

Experimental canopy removal enhances diversity of vernal pond amphibians

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Abstract. Vernal ponds are often treated as protected environments receiving special regulation and management. Within the landscapes where they are found, forest vegetation frequently dominates surrounding uplands and can grow to overtop and shade pond basins. Two bodies of research offer differing views of the role of forest canopy for vernal pond systems. Studies of landscape conversion suggest that removing forest overstory within uplands can cause local extinctions of amphibians by altering terrestrial habitat or hindering movement. Studies of canopy above pond basins imply an opposite relationship; encroachment of overstory vegetation can be associated with local extinctions potentially via changes in light, thermal, and food resource environments. Unresolved uncertainties about the role of forest canopy reveal significant gaps in our understanding of wetland species distributions and dynamics. Any misunderstanding of canopy influences is simultaneously important to managers because current practices emphasize promoting or conserving vegetation growth particularly within buffers immediately adjacent to ponds. We evaluated this apparent contradiction by conducting a landscape-scale, long-term experiment using 14 natural vernal ponds. Tree felling at six manipulated ponds was limited in spatial scope but was nevertheless effective in increasing water temperature. Compared with eight control ponds, manipulated ponds maintained more amphibian species during five years post-manipulation. There was little evidence that any species was negatively influenced, and the reproductive effort of species for which we estimated egg inputs maintained pretreatment population densities in manipulated compared with control ponds. Overall, our experiment shows that a carefully circumscribed reduction of overhead forest canopy can enhance the capacity of vernal ponds to support wildlife diversity and suggests a scale dependence of canopy influences on amphibians. These findings have implications for the connection between current wetland management practices and the goals of wetland stewardship and conservation of wetland-dependent species.

Key words: buffer; canopy; conservation; experiment; forest; frog; salamander; scale transition; upland habitat; wetland management.

INTRODUCTION

Vernal ponds are among the most numerous freshwater environments (Gibbs 1993). Their wide distribution across the landscape can put them into frequent conflict with human activities and their small size makes them vulnerable to modification or destruction (Semlitsch and Skelly 2007). In reaction to a wave of wetland loss, a variety of protections for vernal ponds have been established at local, state, and federal levels in the United States and around the world (e.g., Committee on Characterization of Wetlands 1995, Zinn and Copeland 1998). These protections remain contentious even if their motivations are not. It is clear that vernal ponds serve important hydrological functions (Duffy and Kahara 2011), and it is equally clear that there are many species that depend exclusively or primarily on vernal pond habitats (Semlitsch and Skelly 2007). Many of these

species are also dependent on the uplands that surround them. In temperate biomes, forests often dominate landscapes and can encompass small ponds, completely covering their basins. In these ways, forests can both provide an adjacent distinct environment for aquatic-dependent species (Semlitsch 2000) and also act as a powerful mediator of site conditions within the ponds themselves (Werner and Glennemeier 1999, Skelly et al. 2002).

A number of studies have revealed relationships between forest loss and conversion to other cover types and the presence and abundance of amphibian species (Popescu and Hunter 2011). There is some evidence of thresholds of landscape conversion beyond which wetland-dependent species are consistently absent (Homan et al. 2004). While species differ in their tolerance of forest conversion (Gibbs 1998), a general sense has emerged that forest disturbance near wetlands is detrimental to conservation goals (de Maynadier and Hunter 1999, Semlitsch 2002, Semlitsch and Bodie 2003, Harper et al. 2008, Semlitsch et al. 2009). Subsequent

Manuscript received 5 June 2013; accepted 12 August 2013.
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research has shown that, beyond a reduction of terrestrial habitat for forest dwellers, converted landscapes may be more challenging for dispersing individuals leaving natal ponds (Rothermel and Semlitsch 2002, Rittenhouse et al. 2008, Popescu and Hunter 2011). These conclusions are aligned with wetlands regulations and the development of best management practices that require or recommend avoiding disturbance to forest and other vegetation within a buffer around ponds (e.g., California Natural Resources Agency 2010; Massachusetts Wetlands Protection Act).

