**Importance of forestry practices relative to microhabitat and microclimate changes
for juvenile pond-breeding amphibians**

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Abstract

Balancing the goals of forest management and species conservation is a major challenge. Forestry practices could be refined with greater understanding of the importance of large-scale forestry practices versus smaller-scale microhabitat and microclimate variables in driving demographic vital rates for species of conservation concern. We examined the relative importance of forestry practices, microhabitat, and microclimate on juvenile anuran survival and growth. To do so, we examined three different species: wood frogs (*Lithobates sylvaticus*), American toads (*Anaxyrus americanus*), and southern leopard frogs (*Lithobates sphenoccephalus*), in three different years using terrestrial enclosures. Terrestrial enclosures were placed in forestry treatment plots with unharvested forest, partial cut forest, early successional forest (ESF; i.e. 4-6 year old clearcut) with downed wood removed, and ESF with downed wood retained in central Missouri, USA. We ranked models using an information-theoretic approach to determine whether forestry treatment, microhabitat (logs, canopy cover, leaf litter depth), or microclimate (temperature and soil moisture) best predicted juvenile survival and growth. We found that microhabitat and microclimate, but not forestry practices, were important for survival and growth. However, small sample sizes may have limited our ability to detect forestry treatment effects. Most associations with growth and survival involved microclimate variables. Effects of microhabitat showed positive associations of survival with canopy cover and downed wood and of growth with leaf litter depth. All effects varied by species/year and season, as is common for studies on the effects of forestry practices on amphibians, indicating that it would be useful to maintain a variety of different microhabitats and microclimates to support a diverse anuran community. Because juvenile survival is a population-regulating parameter for many amphibians, it may be prudent to focus on creating favorable microhabitats and microclimates within areas under active forest management. However, it would be useful to repeat this type of study in different eco-regions with different species to determine the generalizability of these results.

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45 **Keywords:** *Anaxyrus*, coarse woody debris, early successional forest, *Lithobates*, temperature, partial cut

1. Introduction

Forestry management practices include a suite of techniques for timber harvest, wildfire risk reduction (Agee and Skinner 2005), and ecological restoration (e.g., Bailey and Covington 2002). One of the biggest challenges of these techniques is balancing the primary goals with the maintenance of biodiversity (Simberloff 1999). Broad-scale meta-analyses show that forest thinning tends to have positive effects for biodiversity (Verschuyl et al. 2011), while others, like clearcuts, tend to have negative effects for at least some taxa or life stages (e.g. juvenile amphibians, deMaynadier and Hunter 1995, Semlitsch et al. 2009). However, there is a large amount of variability in responses to different forestry practices. Some of this variability is explained by the region of study or the focal taxa, but much is also unexplained. One reason for this may be a lack of understanding of the underlying habitat and climatic changes responsible for biodiversity responses.

Forestry practices alter the habitat as a whole, but also affect microclimate (e.g., Carlson and Groot 1997) and microhabitat features, such as leaf litter depth, shading, and coarse woody debris (Riffell et al. 2011). These factors are known to be very important for a variety of taxa (Riffell et al. 2011) and are likely the mechanisms responsible for many of the effects of different forestry practices (deMaynadier and Hunter 1995). To refine management practices, it is important to know which of these factors are most important and whether the local micro-scale conditions or the forestry practices themselves have a greater predictive power for focal taxa response variables. With such knowledge, forestry practices could potentially be adjusted to minimize negative effects on biodiversity or be tailored based on other factors related to the region, topography or target species (Sutton et al. 2014).

Amphibians are strongly affected by forestry practices. Particularly, clearcutting reduces amphibian abundance (e.g., Patrick et al. 2006), survival (deMaynadier and Hunter 1995, Semlitsch et al. 2009), and alters behavior (Semlitsch et al. 2008, Pittman and Semlitsch 2013, Osbourn et al. 2014).

