

Leaf litter input mediates tadpole performance across forest canopy treatments

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Abstract Understanding the mechanisms limiting the distributions of organisms is necessary for predicting changes in community composition along habitat gradients. In many areas of the USA, land originally cleared for agriculture has been undergoing a process of reforestation, creating a gradient of canopy cover. For small temporary wetlands, this gradient can alter abiotic conditions and influence the resource base of wetland food webs by affecting litter inputs. As distributions of amphibians and many other temporary wetland taxa correlate with canopy cover, we experimentally manipulated shade levels and litter types in pond mesocosms to explore mechanisms limiting species performance in wetlands with canopy cover. Most differences between ponds were mediated by litter type rather than direct effects of shading. Although all three amphibian species tested are open-canopy specialists, spring peepers were the only species to show decreased survival in shaded ponds. Pond litter type generally had strong effects on growth and development rates, with tadpoles of two species in grass litter ponds growing to twice the size of, and metamorphosing 7 days earlier than, those in leaf litter ponds. Contrary to our initial hypothesis, shade level and litter type showed very few significant interactions. Our results indicate that the effects of shading cannot be considered in isolation of vegetation changes in pond basins when evaluating the effects of forest succession on temporary pond communities.

Keywords Amphibian · Anuran · Mesocosm · Metamorphosis · Shade

Introduction

During the past century, forest ecosystems in many areas of the USA have increased in area. In fact, the conterminous 48 states have been in a state of net reforestation since 2002 (Kauppi et al. 2006), with modest increases in forestland area in the north, the Rocky Mountain region, and the Pacific coast in the past decade (Alvarez 2007). This pattern is especially evident in the northeast, where abandoned agricultural lands have been undergoing reforestation since the late nineteenth century (Foster 1992; Gerhardt and Foster 2002). Although deforestation remains a serious threat to species conservation worldwide, reforestation and forest succession also generate selective pressure and alter species assemblages.

Changes in forest cover can dramatically impact the structure of both terrestrial and aquatic communities. In forested wetlands, the distributions of several invertebrates [odonates (Corbet 1999); dytiscids, haliplids and hydrophilids (Batzer et al. 2004); physid snails (Palik et al. 2001)] and amphibians (Skelly et al. 1999; Werner and Glennemeier 1999) are correlated with canopy cover. Thus, species assemblages change along a canopy cover gradient and both competitive and predator–prey interactions are altered. Identifying the mechanisms driving species performance in wetlands across a canopy cover gradient is necessary for understanding changes in community structure in the multitude of small wetlands affected by reforestation and forest succession.

Differences in species distributions may be driven by a number of abiotic and biotic changes associated with

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canopy closure over wetlands. Shaded wetlands often show lower temperatures and dissolved oxygen (DO) concentrations than open-canopy wetlands, as well as reduced primary productivity and altered periphyton composition and abundance (Werner and Glennemeier 1999; Skelly et al. 2002; Schiesari 2006). Canopy cover also influences litter input to pond basins, which may generate dramatically different resource bases for aquatic food webs. Closed-canopy wetlands receive primarily allochthonous inputs in the form of senesced leaf litter. In open-canopy wetlands, increased light levels allow the growth of more herbaceous vegetation, including submerged and emergent macrophytes, grasses, and sedges (Colburn 2004), which then dominate benthic substrates (Skelly et al. 2002; Schiesari 2006). Although canopy cover is recognized as an important influence on wetland conditions, litter inputs can also generate dramatic bottom-up effects on aquatic food webs (Rubbo and Kiesecker 2004). Because canopy cover and litter input do not correlate perfectly and some species may exploit habitats created by infrequent combinations, the interaction of canopy cover and litter input may generate unexpected shifts in community composition.

Pond-breeding amphibians are a useful model for investigating canopy-associated changes in community structure in forested wetlands. Amphibian species are distributed unevenly across canopy cover gradients, and the distribution and performance of some larval amphibians are limited in closed-canopy wetlands (Skelly et al. 1999, 2002; Werner and Glennemeier 1999; Relyea 2002; Halverson et al. 2003; Burne and Griffin 2005; Schiesari 2006). In addition, amphibians play important roles in both aquatic and terrestrial food webs (Burton and Likens 1975; Beard et al. 2002), and act as energy vectors between aquatic and terrestrial systems (Gibbons et al. 2006). Therefore, we designed a fully factorial mesocosm experiment exposing larval amphibians to independent manipulations of both canopy cover and litter input. We hypothesized that canopy cover and litter type would show strong, species-specific interactions for three larval anurans.

