

Canopy closure and amphibian diversity in forested wetlands

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Abstract

The crowns of trees and shrubs often overtop temporary wetlands in forested regions. By shading pond basins, canopy can dramatically change the conditions experienced by residents such as amphibians. In this study, we estimated the presence of 8 amphibian species across 17 temporary wetlands at the Yale–Myers Forest in northeastern Connecticut, USA. In addition, we quantified the light environment using a grid of hemispherical canopy photographs to calculate Global Site Factor (GSF) within each wetland. Amphibian richness was low in most wetlands, and most wetlands were relatively shaded. Amphibian richness increased in lighter wetlands. This result was not confounded by relationships with wetland size. Most amphibian species tended to be absent from heavily shaded wetlands ('open canopy specialists'). However, three species were often found in the shadiest wetlands ('canopy generalists'). Field transplant experiments using one canopy generalist and one open canopy specialist showed that development of the generalist was less affected by wetland light levels compared with performance of the specialist. These findings suggest that canopy may be an important determinant of amphibian diversity patterns across wetlands. Further, conservation strategies dependent on universally applied, inviolate shoreline vegetation buffers may inadvertently contribute to species loss. Because species differ in their sensitivity to changes in canopy, these losses may be predictable.

Introduction

Within forested biomes, all freshwater wetlands exist along a gradient defined by the degree to which vegetation shades the basin. Recent evidence suggests that amphibian species are affected by the degree of canopy cover (Skelly et al. 1999; Werner and Glennemeier 1999; Skelly and Freidenburg 2000; Skelly et al. 2002; Halverson et al. 2003; Skelly and Golon 2003). In general, these studies have shown that some species of amphibians

experience lower growth and survival rates, or are less likely to occur, within heavily shaded wetlands. While the mechanisms are not well understood, lower temperatures and the quality of available food resources have been implicated in laboratory and field studies (e.g., Skelly et al. 2002; Skelly and Golon 2003).

While existing studies suggest that shaded wetlands can be challenging environments, it is equally clear that some amphibian species maintain dense populations in such environments. The goals of

this study are to (1) examine the structure and diversity of entire amphibian assemblages as they relate to the degree of vegetation canopy, and (2) experimentally evaluate patterns of performance of two species that differ in their distribution across the canopy gradient. The motivation for this study is 2-fold. First, canopy may be an important driver of amphibian distribution and the composition of assemblages. While other factors such as competition and predation have received close attention by amphibian ecologists, it is less clear that these will provide reliable prediction of community structure in nature. Second, vegetation cover has changed dramatically in recent centuries with the spread and growth of human populations (e.g., Foster 1992; Francis and Foster 2001). In many areas of the world, deforestation is rapid and pervasive. Other areas, such as eastern North America, were previously deforested and have been undergoing reforestation. These new forests are different in structure and composition than those that preceded them and, equally importantly, they are subject to vastly different forces, many of them anthropogenic (Francis and Foster 2001). If the canopies over the ponds affect amphibians and other residents, those interested in managing and conserving amphibians and other residents will do well to understand the nature and degree of canopy-derived impacts.

This study includes both observational and experimental elements. Between 1996 and 1999, we recorded the presence of amphibians (embryos, larvae, and metamorphs) in 17 nonpermanent wetlands. In these same wetlands, we used hemispherical photos to estimate the light environment within the wetland basin. We relate the resulting amphibian distribution and light patterns to each other to evaluate whether the assemblages in nonpermanent wetlands are related to canopy development. These data reveal that very few species are common across the entire canopy gradient. We use field experiments to evaluate the association between performance and the breadth of distribution across the canopy gradient.

Methods

We sampled wetlands at the 3800-ha Yale–Myers Forest in northeastern Connecticut, USA. The 17 nonpermanent wetlands used in this study range

from heavily shaded to relatively open. Maximum surface areas ranged from 40 to 5200 m² and maximum depths were between 25 and 250 cm. All wetlands tend to dry by early to mid summer during years of near average rainfall.