Previous work shows that microhabitat changes from forestry practices are very important for overall amphibian capture rates (including both adults and juveniles; deMaynadier and Hunter 1995), as well as juvenile amphibian survival and desiccation (Rittenhouse et al. 2008). Amphibian capture rates tend to have positive relationships with downed wood, leaf litter depth, canopy closure, and soil moisture (deMaynadier and Hunter 1995). Amphibian physiological adaptations (e.g., permeable skin) make them vulnerable to water loss (Jørgensen 1997). Many species require particular microclimates and microhabitats that minimize desiccation (Peterman et al. 2013, Peterman and Semlitsch 2013). However, it is unclear whether these microscale factors or larger-scale changes in landuse have higher predictive power for amphibian performance, as this comparison has not been made in previous studies for survival or growth (but see Blomquist and Hunter 2009, 2010 for an assessment of adult habitat selection).

In our study, the goal was to assess the importance of habitat-level forestry practices relative to micro-scale (i.e. meters squared) variables (microhabitat and microclimate) in predicting amphibian performance. We focused on juvenile amphibian survival and growth in *in situ* terrestrial enclosures as part of a habitat-scale (i.e. hectares) experiment to evaluate the effects of forestry practices on amphibians (Semlitsch et al. 2009). We focused on juveniles, because their survival rates are especially important for amphibian population dynamics (Biek et al. 2002, Vonesh and De la Cruz 2002). Forestry practices included unharvested forest (control), partial cut forest, early successional forest (ESF; i.e. 4-6 year old clearcut) with downed wood removed, and ESF with downed wood retained. We predicted that forestry practices would be most important for survival (Semlitsch et al. 2009) and that micro-scale variables would be most important for growth.

2. Material and Methods

2.1 Study System

Our study was conducted in central Missouri, USA at Daniel Boone Conservation Area (DBCA), Warren County. The terrestrial habitat is primarily natural, second-growth oak-hickory forest, and there are many permanent, constructed wildlife ponds that support several species of amphibians. DBCA is the site of experimental forestry plots constructed in late 2004 and early 2005 to investigate the effects of forestry practices on amphibians (Semlitsch et al. 2009). Briefly, the four, circular plots (164 m radius) had a small pond in the center, and the surrounding terrestrial area was divided into four quadrants. Each quadrant received one of four forestry treatments: unharvested forest (control), partial cut forest (thinned to 60% stocking level by removing or girdling low quality trees), clearcut with downed wood removed (trees greater than 25cm in diameter were removed and trees under 25 cm were girdled and left standing), and clearcut with downed wood retained (as in removed treatment except trees under 25 cm were felled). The two clearcuts were opposite each other in all plots (Semlitsch et al. 2009). Our study occurred during the 4-6 years after timber harvest, and the vegetation in former clearcuts had grown to be successional, shrubby vegetation (Earl and Semlitsch 2013). Thus, we refer to the former clearcuts as early successional forest (ESF).

We evaluated the impacts of long-term forest management on three anuran species in different years: wood frogs (*Lithobates sylvaticus*) in 2008/2009, American toads (*Anaxyrus americanus*) in 2009/2010, and southern leopard frogs (*L. sphenoccephalus*) in 2010/2011. These species were chosen, because they have large geographic ranges and are relatively common, potentially making our results relevant to areas beyond our study site. In Missouri, all species breed in ponds during spring (March, April). Wood frogs generally breed about one month earlier than the other two species. All three species have larval periods lasting several months, after which they metamorphose and emigrate to the adjacent terrestrial habitat during summer (Hocking et al. 2008). Wood frogs and American toads typically overwinter terrestrially (Green 2005, Redmer and Trauth 2005), whereas leopard frogs overwinter in

permanent bodies of water (Butterfield et al. 2005).