Materials and methods

We tested the effects of canopy cover and litter type manipulations on amphibian larvae with two experiments using outdoor pond mesocosms—a valuable technique for addressing questions unanswered by laboratory and field studies (Rowe and Dunson 1994; Resetarits and Fauth 1998; Boone and James 2005; Chalcraft et al. 2005). Although mesocosms cannot reproduce the complexity of natural systems (Carpenter 1996; Skelly and Kiesecker 2001), they can generate predictions which hold true when tested under large-scale, more natural conditions (Resetarits

and Fauth 1998; Boone et al. 2004). The use of mesocosms can also allow an increased number of treatment combinations and replicates, relative to many field studies. The first experiment was a fully factorial design testing the effects of three canopy cover levels and two litter types on two amphibian species—spring peepers (*Pseudacris crucifer*) and southern leopard frogs (*Rana sphenoccephala*). The second experiment used the same design but began at a later date with gray treefrogs (*Hyla versicolor*). Both experiments took place in 2003 at a fenced research facility at the University of Missouri in Columbia, Missouri, USA. In both experiments, we created an experimental array of polyethylene ponds (1.52 m diameter) and randomly assigned each pond to one of three shade levels and one of two litter types with three replicates per treatment ($n = 18$ per species). We filled each pond with approximately 800 l of tap water, allowed the water to stand 3 days for chlorine to dissipate, and added the assigned litter treatment (1 kg/pond).

While no experimental treatment can accurately recreate the continuum of litter types present in natural wetlands, we chose to test two types (hereafter, “leaves” and “grass”) which represent important energy inputs to wetlands at opposite ends of the canopy cover gradient. Litter for “leaf” treatments was collected from forest with an overstory of oak (*Quercus* sp.) and hickory (*Carya* sp.) similar to the overstory of many closed-canopy ponds in the central hardwood region of the USA. Although open-canopy ponds show a number of vegetative differences relative to closed-canopy ponds (e.g., increased aquatic macrophyte growth), one of the more consistent patterns is an increase in growth of sedges and grasses (Batzer et al. 2000; Skelly et al. 2002). “Grass” litter was raked and cut from around a partially dried open-canopy pond and consisted of mixed cool-season grass (Poaceae) and sedge (Cyperaceae) stems and leaves. Both leaf and grass litter treatments utilized dead material from the previous growing season, as is present in the basin of temporary wetlands that fill in the spring (R. D. S., personal observation). Litter was collected from the Thomas S. Baskett Wildlife Research and Education Area (Boone County, Mo.) and air-dried in the sun for approximately 2 weeks prior to use.

On 4, 7, and 15 April (experiment 1) and 22, 23, and 26 July (experiment 2), we inoculated each experimental pond with mixed phyto- and zooplankton collected from multiple natural ponds in the Baskett Research Area. Although zooplankton do not serve as a food source for the anuran species in our study, we were interested in simulating complex communities found in natural ponds.

High-, intermediate-, and low-shade treatments were created by fashioning lids for the ponds from three levels of high-density polyethylene PAK knit shade cloth (77, 52, and 27% shade, respectively; Hummert International,

St. Louis, Mo.). The low-shade lids provided a minimal level of shade, comparable to fiberglass screen lids used in other pond mesocosm experiments to exclude invertebrate predators. The high-shade level was comparable to light conditions in closed-canopy wetlands (Skelly et al. 2002) and was above the shade threshold at which spring peepers tend to disappear from small wetlands (Halverson et al. 2003). Lids were placed on ponds on 10 April (experiment 1) and 21 July (experiment 2).