We estimated the light environment at each wetland using hemispherical photographs of the forest canopy (Halverson et al. 2003). This technique yields an estimate of solar radiation flux at the point where the photograph was taken. Estimates of photon flux based on hemispherical photographs closely correspond to average direct sensor measurements (Chazdon and Field 1987; Becker et al. 1989).

We flagged sampling points in a Cartesian grid oriented to true North and spaced 5 m apart within the boundary defined by the spring maximum shoreline. Using a camera with a fisheye lens offering a 180-degree field of view, we took two photographs at each sampling point, the first during the summer of 1999 and the second during the winter of 1999–2000. For each photograph, the camera was aimed straight up using a self-leveling tripod and oriented so the ‘top’ of the photograph pointed to true north. One set of photographs was taken when there were no leaves on surrounding deciduous vegetation and a second set when deciduous leaves were fully developed. For all photographs, the camera was placed as close to the water surface as practicable to include shading due to understory plants as well as overstory trees.

The photographs were analyzed using Hemi-viewtm (Delta-T 2001), a computer program in which each pixel of a digital image is characterized as being either open sky or an obstruction based on a gray-scale threshold set by the user. The program estimates angular coordinates of the sun through the day and year, and during those times the sun is unobstructed, it calculates the amount of cosine-corrected direct beam radiation incident upon the site of interest. Diffuse radiation is calculated in a similar manner. Necessary parameters for this program were estimated from the National Solar Radiation Database (2001) for Hartford, CT (approximately 40 km from the study site) from 1960–1990.

Light estimates based on hemispherical photographs were characterized in terms of the global site factor (GSF): the ratio of the amount of light estimated to strike a particular point to the amount

of light estimated to strike a similarly located point with an absolutely open sky. We used two estimates based on these GSF values. Average GSF is the overall average across the photographs taken during the period when deciduous trees have their leaves. A second measure, enclosure GSF, is based on the single leaf-on photograph taken closest to the location of enclosures placed in the wetlands during 1999 and 2000.

We measured the presence-absence distribution of amphibian species in each of the 17 wetlands (listed in Halverson et al. 2003). From 1996 to 1999, wetlands were visited several times annually between March and July. During March and April, wetlands were visually inspected for egg masses of wood frogs (*Rana sylvatica* LeConte) and spotted salamanders (*Ambystoma maculatum* Shaw). During most years, wetlands were visited three times between early May and early June. During these visits, wetlands were visually inspected for larval amphibians and eggs, and time-constrained dipnet sampling (scaled to wetland size; Halverson et al. 2003) was conducted throughout the wetland. We detected 8 species including 5 frogs (American toad [*Bufo americanus* Holbrook], gray treefrog [*Hyla versicolor* LeConte], spring peeper [*Pseudacris crucifer* Wied-Neuwied], green frog [*R. clamitans* Rafinesque], and wood frog) and 3 salamanders (spotted salamander, marbled salamander [*A. opacum* Gravenhorst], and red-spotted newt [*Notophthalmus viridescens* Rafinesque]). We defined a species as present if eggs, larvae, or metamorphs were collected within the pond during more than one year between 1996 and 1999.

We conducted field enclosure experiments within 6 natural wetlands at the Yale-Myers Forest (Blacksmith, Boulder, Dentist, French House Beaver, Quarry, Woodpile) during consecutive years (1999, 2000). The experiments were conducted identically each year: wood frog and spring peeper larvae were reared in single species enclosures from shortly after hatching until metamorphosis in an array of wetlands that spanned the canopy gradient. During both years, we placed six $0.64 \times 0.64 \times 0.71$ m open-bottomed enclosures in each wetland. Enclosure locations were chosen to be equivalent in depth (ca. 25–50 cm depending on the wetland) and to be representative of the conditions within each wetland. Enclosures were constructed of wooden frames and were covered with black fiberglass window screening (1.5-mm mesh).