2.2 Experimental Design

To examine the importance of forestry practices, microhabitat and microclimate on juvenile survival and growth, we used *in situ* terrestrial enclosures within experimental forestry plots at DBCA (Earl and Semlitsch 2013). Terrestrial enclosures (3 m x 3 m enclosures made from hardware cloth) allowed us to increase our detection probability and manipulate variables of interest (Harper et al. 2009). Enclosures were constructed in the center of forestry quadrants (Hocking and Semlitsch 2007, Semlitsch et al. 2008, 2009) in 2004 for another experiment (Harper 2007, Todd et al. 2014). We created two treatments: density (high or low) and forestry treatment, both of which have been shown to affect juvenile survival (Todd and Rothermel 2006, Harper 2007, Harper and Semlitsch 2007).

We used aquatic mesocosms (1000 L cattle water tanks) to raise tadpoles to metamorphosis for placement in terrestrial enclosures. Although not part of the analysis presented in this study, we established two treatments in the aquatic environment: litter input (1 kg leaves, 1 kg grass, or none) and mesocosm placement (edge or center) within control forest and ESF quadrants (Earl and Semlitsch 2012, 2013). Hatchlings were added to aquatic mesocosms and collected at metamorphosis. Metamorphs were then placed into terrestrial enclosures such that one (low density) or two (high density) metamorphs from each aquatic treatment were present in each terrestrial enclosure. Thus, there was equal representation among aquatic treatments in each terrestrial enclosure, and previous analyses show that treatments in the terrestrial environment explained more variation in juvenile survival than that of the aquatic treatments (Earl and Semlitsch 2013). However, the aquatic treatments likely created greater variation among individuals than would be found in natural populations. The target scenario for terrestrial enclosures was 12 individuals in the low-density treatment (1.33 individuals/m²) and 24 individuals in the high-density

treatment (2.67 individuals/m²), which are within natural juvenile densities (Harper and Semlitsch 2007). However, low survival in some aquatic treatments limited our ability to attain target densities. We used density as a continuous variable in analyses, because there was considerable variation in actual densities among terrestrial enclosures.

2.3 Terrestrial Enclosures

Two terrestrial enclosures were placed in pairs in each forestry treatment of the four experimental plots (total N = 32 terrestrial enclosures). Only three circular plots were used for wood frogs in 2008/2009 (N = 24 terrestrial enclosures). Also, two enclosures in the ESF with downed wood retained treatment were not used for leopard frogs due to extensive damage to the walls of those enclosures. Each pair of enclosures was placed 100 m from the plot's central breeding pond in fall of 2004 using the methods described in Harper (2007). Briefly, enclosures were 3 x 3 m made from galvanized steel hardware cloth with 0.32 cm mesh, which allowed small invertebrate prey to move in and out of enclosures. Hardware cloth was buried 30 cm below ground and extended 80 cm above ground with a 10 cm lip bent inward around the top to prevent escape. The amount of downed wood in each enclosure was standardized by forestry treatment, based on data from Shifley and Brookshire (2000). We removed all downed wood from ESF enclosures with downed wood removed. We added 2 m downed wood of decay class 3 as one log to enclosures in the control forest, partial cut and ESF with downed wood retained. Class 3 downed wood (Maser et al. 1979) are logs that are still round, but are faded, without twigs, and have very little bark. This type of downed wood likely occurred before the application of forestry treatments. Downed wood from treatment application is decay class 1, which includes round logs with intact twigs and bark (Maser et al. 1979). We added 3 m class 1 downed wood as a single log to each partial cut enclosure and 9 m of class 1 downed wood as two logs to enclosures in the ESF with downed wood retained treatment.

All added logs were 15 cm in diameter. In spring 2005, leaf litter depth was standardized by treatment to 2 cm in the two ESF treatments and 4 cm in the partial cut and control forest. These depths were based on the averages of measurements taken throughout the forestry treatment quadrants (Rittenhouse, Harper, Hocking, Conner and Semlitsch, unpublished data). After 2005, leaves were allowed to accumulate and logs were allowed to decay naturally (Earl and Semlitsch 2013).