The three anuran species tested in these experiments are native to central Missouri. Both spring peepers and southern leopard frogs are early spring breeders. Because shade-mediated differences among wetlands could be more dramatic after leaf-out in summer months, we also tested gray treefrogs, a summer-breeding species. Although comparative data from the Midwest are limited (but see Hocking and Semlitsch, *in press*), surveys from the northeastern US indicate that all three of these species or close relatives tend to be absent from closed-canopy ponds (Skelly et al. 1999; Werner and Glennemeier 1999; Halverson et al. 2003).

Amplectant pairs (spring peepers and gray treefrogs) or egg masses (leopard frogs) were collected from ponds in the Baskett Research Area. Clutches were maintained in individual aquaria in the laboratory at 24°C. At the free-swimming stage (stage 25; Gosner 1960), a minimum of three clutches per species was thoroughly mixed in order to homogenize genetic influences. On 21 April (experiment 1) and 23 July (experiment 2) we added 40 tadpoles of a single species to each pond. This density is well within the range of larval anuran densities in natural wetlands (Morin 1983). Although spring peepers and southern leopard frogs may coexist in natural ponds, we chose to test each species separately in experiment 1 to minimize interspecific competition and potential confounding of densities, which may occur if the two species have asymmetric impacts on the aquatic habitat.

We monitored ponds at least every other day. On 5 May, 19 May, and 3 June (experiment 1) and 6 August and 20 August (experiment 2), we recorded temperature, pH, and DO for each pond, with a 12-h daylight profile of temperature and DO on 29 May. In addition, we sampled periphyton and phytoplankton resources available for tadpole grazing. For periphyton samples, we took three scrapings (38 mm × 30 mm) with a razor blade at a consistent depth from three areas of each pond. Scrapings were placed on glass fiber filters (47 mm) and stored in 20-ml scintillation vials filled with 15 ml of acetone with magnesium buffer. These samples were covered with foil and refrigerated for less than 24 h until analysis with a fluorometer (10-AU; Turner Designs, Sunnyvale, Calif.). Total chlorophyll-*a* levels were determined with fluorescence readings before and after acidification with 0.1 N hydrochloric acid. For

phytoplankton samples, three 1-l water samples were taken from different areas of each pond and mixed. Composite samples (100 ml each) were stored on ice in glass bottles. The same day, samples were vacuum filtered through glass fiber filters, which were placed in 15 ml acetone with magnesium buffer in scintillation vials. Sample preparation and fluorometric analyses were completed as described above.

As tadpoles neared metamorphosis, we monitored the ponds daily and removed animals when at least one front leg erupted (stage 42; Gosner 1960). The metamorphs were then held in the laboratory through tail resorption (2–4 days), at which time the date and their mass was recorded. All “days to metamorphosis” calculations were made using the date of complete tail resorption, rather than capture date, because some metamorphs were captured at different stages in the tail resorption process. Metamorphs were collected from 26 May to 12 July (experiment 1) and 11 August to 4 September (experiment 2) and experiments ended on 17 July and 4 September, respectively. When ponds were drained, we searched the substrate and recorded the number and Gosner stage of any remaining tadpoles. Less than 1% ($n = 18$) of the initial number of tadpoles added had not metamorphosed at this time.

For each experimental pond, we first calculated percent survival as the number of metamorphs and remaining tadpoles divided by the number of tadpoles initially added. We used percent survival as a covariate for analyses of days to and mass at metamorphosis because these traits are highly sensitive to density changes (Wilbur 1997). Any significant changes in survival can otherwise confound analyses of treatment effects on days to and mass at metamorphosis. We calculated percent metamorphosis as the number of metamorphs divided by the number of tadpoles initially added. We analyzed the effect of canopy and litter treatments on percent metamorphosis, days to metamorphosis, and mass at metamorphosis using univariate two-way ANOVA, with comparisons of means or least square means (with covariates) between treatment groups. Results for each species were analyzed separately. One pond in experiment 2 (medium shade, grass litter) showed complete mortality for an unknown reason and was excluded from all analyses. The influence of shade and litter treatments on biotic (phytoplankton and periphyton levels) and abiotic (temperature, pH, DO) pond characteristics was determined using a two-factor repeated measures ANOVA for each variable. Percent metamorphosis values were arcsine square-root transformed and phytoplankton and periphyton values were log-transformed prior to analysis to meet assumptions of normality and homoscedasticity. Percent survival values were not transformed prior to use as covariates. All analyses were completed in SAS (SAS Institute, version 8) with $\alpha = 0.05$.