Interestingly, results from forest conversion research stand in contrast to an independent set of studies that have examined the role of canopy conditions over pond basins. Comparisons of shaded and open ponds reveal average water temperature differences of $\sim 2^{\circ}\text{C}$ and differences of up to 6° or 7°C in maximum daily temperature (e.g., Freidenburg and Skelly 2004). Beyond such physical effects, shading also influences patterns of primary production and the composition of microbial communities (Batzer et al. 2000) with corresponding implications for food chains within shaded vs. open ponds (Werner and Glennemeier 1999, Skelly et al. 2002). Studies of amphibians and canopy have revealed that heavily shaded ponds are species poor relative to open canopy ponds (Werner et al. 2007a). The primary driver of this pattern is the relative shading intolerance of most amphibian species in contrast to a smaller subset of species that appear to be relatively insensitive to canopy conditions (Skelly et al. 2005). While most observational studies of canopy influences consist of cross sectional observations (e.g., Skelly et al. 2005, Werner et al. 2007a), longitudinal observations in at least one system reveal an analogous pattern: encroachment of overstory vegetation at individual ponds was associated with species loss (Skelly et al. 1999).

Dissonance between research on forest conversion and canopy influences inspired us to carry out an experiment using entire natural ponds. We hypothesized that the influence of forest disturbance on pond-dependent amphibians may be strongly scale dependent. When a small number of trees are removed near a pond, the influence on wetland site conditions may be large but the influence on terrestrial habitat may be minimal. We predicted that strategic removal of a small number of trees would alter the conditions in manipulated vernal ponds in ways that would foster the presence of amphibian species intolerant of shaded conditions. We predict an overall increase in the number of species supported because we expect canopy-tolerant species to persist as well. To test these predictions, we cut trees near the southern shorelines of six shaded vernal ponds and compared the subsequent patterns of species presence and absence to a set of eight shaded ponds at which the canopy was unmanipulated. We followed species distributions for five years post-manipulation. In addition, in an effort to evaluate the welfare of canopy-

tolerant species, we estimated population sizes of two species for nine years post-manipulation.

METHODS

The Yale Myers Forest (Connecticut, USA) covers 3213 ha and is administered by the Yale School of Forestry and Environmental Studies. Study ponds were selected because they were typical in size (averaged 1300 m^2 in area and 89 cm in maximum depth) and had well-developed canopies. All 14 ponds were known to support amphibians prior to their inclusion in this study. At six of the ponds, canopy was manipulated by felling trees. Ongoing research in some Yale-Myers ponds prevented us from selecting ponds at random but the six “cut” ponds were selected such that cut vs. control ponds were comparable in maximum depth (t test, $df = 12$, $t = 1.139$, $P = 0.277$), surface area (t test, $df = 12$, $t = 1.824$, $P = 0.107$) and pretreatment canopy cover (t test, $df = 12$, $t = 1.134$, $P = 0.302$) and so that ponds of the two treatments were interspersed geographically. Cutting took place along the portion of the southern shoreline centered on true south and covering a 90° arc. All trees up to 25 m from the shoreline were felled. Trees were felled away from the pond, and left intact and in place. Debris that fell in the pond basin was removed. All cutting took place during the winter of 2001–2002 and was completed prior to the onset of the 2002 spring breeding season. The remaining eight control ponds were left unmanipulated.

We recorded water temperature during 2002 in all ponds using Hobo temperature loggers suspended 10 cm below the water surface and 2 m from the shoreline. Two loggers were deployed in each pond: one near the north shore and one near the south shore. Beginning in 2001 and through 2006, we visited ponds to sample for eggs and larvae of amphibian species. Prior to cutting during 2001, we sampled eight control ponds and three ponds within the cut treatment. During subsequent years, all ponds were sampled. Ponds were visited two to four times per field season; all ponds received the same number of visits in a given year. Species were detected during visual searches for eggs and by dipnetting for larvae.