We assigned individual metamorphs to terrestrial enclosures and individually marked them by clipping three toes each. Toe-clipping individuals reduces return rates by approximately 4-11% for each toe clipped after the first (McCarthy and Parris 2004), however these effects may be species-specific (Funk et al. 2005) and the species in this study have not been assessed. To assign metamorphs to terrestrial enclosures, we randomly chose a forestry treatment in each forestry plot to start and then systematically added individuals to the low-density and high-density terrestrial enclosure of each forestry treatment going clockwise around the plot. Once one individual from an aquatic treatment was present in each terrestrial enclosure we then continued clockwise to add the second metamorph to each high-density terrestrial enclosure. This method of assignment resulted in no statistical difference in metamorphic snout to vent length (SVL), mass, body condition, or length of larval period among treatments (Earl and Semlitsch 2013).

We searched terrestrial enclosures for juvenile frogs in two censuses for each species (Table 1). The first census occurred late in September to assess survival and growth over the summer, or after approximately two months. In Missouri, September is when the temperatures start to decline after summer. The second census occurred the following May to assess survival and growth over the winter, or after approximately 10 months. The September censuses consisted of two searches and May censuses consisted of at least two searches of each enclosure performed on different days. Additional searches were performed in May until the number of individuals captured reached sample stability (i.e. it appeared

we detected all but two or fewer individuals), which we determined by examining sample accumulation curves (Orlóci and Pillar 1989, Gotelli and Colwell 2001). For each search, 2-3 people surveyed the entire area of the pen by disturbing leaf litter, turning over cover objects, and investigating large holes for a minimum of 30 person minutes. Greater time was spent in pens with more complex vegetation structure and with a larger number of detected individuals to ensure the capture of all surviving individuals that had been detected. After each census, juveniles were measured for SVL to the nearest mm and mass to the nearest mg. After the September census, all frogs were returned to their enclosure of origin. After the May census, all frogs were sacrificed using a lethal dose of MS-222 and preserved for later examination (Earl and Semlitsch 2013).

2.4 Microclimate and Microhabitat Variables

To assess the microclimate, we placed an iButton (model DS1291G, Embedded Data Systems, Lawrenceburg, KY) temperature logger and a soil moisture probe (Watermark, Irrometer Co., Riverside, California) in each terrestrial enclosure. iButtons were coated with two layers of a synthetic rubber coating (Plasti Dip, Performix, St. Louis Park, MN) and placed in a small, resealable plastic bag to prevent water damage. iButtons recorded temperature every four hours and were deployed underneath the leaf litter approximately 10 cm from the middle of one side of the enclosure for most of the period between metamorphosis and the September census and all of the period between the September and May census (Table 1). In several cases, leaves in enclosures were moved by wind or wildlife, uncovering iButtons, resulting in them registering extreme temperature values. The data for these enclosures were recorded as missing. This occurred in 0-2 enclosures per data set. Soil moisture probes were installed at the center of each pen. Soil moisture measurements (kPA) were taken during periods of drought and following heavy rains to determine the maximum and minimum soil moisture in each pen. We measured at least one wet

and one dry period in each census interval.

Microhabitat variables were assessed in July each year and included canopy cover, leaf litter, and number of logs in each pen. We measured canopy cover using a convex spherical densiometer (Ben Meadows, Janesville, WI, USA) and leaf litter depth to the nearest 0.5 cm, taking each measurement at the center of each side of each enclosure. Logs were counted and each assessed for decay class (Maser et al. 1979).