Results

Tadpole response

Percentage of tadpoles surviving through metamorphosis differed by species. Overall, survival of southern leopard frogs ($93.89 \pm 1.99\%$) was higher than that of spring peepers ($73.19 \pm 5.76\%$) and gray treefrogs ($67.06 \pm 7.70\%$). Shade treatment significantly affected survival for spring peepers ($F_{2,12} = 4.73$, $P = 0.0306$), but not for leopard frogs ($P = 0.2107$) or gray treefrogs ($P = 0.6912$) (Fig. 1a). Spring peeper survival decreased by 30% in high-shade ponds, when compared to low and medium treatments. Spring peeper survival was not affected by litter type ($P = 0.7477$). Leopard frogs had higher survival in grass ponds than leaf ponds ($F_{1,12} = 6.72$, $P = 0.0236$). Gray treefrog survival was also significantly affected by litter type ($F_{1,11} = 7.51$, $P = 0.0192$), but in the opposite direction from leopard frogs (Fig. 1b). Survival of gray treefrogs was nearly twice as high in leaf litter ponds ($84.16 \pm 9.94\%$) as grass ponds ($47.92 \pm 10.74\%$).

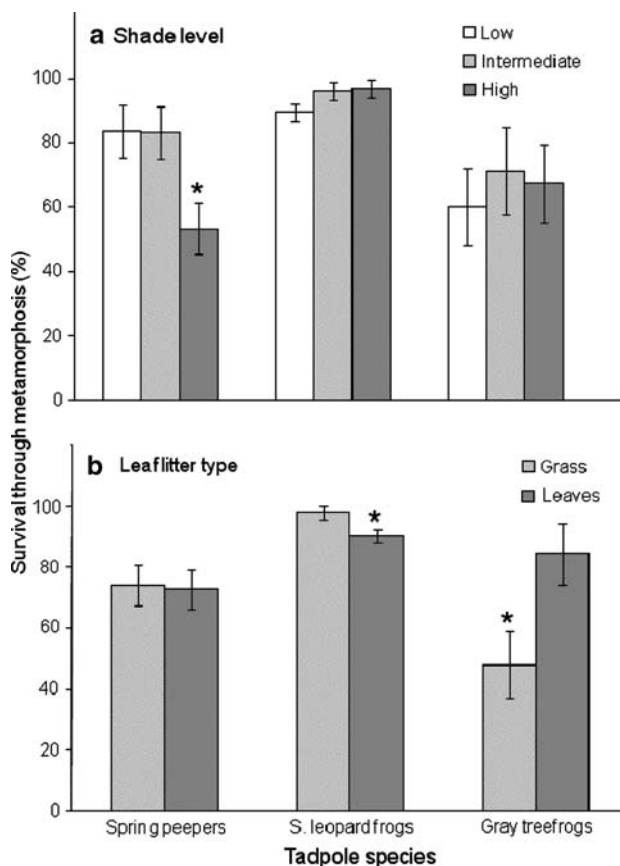


Fig. 1 Percent survival through metamorphosis of spring peeper (*Pseudacris crucifer*), southern leopard frog (*Rana sphenocephala*) and gray treefrog (*Hyla versicolor*) tadpoles in **a** shade treatments (low, intermediate, high) and **b** leaf litter treatments (grass or leaves), means \pm 1 SE. Asterisks indicate treatments that are significantly different from other treatments within species

Shade treatment did not significantly affect time to metamorphosis for any of the three species tested (spring peepers $P = 0.1303$; leopard frogs $P = 0.1611$; gray treefrogs $P = 0.8163$) (Fig. 2a). Litter treatment, however, showed strong effects for two of the three species (Fig. 2b). For both spring peepers and leopard frogs, tadpoles in grass ponds metamorphosed an average of 7 days faster than their counterparts in leaf ponds (spring peepers $F_{1,11} = 33.47$, $P = 0.0001$; leopard frogs $F_{1,11} = 136.81$, $P < 0.0001$). Gray treefrog time to metamorphosis was not related to litter type ($P = 0.1687$). However, the shade by litter interaction was significant for gray treefrogs ($F_{2,10} = 5.26$, $P = 0.0275$) (Fig. 3). Under low-shade conditions, treefrogs metamorphosed more quickly in grass litter ponds. As shade level increased, days to metamorphosis values converged between the two litter treatments. Contrary to our initial hypothesis, no other shade by litter interactions were statistically significant for any of the tadpole response variables tested.

