014).

In summary, the best vernal pool conservation strategies include case-by-case regulatory approaches coupled with broader landscape-scale initiatives that capture the full suite of vernal pool ecosystem services by maximizing connectivity among wetlands and forests. Flexible conservation strategies that reduce landowner and manager costs while achieving ecological objectives will have the greatest probability of success in maintaining fully functioning landscapes. We can move toward this paradigm by tailoring conservation to local needs through stakeholder-generated solutions often coupled with government engagement at multiple levels.

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