For two species, wood frogs (*Rana sylvatica*) and spotted salamanders (*Ambystoma maculatum*), we collected annual records of egg mass inputs (2001–2011). We recorded the number of wood frog egg masses in each pond as well as the number of spotted salamander egg masses detected during a time-constrained search (masses/person minute). These responses can act as an index of population size (Werner et al. 2009) and offer an opportunity, for some resident species, to evaluate population responses beyond presence and absence.

RESULTS

Felling overstory trees along the Southern shoreline (90° arc extending 25 m) affected the thermal environment in cut ponds. While temperatures did not differ

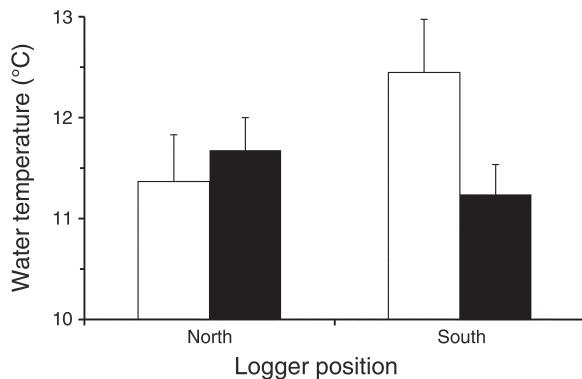


FIG. 1. Water temperature in 14 vernal ponds between 14 March and 30 June 2002. Ponds were divided into those that had trees felled along the southern shore, creating a more open canopy above the pond basin (cut, $n = 6$ ponds, open bars), and those that were not manipulated (control, $n = 8$ ponds, solid bars). In each pond, a temperature logger was placed 10 cm below the surface 2 m from the northern and southern shorelines, respectively. Values are means + SE.

between treatments near the unmanipulated northern shoreline of the ponds (Fig. 1; t test, $df = 12$, $t = 0.676$, $P = 0.51$), at southern logger locations cut ponds averaged 1.1°C warmer than control ponds (Fig. 1; t test, $df = 12$, $t = 2.83$, $P = 0.015$).

In 2001, prior to cutting, the number of species supported in ponds destined for cut vs. control treatments was not distinguishable (Fig. 2; t test, $df = 9$, $t = 1.40$, $P = 0.195$). During the five years posttreatment, cut ponds averaged 1.2 more species each year than control ponds (Fig. 2; t test, $df = 12$, $t = 2.46$, $P = 0.030$). Maximum observed richness was 1.7 species higher in cut ponds (t test, $df = 12$, $t = 3.95$, $P = 0.002$). A repeated-measures ANOVA revealed an effect of year on species richness (Wilks' lambda = 0.19, $F_{4,9} = 9.87$, $P = 0.002$) but no evidence of an interaction between pond treatment and year (Wilks' lambda = 0.54, $F_{4,9} = 1.64$, $P = 0.246$).

To further explore the differences in richness between pond treatments, we estimated post-manipulation prevalence of seven species within cut and control ponds. Species were categorized as canopy tolerant or intolerant following Skelly et al. (2005). Species known to be canopy tolerant (marbled salamanders [*Ambystoma opacum*], spotted salamanders, wood frogs) were equivalent in prevalence between cut and control ponds (Fig. 3; Z tests, $P > 0.872$ for each species). Of the species known to be canopy intolerant, three of them (gray treefrog [*Hyla versicolor*], green frog [*Rana clamitans*], and spring peeper [*Pseudacris crucifer*]) were more prevalent in cut ponds vs. control ponds (Fig. 3; Z tests, $P < 0.015$ for each species). One species categorized as canopy intolerant, the red-spotted newt (*Notophthalmus viridescens*), was equivalent in prevalence between treatments (Fig. 3, Z test, $P = 0.347$). The distinction in response to manipulations between tolerant and intolerant species is illustrated using two species