2.5 Statistical Analysis

All analyses were performed in SAS 9.4 (SAS Institute, Cary, NC) and involved variables averaged for each replicate enclosure. We calculated the growth in SVL (mm/day) and mass (mg/day) of each individual found to be alive from metamorphosis to the September census and between the September and May censuses by subtracting the earlier size from the later size and dividing by the number of days between measurements. We found SVL and mass growth to be highly correlated for all species in both time periods (all $r > 0.72$, all $p < 0.005$) except for leopard frogs in May, which had a more moderate correlation ($r = 0.55$, $p = 0.04$). As such, we only analyzed data for growth in mass, because it was more variable than growth in SVL. For survival, we adjusted the raw numbers of individuals caught at each census with detection probabilities generated from Cormack-Jolly-Seber mark-recapture models in program MARK (White and Burnham 1999) that used each individual as a replicate instead of each terrestrial enclosure from previous work (Earl and Semlitsch 2013). We used the null survival model (survival varied by time period, but with no covariates or factors) and the best detection model from each analysis. Previous results had shown that detection probabilities were affected by SVL at metamorphosis for American toads and leopard frogs and by habitat (ESF or forest) for leopard frogs only. Neither SVL nor habitat affected detection probabilities for wood frogs (Earl and Semlitsch 2013). Because SVL at

metamorphosis did not differ among replicates, we used the overall average SVL for detection probability estimates. To adjust survival estimates, the number of surviving individuals was calculated by dividing the number of individuals captured with the appropriate detection probability for each enclosure.

For temperature data, we calculated the average daily minimum, maximum, standard deviation, and average temperature for each enclosure in each time period. For soil moisture, the lowest soil moisture was likely to be the most limiting for amphibians (Rittenhouse et al. 2008), so we calculated the minimum and the range of values for each enclosure in each time period. The soil moisture scale (kPA) was reversed (original scale was from 0 to 200, so we subtracted the measurement from 200), so that high values represented high soil moisture and low values represented low soil moisture. We examined Pearson's product moment correlations between each group of variables (temperature, soil moisture, and microhabitat), for each year to help decide which variables to include in models. We also examined the effect of forestry treatments on continuous variables using MANOVAs (proc glm) for each group of variables and each year. For cases where the MANOVA indicated a significant effect, we performed one-way ANOVAs. For log counts, we used Poisson regression (proc genmod) to examine effects of forestry treatments.

To determine the importance of forestry treatments, microhabitat, and microclimate to juvenile growth and survival, we created eight models (Table 2). These included an intercept-only null model, one forestry treatment model, one individual density model, two microhabitat models, and three microclimate models. Forestry treatment and density models were included, because these factors are known to greatly affect juvenile amphibian survival and growth (Todd and Rothermel 2006, Harper and Semlitsch 2007, Berven 2009, Todd et al. 2014). Two microhabitat models were specified. One focused on cover, leaves and downed wood, that can provide prey resources and a refuge from predators and dehydration (e.g., Heatwole 1962, Otto et al. 2013, O'Donnell et al. 2014). We called the second microhabitat model the

forestry model, because it contained variables typically measured in forestry studies: leaf litter depth and canopy cover, both of which are important for amphibian survival (e.g., Walton 2005, Todd and Rothermel 2006). While canopy cover may not be a microhabitat variable itself, it serves as a good proxy for understory vegetation (e.g., Ehrenreich and Crosby 1960). We included microclimate models focused on temperature and soil moisture averages and variability. Temperature and moisture greatly affect dehydration rates (e.g., Preest and Pough 1989, Peterman et al. 2013) and can affect predator-prey interactions (e.g., Barton et al. 2009), potentially affecting both survival and growth. Climate variability has recently been shown to affect population dynamics and vital rates (García-Carrerras and Reuman 2013, Vasseur et al. 2014).