Litter treatment had a highly significant effect on mass at metamorphosis for all three species (spring peepers

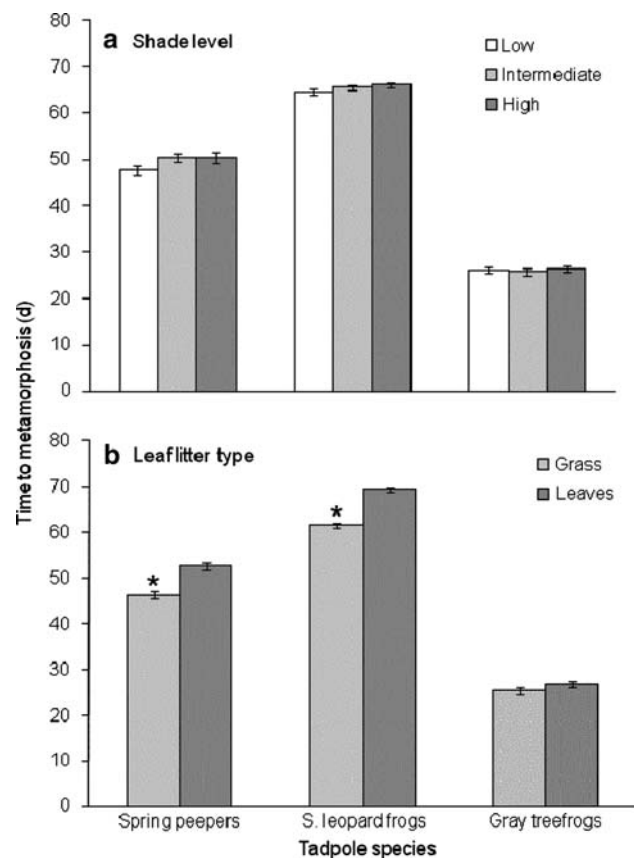


Fig. 2 Time to metamorphosis of spring peeper, southern leopard frog and gray treefrog tadpoles for **a** shade treatments (low, intermediate, high) and **b** leaf litter treatments (grass or leaves), means \pm 1 SE. Asterisks indicate treatments that are significantly different from other treatments within species. *d* Days

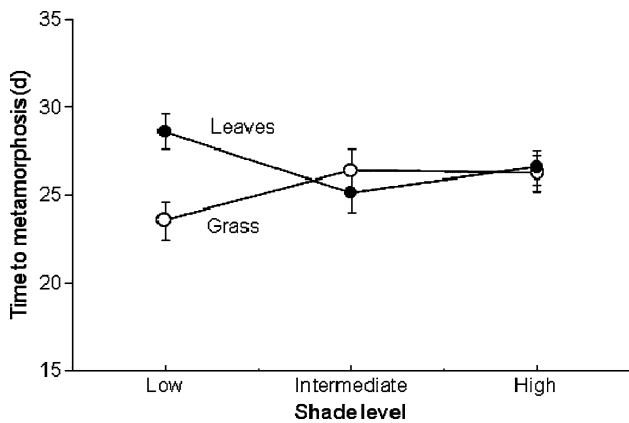


Fig. 3 Interaction of shade and litter treatment for time to metamorphosis of gray treefrogs ($F_{2,10} = 5.31, P = 0.0268$), means \pm 1 SE

$F_{1,11} = 37.56, P < 0.0001$; leopard frogs $F_{1,11} = 425.42, P < 0.0001$; gray treefrogs $F_{1,10} = 71.46, P < 0.0001$). For each species, metamorphs from leaf litter ponds were smaller than those from grass ponds (Fig. 4b). This effect was most pronounced for southern leopard frogs, with a mean mass of 2.52 g in grass ponds, versus 1.20 g in leaf ponds. Southern leopard frogs were the only species to show mass differences among shade treatments ($F_{2,11} = 8.94, P = 0.0049$), with larger metamorphs emerging from medium-shade ponds (Fig. 4a).