Enclosures were placed in a rectangular array, with no enclosure less than 15 cm from its nearest neighbor. Fiberglass screening skirts at the lower edge of the enclosures were sealed to the benthic substrate by placing rocks around the perimeter of the enclosure base. After placement, enclosures were cleared by repeatedly dipnetting the water column. Each enclosure was dipnetted for three 2-min intervals and all macroinvertebrates (e.g., beetle larvae) and vertebrates (tadpoles and salamander larvae) were removed. Following clearing, a lid of fiberglass screening was placed over the enclosure. In each pond, enclosures were paired with their neighbor to the east or west and treatment (spring peeper or wood frog) was allocated by a coin flip.

During both years, wood frogs were collected as recently laid eggs from multiple wetlands (2 wetlands in 1999 and 3 wetlands in 2000). Embryos were placed into, and larvae were reared in, wading pools and given access to a mix of senesced deciduous leaves and pelleted rabbit chow. During both years, spring peepers (which lay their eggs singly) were collected as eggs and recent hatchlings from 2 open-canopy wetlands. Prior to stocking, larvae were reared in wading pools and given access to a mix of senesced deciduous leaves and pelleted rabbit chow. For both species, larvae from the wetlands were mixed together and used haphazardly to stock enclosures. Six wood frog larvae (Gosner Stage 25; Gosner 1960) were stocked into 3 of the enclosures (stocking dates: 23 April 1999; 5 May 2000) and 6 spring peeper larvae (Gosner Stage 25) were stocked into each of the remaining 3 enclosures (Stocking Dates: 10 May 1999; 17 May 2000). Earlier stocking of wood frogs during each year reflects their earlier breeding phenology. Larvae in enclosures were allowed to reach metamorphosis (Gosner Stage 42 or greater) unless pond drying intervened. Metamorphs were collected from each enclosure every 2–3 days during the metamorphic period. During 1999, a relatively dry year, three of the wetlands dried in mid to late June, prior to the onset of metamorphosis (Blacksmith, Boulder and Quarry Ponds). During 2000, a cooler, wetter year, two of the wetlands (Boulder, Quarry) dried in mid July after amphibians had already begun metamorphosing, but before all individuals had completed metamorphosis. In all wetlands that dried, remaining larvae were recovered from the bottoms of the enclosures on the first

day when water no longer covered the entire bottom of at least one of the 6 enclosures.

Analyses of 1999 and 2000 field experiments were conducted separately. For each species in each wetland, we calculated average developmental rate (Gosner Stages per day between stocking and collection). We scaled our developmental responses as the proportion of the rate observed in the fastest developing wetland. This transformation allowed us to evaluate the degree to which development rates were depressed in each species across the range of wetlands in the experiment. To determine whether this measure of development rate changed with light environment in the experiment, we performed linear regressions (one for each of the species) in which the independent variable was the GSF measured from the single photo closest to the array of enclosures in that wetland. One of the six wetlands included in the experiments (French House Beaver) was not among the 17 wetlands in which GSF was measured using photographs. In order to estimate the GSF for the enclosure location at this wetland, we measured % canopy cover using a spherical densiometer and then estimated leaf-on GSF using a linear regression ($R^2 = 0.94$) we had calculated previously between GSF- and densiometer-derived percent canopy.

Results

None of the 17 wetlands contained all amphibian species discovered during the survey. One wetland (Dentist) contained 7 of the 8 species, however, most wetlands held 3 or fewer species. Linear regression revealed that amphibian richness was related to GSF (Figure 1; $n = 17$, $R^2 = 0.39$, $p = 0.007$). By contrast, pond surface area was not related to GSF, nor was it a significant predictor of amphibian richness (linear regression, $p > 0.10$ in each case).