We ran models (proc mixed) for each species/year and each census period separately and included the treatment quadrant as a random variable to account for the lack of independence between the two enclosures placed in each treatment quadrant. Dependent variables were summarized for each enclosure, and assumed to have a normal distribution. For wood survival from September to May and both growth time periods, we were unable to include the random variable due to limited sample sizes. These data sets only had one or two pairs of enclosures in the same treatment plot. We also were unable to include the microclimate average and variation model in model selection for growth data from September to May due to insufficient degrees of freedom. Models were ranked using Akaike's Information Criterion corrected for small sample sizes (AIC_c), where the lowest value indicates the best-supported model (Burnham and Anderson 2002). We considered all models within 2 AIC units of the best model to be competing models. We used this framework to report the most likely models, although clearly other models may be useful (Burnham et al. 2011). We used model-averaging to estimate parameter values and standard errors for all parameters included in models with a model weight of 0.10 or greater. Model-averaging used all candidate models. For models not containing a specific parameter, we used an estimate and standard error

of zero in the average. We arcsine square-root transformed juvenile survival and log transformed leopard frog growth from September to May to meet assumptions of normality and homoscedasticity.

3. Results

Survival and growth were highly variable for all three species and both time periods. Survival from metamorphosis to September was lower than survival from September to May for both wood frogs (2008/2009) and American toads (2009/2010). Southern leopard frog (2010/2011) survival was higher from metamorphosis to September than from September to May. Growth rates were greater from metamorphosis to September than from September to May (Table 3).

3.1 Microhabitat and Microclimate

Canopy cover and leaf litter depth were highly correlated in 2008 ($r = 0.81$, $p < 0.0001$) and moderately correlated in 2009 ($r = 0.64$, $p < 0.0001$) and 2010 ($r = 0.63$, $p = 0.0003$). The number of logs was not significantly correlated with canopy cover or litter depth in any of the three years (all $r < 0.34$, all $p > 0.06$). The minimum and range of the soil moisture index were negatively correlated in both seasons in all three years (all $r < -0.62$, $p < 0.0003$). There were also correlations between the average daily temperature standard deviation and the average temperature from metamorphosis to September (all $r > 0.50$, all $p < 0.006$) but not from September to May (all $r < 0.31$, all $p > 0.16$).

MANOVAs indicated no overall effect of forestry treatment on temperature (all $p > 0.07$) or soil moisture (all $p > 0.06$) variables in all three years. However, forestry treatment did significantly affect the habitat variables (2008: $F_{6,38} = 13.01$, $p < 0.0001$; 2009: $F_{6,54} = 11.20$, $p < 0.0001$; 2010: $F_{6,48} = 5.09$, $p = 0.0004$). Both ESF treatments had lower canopy cover and leaf litter depths than the partial cut forest and the control forest in 2008 and 2009, but in 2010, the ESF with downed wood removed had lower canopy

cover and leaf litter depths than all other treatments (Figure 2A, B). The ESF with downed wood retained and partial cut forest had higher numbers of logs than the control forest and the ESF with downed wood removed (all $\chi^2 > 5.40$, all $p < 0.02$) in all three years (Figure 2C).

3.2 Model Selection

For models predicting juvenile survival, the null model was often the best-supported model or a competing model. Competing models included microhabitat, microclimate, or the density model, but never the forestry treatment model (Table 4). For wood frogs from metamorphosis to September, survival had a positive association with the number of logs and a negative association with temperature variability (Table 5). The microhabitat forestry model had the greatest support with the microhabitat cover, null, and microclimate variation models competing. Model-averaging showed that the number of logs and temperature standard deviation parameters had confidence intervals that did not overlap zero (Table 5). For wood frog survival from September to May, the null was the best-supported model with the density model competing (Table 4). However, model averaging resulted in all parameters with confidence intervals overlapping zero (Table 5). American toad survival to September was best predicted by the microhabitat forestry model with no models competing (Table 4). Canopy cover had a positive effect on survival (Table 5), but all other variables had confidence intervals that overlapped zero (Table 5). For American toads from September to May, survival increased with the average temperature and had a negative relationship with density (Table 5). The density model was the best-supported model with the null and average temperature models competing (Table 4). For southern leopard frogs, survival from metamorphosis to September had a negative relationship with the average temperature. The null model had the greatest support for survival from metamorphosis to September with the microclimate average and variability, density, and microclimate average models competing (Table 4). Model-averaging revealed

only one parameter (average temperature) estimate with a confidence interval that did not include zero (Table 5). For leopard frog survival from September to May, the density model was the best with no competing models (Table 4). Survival increased with density (Table 5).