Environmental variables and primary productivity

Shade treatment had a highly significant effect on pond temperature in both experiment 1 ($F_{2,31} = 76.80, P < 0.0001$) and experiment 2 ($F_{2,13} = 66.23, P < 0.0001$). Slightly lower temperatures were associated with shaded ponds at each time period (overall mean difference = 1.3°C). In a 12-h daylight profile, temperatures were the same among shade treatments at the first sampling period (0730 hours), but diverged by mid-morning (1030 hours). Differences between high- and low-shade ponds were up to 2.1°C in the morning and 3.4°C in the afternoon. Shade treatment also affected pH for both experiment 1 ($F_{2,31} = 3.50, P = 0.0425$) and experiment 2 ($F_{2,13} = 14.12, P = 0.0006$). Increasing shade was associated with lower pH values, but the range of pH means among shade treatments was relatively small (7.3–8.4).

DO levels showed strong differences between shade treatments ($P < 0.0001$ in both experiments). Mean DO levels showed an inverse relationship with shade. Over both experiments, DO was lower at each sampling period in high-shade ponds (1.63–3.43 p.p.m.) than intermediate- (2.98–4.72 p.p.m.) and low-shade ponds (4.80–6.99 p.p.m.). Low-shade ponds showed greater midday DO increases than high-shade ponds, indicating higher levels of primary productivity associated with increased light.

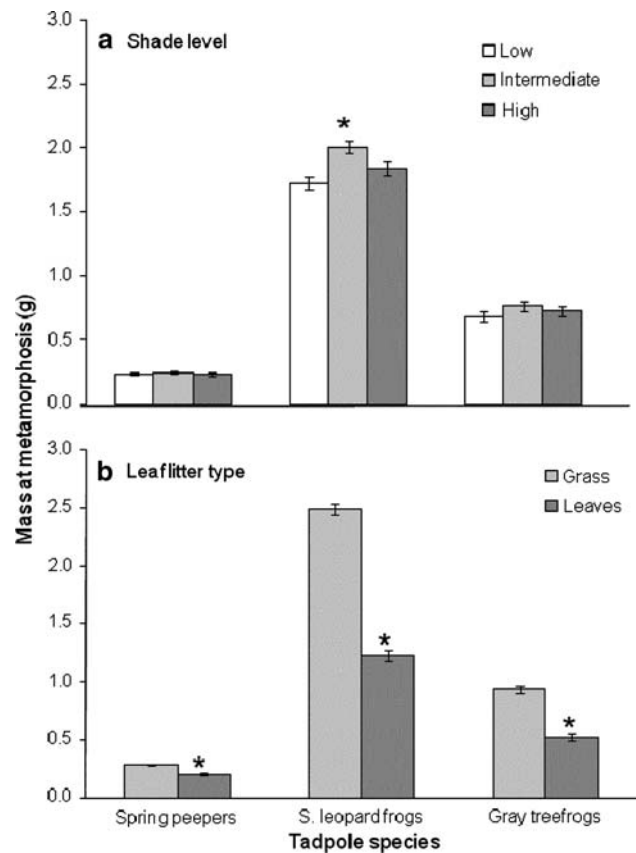


Fig. 4 Mass at metamorphosis of spring peeper, southern leopard frog, and gray treefrog tadpoles for **a** shade treatments (low, intermediate, high) and **b** leaf litter treatments (grass or leaves), means \pm 1 SE. Asterisks indicate bars that are significantly different from other treatments within species

Phytoplankton levels responded strongly to both shade ($F_{2,31} = 10.28, P = 0.0004$) and litter treatment ($F_{1,31} = 36.51, P < 0.0001$) in experiment 1. At every sampling period, low-shade ponds had the highest levels of phytoplankton (low shade = 3.09–6.52 $\mu\text{g/l}$, high shade = 1.03–5.45 $\mu\text{g/l}$). In addition, ponds with grass litter always contained more phytoplankton than those with leaf litter. In experiment 2, shade treatment no longer had a significant effect on phytoplankton levels, but the effect of litter remained highly significant ($F_{1,13} = 83.05, P < 0.0001$). Grass litter ponds were variable, but supported levels of phytoplankton that were up to 10 times greater than leaf ponds.