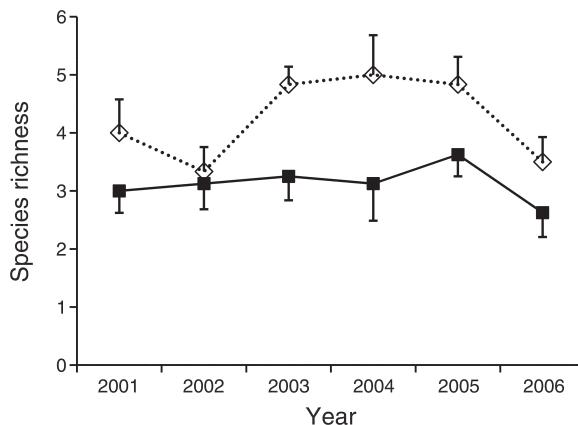


FIG. 2. Amphibian species richness detected as eggs or larvae within ponds at the Yale Myers Forest (Connecticut, USA) during the period 2001–2006. Ponds were divided into those that had trees felled along the southern shore, creating a more open canopy above the pond basin (cut, $n = 6$ ponds, open symbols and dashed line), and those that were not manipulated (control, $n = 8$ ponds, solid symbols and solid line). Canopy manipulation took place during the winter of 2001–2002 and was completed prior to the 2002 breeding season. During 2001, eight control ponds and three ponds in the cut treatment were sampled. All ponds were sampled each year subsequently. Values are means \pm SE.

in Fig. 4. Gray treefrogs were entirely absent from the ponds in the experiment prior to the manipulation of canopy. Following cutting, treefrogs colonized manipulated ponds reaching two-thirds of them by the last year

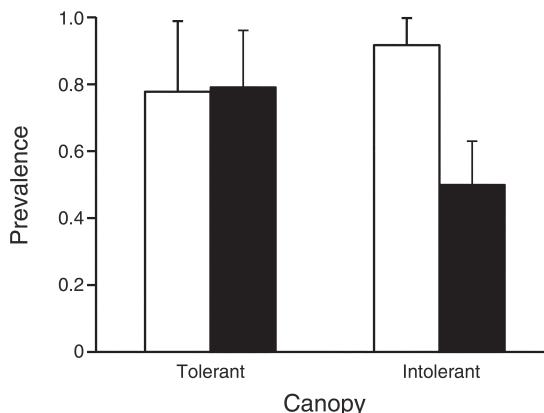


FIG. 3. Post-manipulation prevalence (2002–2006) of canopy-tolerant and canopy-intolerant species within 14 vernal ponds at the Yale Myers Forest (Connecticut, USA). Canopy tolerance was defined according to Skelly et al. (2005). Three tolerant species included marbled salamanders, spotted salamanders, and wood frogs. Four intolerant species included red-spotted newts, gray treefrogs, spring peepers, and green frogs. Ponds were divided into those that had trees felled along the southern shore creating a more open canopy above the pond basin (cut, $n = 6$ ponds, open bars) and those that were not manipulated (control, $n = 8$ ponds, solid bars). Canopy manipulation took place during the winter of 2001–2002. Presence was defined by the detection of eggs or larvae. Values are means + SE.

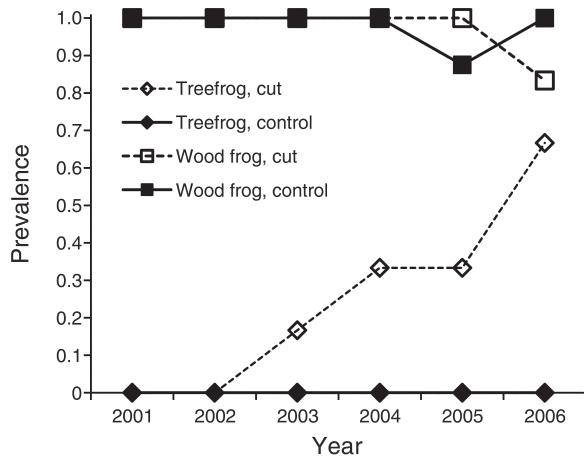


FIG. 4. Prevalence by year of two amphibian species (gray treefrogs and wood frogs) within 14 vernal ponds, 2001–2006. Ponds were divided into those that had trees felled along the southern shore creating a more open canopy above the pond basin (cut, $n = 6$ ponds) and those that were not manipulated (control, $n = 8$ ponds). Canopy manipulation took place during the winter of 2001–2002. Presence was defined by the detection of eggs or larvae.

of sampling. By contrast, they remained entirely absent within control ponds. The response of wood frogs, a canopy-tolerant species, showed no detectable influence of the manipulation: the species was present in all ponds at the start of the study and remained present within virtually all ponds in both treatments during each year of the study.