In the field enclosure experiments, the highest rate of development for each species was achieved in the wetland with the most light (Dentist Pond) during both years (Figure 2). For each species, development rates increased with GSF measured at the location of the enclosures (spring peeper linear regression: 1999, $n = 6$, $R^2 = 0.72$, $p = 0.033$; 2000, $n = 6$, $R^2 = 0.85$, $p = 0.008$; wood frog linear regression: 1999, $n = 6$,

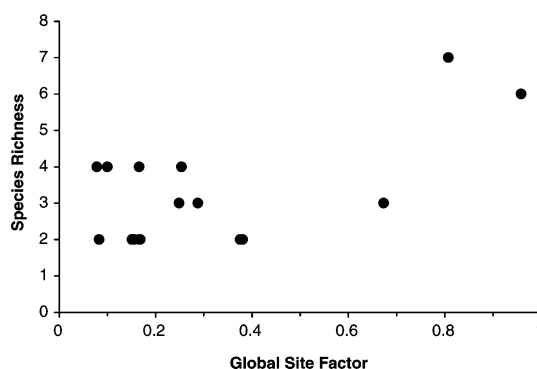


Figure 1. Species present in each of 17 nonpermanent wetlands at Yale–Myers Forest, Connecticut, USA between 1996 and 1999. Mean GSF (Global Site Factor) is an estimate of light environment in each wetland calculated during the summer months when deciduous leaves are present. GSF ranges from 0 in total darkness to 1 if light from the sun is entirely unobstructed.

$R^2 = 0.72$, $p = 0.032$; 2000, $n = 6$, $R^2 = 0.93$, $p = 0.002$). A paired comparison showed that spring peeper development was more strongly depressed than wood frog development across the wetland array (paired t -test: 1999, $df = 5$, $p = 0.005$; 2000, $df = 5$, $p = 0.045$). In the darkest wetlands, spring peeper development rate dropped by as much as 44%, while wood frog development rate dropped by ca. one-third or less.

Discussion

The results of this study suggest that nonpermanent wetlands in forested biomes can often be low in amphibian diversity and that amphibian diversity may be constrained by local canopy development. Southern New England is typical of forested regions in North America and other continents: woody vegetation frequently grows in proximity to the shoreline and even within the basin of depressional wetlands. The resulting canopy can deeply shade these freshwater environments. The most shaded wetlands in this study have light environments comparable to terrestrial understory in well-developed forests (e.g., Chazdon and Field 1987; Canham 1988).

We found that a subset of the local species pool is reliably present within heavily shaded wetlands (Table 1). For example, both wood frogs and spotted salamanders were present in all, or nearly all wetlands. These species appear to persist