Results for periphyton levels differed between experiments. In experiment 1, shade treatment showed a strong effect on periphyton growth ($F_{2,31} = 8.92, P = 0.0009$). Periphyton levels were consistently lowest in low-shade ponds and highest in the most shaded ponds, although variability was high in all treatments. In experiment 2, litter treatment was the dominant influence on periphyton levels ($F_{1,13} = 15.30, P = 0.0018$), with higher levels of periphyton associated with grass litter ponds. No significant shade

by substrate interactions were detected for any of the environmental variables.

Discussion

Our results demonstrate that shade and associated changes in litter input to wetlands can dramatically affect abiotic conditions, primary productivity, and larval amphibian performance. Most of the differences seen between experimental ponds were mediated by litter differences, as opposed to direct effects of shading (e.g., temperature changes)—a pattern revealed by independent manipulations of shade level and litter type. Because canopy cover acts as a selective sieve (Skelly et al. 2002) for species inhabiting wetlands, it is important to understand the mechanisms driving canopy-related changes in community structure. Our results highlight the importance of pond basin vegetation changes in explaining shifts in amphibian communities along canopy cover gradients.

The lack of shading effects was surprising, given that increasing canopy cover led to lower water temperatures in our ponds. Although cooler temperatures are known to slow amphibian development rates and lead to delayed metamorphosis (Moore 1939; Smith-Gill and Berven 1979; Harkey and Semlitsch 1988), temperature differences in our study were not associated with differences in time to metamorphosis. This lack of effect may have resulted because: (1) differences in temperature in our outdoor mesocosm experiment were less pronounced than those that would be found in natural wetlands, or (2) temperature differences were swamped by stronger effects of resource availability mediated by pond litter type. The maximum mean temperature difference between open- and closed-canopy treatments in our study (2.4°C) was more modest than mean differences reported for natural wetlands by Skelly et al. (2002; 5°C), but was similar to differences found by Schiesari (2006; 2.5°C) and Werner and Glennemeier (1999; 1.7°C). Thus, temperature differences in our study were within a reasonable range for natural wetlands. We suggest that under natural conditions, resource availability influences time to metamorphosis more readily than does temperature.

In contrast to the weak effects of shade, the changes elicited by litter inputs were strong and affected all species. Ponds with grass litter consistently showed higher primary productivity and metamorphs that were both earlier and larger than in leaf litter ponds, indicating greater quantity and/or quality of food resources for tadpoles. This finding is consistent with recent studies on natural benthic substrates (Skelly and Golon 2003; Schiesari 2006), but is the first to link a difference in resource quality directly to litter inputs. In general, grass litter decomposes at a faster rate than deciduous leaf litter in aquatic systems (Webster and

Benfield 1986), increasing the availability of nutrients and facilitating growth of microbes. We believe this nutrient release drove the increased productivity and faster tadpole growth rates observed in grass litter ponds. Alternatively, humic acids and tannins released into the water by the deciduous leaf litter may have attenuated photosynthetically active radiation, possibly inducing productivity differences.

Contrary to our initial hypothesis, canopy cover and litter type had few interactive effects on larval anuran survival, growth, and development. Although both shade level and litter influenced tadpole performance, these effects were largely independent. Only gray treefrog time to metamorphosis showed a significant interaction, with metamorphs emerging sooner from grass litter ponds under low-shade conditions but not in intermediate- or high-shade treatments.