As a further examination of the response of canopy-tolerant species to canopy manipulation, we used egg mass responses as proxies for population densities of wood frogs and spotted salamanders (Werner et al. 2007a). Wood frogs (Fig. 5) had equivalent abundances within control and cut ponds prior to the manipulation of canopy (t test, $df = 8$, $t = 0.515$, $P = 0.621$). Following cutting, wood frog abundances were indistinguishable between cut and control ponds (t test, $df = 12$, $t = 0.287$, $P = 0.782$). A repeated-measures analysis showed a marginal influence of year (Wilks' lambda = 0.12, $F_{8,5} = 4.65$, $P = 0.054$), but there was no interaction between the effects of year and treatment (Wilks' lambda = 0.70, $F_{8,5} = 0.27$, $P = 0.952$). We found comparable responses for spotted salamanders: abundances were indistinguishable between treatments both before and after canopy manipulation.

DISCUSSION

Our manipulation of forest adjacent to vernal ponds was deliberately modest in scale. The footprint for tree felling (90° arc radiating 25 m from the shoreline) averaged just a bit over 1000 m², roughly the same area as the typical pond surface within our study. Nevertheless, this disturbance had a readily detectable, and overall positive, effect on vernal-pond-dwelling amphibians. Manipulated ponds were warmer (Fig. 1) and

supported more amphibian species compared with control ponds (Fig. 2). Canopy-intolerant species benefited from the manipulation (Figs. 3, 4) and we uncovered no evidence that canopy-tolerant species were harmed (Fig. 5).

Our experimental findings add weight to inferences that have been drawn from a number of observational studies of vernal pond forest canopies. Multiple investigators have shown in cross-sectional studies that open canopy ponds support greater amphibian species richness than closed canopy ponds (Halverson et al. 2003, Werner et al. 2007b). The size of the observed canopy effect from prior studies is comparable to the response estimated in this study. The responses are comparable in detail as well. Observational studies have noted the regularity of compositional differences across the canopy gradient (Skelly et al. 1999, 2005, Werner et al. 2007a). A relatively small number of species are known to tolerate deeply shaded conditions, while most other species seem able to thrive in unshaded ponds (Halverson et al. 2003). We used categorizations from a previous study (Skelly et al. 2005) to investigate distinctions in experimental responses by canopy-tolerant and canopy-intolerant species. We found that canopy generalists tended to be equal in their prevalence across the canopy treatments while intolerant species tended to be more prevalent in our manipulated ponds. As we expected, canopy manipulation generally tended to have a positive or neutral effect on species depending on their canopy tolerance.

While our findings are consistent with prior observational studies of pond canopy, they might be construed as being inconsistent with prior research on disturbance within terrestrial uplands surrounding vernal ponds.

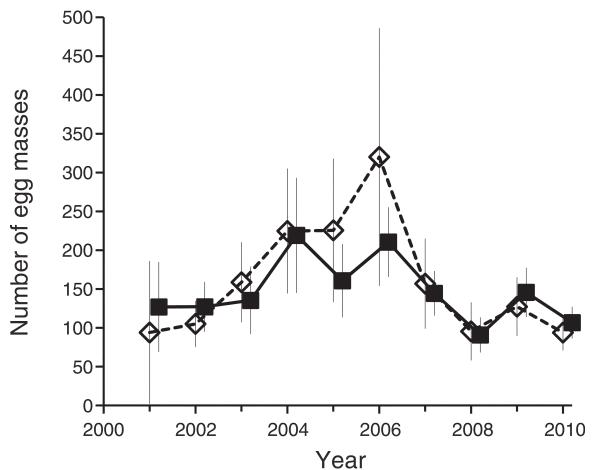


FIG. 5. Wood frog egg masses present in 14 vernal ponds, 2001–2010. Ponds were divided into those that had trees felled along the southern shore, creating an opening in the canopy above the pond basin (cut, $n = 6$ ponds, open circles and dashed line), and those that were not manipulated (not cut, $n = 8$ ponds, solid circles and solid line). Canopy manipulation took place during the winter of 2001–2002. Values are means \pm SE.