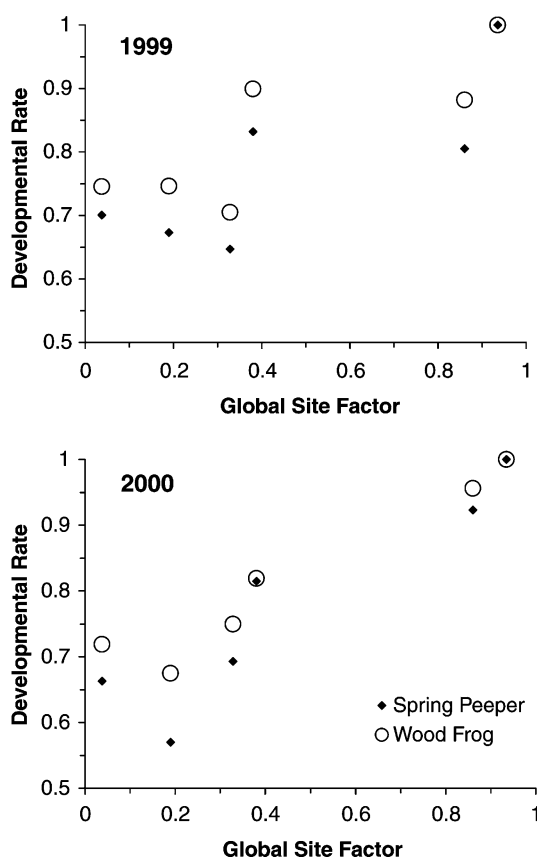


Figure 2. Developmental rate of spring peepers (filled diamonds) and wood frogs (open circles) raised in a field enclosure experiment in six natural wetlands at the Yale–Myers Forest. For each species, developmental rate is scaled according to the fastest rate seen in that species in the experiment (Dentist Pond in both cases). For the remaining wetlands, developmental rate represents the proportion of the rate seen in Dentist Pond. GSF is a measurement of the light environment taken while deciduous leaves are present and based on the hemispherical photograph taken in each wetland that is closest to the location where enclosures were placed during the experiment.

regardless of canopy conditions. A third species, the marbled salamander, was present in relatively few wetlands, but all of those were shaded. The remaining species are to varying degrees, specialists that are found primarily within less shaded environments (note mean GSF experienced in the last column of Table 1). It is this among species heterogeneity in associations across the canopy gradient that generates the relationship seen in Figure 1.

While the intention of this study was to evaluate the role of canopy, it is possible that canopy is associated with other measures already known to

impact diversity of amphibians and other species. If this is true, interpretations of natural history patterns described here may be erroneous. As an example, larger wetlands may have more species simply through a species–area relationship (e.g., due to passive sampling, or because of higher habitat diversity). At the same time, larger wetlands might be expected to have higher light environments because tree canopies rooted along the shoreline cannot interdigitate above very large basins. However, area was a poor (and nonsignificant) predictor of both GSF and amphibian richness. In part, the explanation for this lack of relationship is clear. While very large wetlands may be less likely to have dense tree canopies above them, some small wetlands in our study area also have little vegetation above their basins. At the Yale–Myers Forest, the absence of forest canopy above small wetlands has two primary causes: timber extraction and the activities of beaver (*Castor canadensis* Kuhl).

Linking patterns of distribution and community structure to the attributes of individual species is a major goal of ecology and a critical challenge for conservationists and managers. For amphibians living in nonpermanent wetlands, canopy may be related to distribution and community richness because it impacts the performance of larvae. Variable degrees of specialization across the canopy gradient may reflect differential degrees to which species are able to maintain high performance under challenging conditions. In a prior observational study of spring peepers and wood frogs, we found that development rates of both species were positively related to light level across the same set of wetlands used in this study (Halverson et al. 2003). The results of the experiments reported here show that potential confounding factors in the observational study (e.g., differences in breeding phenology among wetlands, localized adaptation) do not compromise the central result. In experimental enclosures in six different wetlands conducted during two years using controlled, identically timed stocking, a critical life-history trait in amphibians, larval development rate, is strongly related to the degree of canopy cover in nonpermanent wetlands.

Our field experiments also enable us to conclude that spring peepers and wood frogs are differentially affected by canopy across the gradient. During two consecutive years, relative rates across

Table 1. Salamander and frog species found in 17 nonpermanent wetlands at Yale–Myers Forest between 1996 and 1999.

Species	Common name	Presence	Global Site Factor	
			Minimum	Mean
<i>Bufo americanus</i>	American toad	1	0.807	0.807
<i>Rana clamitans</i>	Green frog	3	0.167	0.644
<i>Pseudacris crucifer</i>	Spring peeper	5	0.287	0.621
<i>Notophthalmus viridescens</i>	Red-spotted newt	4	0.167	0.545
<i>Hyla versicolor</i>	Gray treefrog	5	0.079	0.439
<i>Ambystoma maculatum</i>	Spotted salamander	17	0.079	0.312
<i>R. sylvatica</i>	Wood frog	16	0.079	0.307
<i>A. opacum</i>	Marbled salamander	4	0.079	0.170