Alterations in larval amphibian survival and performance have the potential to induce cascades of community changes in wetlands. Amphibians are abundant consumers within wetlands and, in the case of salamanders, act as keystone predators (Morin 1981; Fauth and Resetarits 1991; Wissinger et al. 1999). Resources consumed by amphibian larvae in wetlands are transferred to terrestrial habitats following metamorphosis; this biomass transfer can be large (up to 1,500 kg/year from one isolated wetland; Gibbons et al. 2006). Differential larval survival generated by shade level and litter type directly affects the biomass entering terrestrial ecosystems by controlling juvenile recruitment. In addition to differential survival, altered larval performance influences amphibian population dynamics. Individuals that metamorphose early and at a larger size (as generally seen in our grass litter ponds) can reach first reproduction at a younger age and larger size than their later or smaller counterparts, thus potentially increasing adult fitness (Semlitsch et al. 1988).

Our results support the idea that changes in canopy cover likely contribute to wetland community structure through a combination of species sorting and habitat selection (Binckley and Resetarits 2005). In our study, survival of spring peepers decreased in high-shade conditions, and survival of southern leopard frogs and gray treefrogs was tied to litter type. Therefore, conditions in shaded wetlands can cause differential mortality and potentially limit the distribution of amphibian species. Distributions may be further altered through behavioral selection of habitat. Many inhabitants of temporary wetlands have been shown to discriminate among oviposition sites [treefrogs (Resetarits and Wilbur 1989; Rieger et al. 2004; Resetarits et al. 2005; Binckley and Resetarits 2007), odonates (Corbet 1999), various coleopterans (Binckley and Resetarits 2005, 2007), and mosquitoes (Reiskind and Wilson 2004)]. When given a choice among oviposition sites, several of these taxa

demonstrate a preference for open-canopy habitats (Resetarits et al. 2005; Hocking and Semlitsch, *in press*). By quantifying differences in larval performance associated with both canopy cover and litter, our study provides evidence for why ovipositioning in shaded ponds with a leaf litter base might be maladaptive for some amphibian species when effects of predation and interspecific competition are low.

The same conditions that limited survival and performance of amphibian larvae in our pond mesocosms could be detrimental for other temporary wetland species. Low DO levels (≤ 2 p.p.m.) were common in our most shaded ponds, and may have caused the shade-associated spring peeper mortality. Although many wetland invertebrates are able to behaviorally escape low DO conditions, the levels observed in our shaded ponds may adversely affect invertebrates with poor swimming ability (e.g., conchostracans; Moore and Burn 1968). In addition, deciduous leaf-based litter inputs were associated with considerably lower primary productivity than grass-based litter, possibly due to differences in nutrient release. This pattern apparently led to a lack of food resources for the tadpoles in our study, as metamorphs of all three species were smaller in leaf versus grass litter ponds. Other grazers in temporary wetlands may be similarly limited and changes in litter input may induce even more dramatic effects on organisms feeding directly on detritus (e.g., shredders; Colburn 2004).

In our study, all three species of shade-limited anuran larvae showed unique responses to shade and litter manipulations. Several positive responses (e.g., increased size, faster development) occurred with litter types representing open-canopy wetlands. However, grass and sedge litter was also associated with increased mortality for gray treefrogs, indicating that responses to open-canopy substrates may not be uniformly positive. In addition, regarding population regulation, open-canopy characteristics (e.g., increased temperatures) which benefit tadpoles in the larval environment may be detrimental to juveniles and adults if forest cover is also lacking in the surrounding terrestrial habitat (deMaynadier and Hunter 1999; Semlitsch and Bodie 2003; Rothermel and Semlitsch 2006; Rittenhouse et al., *in review*).

Canopy closure over wetlands and associated changes in litter inputs strongly influence both abiotic (e.g., temperature, nutrient levels) and biotic (primary productivity) conditions in aquatic habitats and cause substantial differences in the survival, growth and development of amphibian larvae. Therefore, gradients of canopy cover and litter likely act in concert with hydroperiod to shape temporary wetland communities (Wellborn et al. 1996; Schneider and Frost 1996). Our study indicates that the performance of several amphibian species within open-canopy wetlands may be largely driven by changes in resource base that are directly

linked to litter inputs. In addition, this experiment reveals a surprising paucity of interactions between canopy cover and litter type. By experimentally investigating how shade-limited species respond to canopy treatments, we can better understand the processes driving temporary pond community dynamics in changing forest landscapes.

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