Across both observational and experimental studies, disturbance within terrestrial landscapes surrounding vernal ponds has been associated with loss of amphibians and other wetland-dependent species. The distinction is most likely attributed to the small scale of disturbance in this study. Most researchers have concluded that disturbance driven species losses stem from conversion of habitat near vernal ponds (Homan et al. 2004) as well as the creation of open environments, which are difficult for terrestrial amphibians to cross (de Maynadier and Hunter 1999). In our study, the dimensions of the disturbance were minimized. Studies of vernal pond amphibians have documented a typical movement distance of ~120 m from their natal pond (Semlitsch 1998, Semlitsch and Bodie 2003, Semlitsch and Skelly 2007). Within a radius of 120 m around our average study pond is an area of approximately 60 000 m². Our manipulation affected just 2% of this area.

We suggest that the loss of habitat caused by our experimental disturbance was negligible while the influence on site conditions within the vernal ponds was substantial. This interpretation is supported by studies of critical thresholds for pond occupancy, which have estimated, for example, that the local extinction of species such as spotted salamanders and wood frogs tend to occur after a majority of forest cover within a radius of 300 m is lost (Homan et al. 2004). These and other results on the influence of forest loss within vernal pond uplands strongly imply that a small-scale manipulation of cover may be unlikely to have a detectable negative effect particularly if it is concentrated along just a portion of the shoreline. And the effect of disturbance on upland habitat in this study may be much more modest than that inferred from some other studies in which forest has been converted to other land uses such as agriculture, residential, and commercial development (e.g., Homan et al. 2004). In our manipulation, trees and their canopies were left intact and in place. The resulting masses of downed trees and the vegetation that quickly emerged among them created a complex and well shaded environment that may not have posed much of an obstacle to dispersing amphibians.

Conclusions

The motivation for restricting disturbance near freshwater wetlands is well founded. Large-scale conversions are associated with loss of wetland dwelling species that also depend on forested upland environments (e.g., Gibbs 1998). However, the results of our experiment provide strong support for inferences gained from observations of canopy effects on wetlands across a diversity of regions: many wetland-dependent species are relatively intolerant of closed canopy conditions (Skelly et al. 1999, 2005). For these species, a surgical reduction of canopy may increase the conservation value of wetland habitats as has been shown in other contexts (Pike et al. 2011). Our findings suggest that, in addition to positive effects on canopy-intolerant species, there

may be few if any negative influences on canopy-tolerant species.

During the last two centuries, the number of small freshwater wetlands has plummeted particularly within developed landscapes (Gibbs 1999). Those that remain can be relatively isolated from each other limiting the capacity of species to move from one location to the next (Semlitsch and Skelly 2007). Under these conditions, there may be significant value in promoting site conditions within remaining vernal ponds that support the maximum diversity of species. While successful interventions to support wildlife are often labor intensive and costly, our findings suggest that even a modest manipulation can have substantial and durable positive influences on wetland-dependent species. Within the context of current policies and regulations, we suggest that it is worth considering how manipulations of vegetation near wetland basins may be useful in promoting the goals of stewardship and protection of these environments and their dependent species.

ACKNOWLEDGMENTS

We thank M. Ashton for supporting our work at the Yale Myers Forest and T. Bernier for an expert job felling trees. We also thank the many people who provided field assistance including N. Cothran, H. Dohna, N. Freidenfelds, A. Halverson, M. Holland, E. Lee, E. McEvoy, M. Urban, and annual egg mass survey crews. M. Atwood, M. Lambert, A. Middleton, M. Rogalski, and O. Schmitz provided helpful comments on an earlier version of the manuscript. This research was supported by grants from the NIH/NSF Ecology of Infectious Disease Program, from the National Science Foundation, and by a Fellowship from the John Simon Guggenheim Memorial Foundation.

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