Presence indicates the number of wetlands where the species was found. Global Site Factor (GSF) indicates the minimum GSF where a species was present. Mean GSF is tallied across all of the wetlands where a species was present. Species are rank-listed in descending order by the average GSF of the wetlands where they were present.

wetlands showed that development of spring peepers responded more strongly to the canopy gradient compared with wood frogs. The decreased ability of spring peepers to maintain rapid development rates in shaded wetlands may contribute to their limited distributions in non-permanent wetlands. As indicated by the results of these field experiments, pond drying frequently occurs before or during the metamorphic periods of amphibians (also reviewed by Wellborn et al. 1996; Skelly 2001). The ability of wood frogs to maintain their development rate in shaded wetlands, coupled with their earlier breeding time, may be critical to their broad distribution across the canopy gradient. Being able to use a wide range of wetlands reduces inter-wetland distance for dispersing animals, may increase the likelihood of rescue effects, and can reduce the likelihood of regional extinction (Gibbs 1993; Carlson and Edenhamn 2000). Conversely, specialist species like spring peepers may depend on dynamic environments that generate a diversity of habitat types, some fraction of which are suitable for them.

In fact, the implications for light-dependent distributional patterns on amphibian dynamics are potentially of broad significance. First, it appears that the distribution of several amphibian species including spring peepers may depend on disturbance. In the absence of vegetation removing disturbances, canopies can overtop wetlands in a matter of decades or less (e.g., Battaglia et al. 2002). At the scale of an individual wetland, wind, fire, beaver, tree disease, and in their absence, human intervention may be required for the long-term persistence of some amphibians. Relatedly, a

number of the species that utilize open canopy environments as embryos and larvae often live in well-developed forests as adults (e.g., *N. viridescens*, *P. crucifer*). Because the movement range of most amphibians is relatively restricted, these habitat use patterns suggest that some species may have evolved to exploit shifting habitat mosaics (e.g., Gill 1978).

Conservation implications

In the United States and elsewhere, regulatory frameworks often feature terrestrial buffers surrounding the basins of freshwater wetlands (e.g., Calhoun et al. 2003). These buffers typically include zones nearest the shoreline in which vegetation, including woody vegetation, is promoted and protected. While the motivation for buffers often includes maintenance of water quality, increasingly, buffers are being nominated as a conservation tool for wetland dependent species (e.g., Semlitsch and Bodie 2003).

The case for buffers as wetland conservation tools is well supported (Dodd and Cade 1998; Semlitsch 1998, 2000, 2002; Semlitsch and Bodie 2003). Without appropriate terrestrial habitats, animals such as amphibians that depend on both aquatic and terrestrial realms cannot persist (Waldick et al. 1999). In addition, shoreline vegetation may have important effects on the movement of emigrating metamorphs (deMaynadier and Hunter 1999; Rothermel and Semlitsch 2002). Recent work suggests the width of biologically effective buffers may be greater than has been thought previously,

and certainly well beyond most current regulated buffers (Semlitsch and Bodie 2003). However, while the need for buffers is well established, the temporal dynamics of buffer vegetation have not been closely considered by biologists, regulators, and managers, but see Palik et al. (2001). Recent suggestions to regulators and managers reinforce the concept that vegetation closest to wetlands should receive the highest level of protection (Semlitsch and Bodie 2003). As suggested by others, it seems clear that a long-term perspective is needed in developing practices that will promote and maintain wetland-dependent species (Semlitsch 2002). The results of this study imply that inviolate shoreline buffers, universally applied, may not efficiently conserve amphibian species dependent on nonpermanent wetlands. Coupled with active programs of beaver removal and fire suppression, wetland conservation efforts could even allow inadvertent local losses of amphibian populations as forests grow and increasingly shade wetlands. Carefully planned, selective removal of shoreline trees may be an effective means to maintain or increase local amphibian diversity. This hypothesis is being evaluated in a replicated, whole wetland manipulation experiment at the Yale–Myers Forest.

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