Juvenile growth was best predicted by different models for each species/year and time period. For wood frog growth during both periods, the null model was best supported with no competing models (Table 6). For metamorphosis to September, model averaging showed that growth increased with increasing temperature and soil moisture variability, and decreased with the average temperature (Table 7). For wood frog growth from September to May, growth had a negative relationship with juvenile density (Table 7). American toad growth from metamorphosis to September was best predicted by the microclimate average model with the climate average and variability model competing (Table 6). Growth from metamorphosis to September had a positive association with temperature and a negative association with soil moisture range (Table 7). For American toad growth from September to May, the null model had the greatest support with the microhabitat cover model competing (Table 6). Growth was shown to be higher in habitats with greater leaf litter depths, as indicated by model-averaging (Table 7). Southern leopard frog growth from metamorphosis to September was best predicted by the density model with four other models competing (Table 6). However, only one parameter estimate had a confidence interval that did not include zero (Table 7) that indicated a negative relationship between juvenile growth and density. For leopard frog growth from September to May, the climate variation model was best with the microhabitat cover model competing (Table 6). Model averaging showed that growth increased with leaf litter depth and temperature variability and decreased with soil moisture (Table 7).

4. Discussion

Previous work has established that forestry practices, microclimate, and microhabitat can all

influence amphibian behavior, growth and survival (Rittenhouse et al. 2008, Semlitsch et al. 2009, Blomquist and Hunter 2010, Osbourn et al. 2014). Understanding which of these major factors most influences population dynamics could help refine forest management techniques (Sutton et al. 2014) to conserve amphibian populations. We found that microclimate and microhabitat were important for predicting juvenile anuran survival, an important population vital rate (Biek et al. 2002, Vonesh and De la Cruz 2002), but forestry treatment was not. These results are likely due to the importance of microsite conditions for juvenile amphibians and the diminished effects of forestry practices with increased time since harvest (i.e. 4-6 years). These results suggest that focusing on creating favorable microhabitats and microclimates within harvested areas will likely help maintain viable amphibian populations in forests where managers are attempting to balance human use and conservation. In a similar study, a mixture of forestry treatments, microhabitat, and microclimate variables were found to affect lizard captures (Sutton et al. 2014), and Blomquist and Hunter (2009, 2010) found that all three types of factors affected adult anuran habitat selection.

Anuran juvenile survival and growth had the most associations with microclimate variables. The average temperature effects depended on season. Cooler microclimates enhanced southern leopard frog survival in summer, and warmer microclimates enhanced American toad survival over the winter. This ability for different microhabitats to buffer extreme temperatures allows juveniles to better deal with less favorable temperatures (Seebacher and Alford 2002). Temperature can also influence growth rates. In the laboratory, ectotherms like amphibians grow faster with warmer temperatures (Marian and Pandian 1985, Hayes et al. 1993), though this is not always true under field conditions (Cohen and Alford 1993). Under natural conditions, temperature can affect water loss (Peterman et al. 2013), the use of cover objects (Joppa et al. 2009), and predator-prey interactions (Anderson et al. 2001, Barton et al. 2009), all of which may affect the relationship between growth rates and temperature. In our study, warmer summer

temperatures resulted in lower growth rates for wood frogs and higher growth rates in American toads. Wood frogs are at the southern edge of their geographic range in Missouri (Redmer and Trauth 2005), which may make them more prone to heat stress at our study site than in other areas of their range. As such, higher temperatures may have limited their growth due to missed foraging opportunities from needing to use cover objects that moderate temperature extremes (Scheffers et al. 2014) more frequently.

Juvenile frogs' response to temperature variability was more nonintuitive, exhibiting varied effects. Temperature variability has been predicted to negatively impact ectotherm populations (Vasseur et al. 2014). Consistent with this, wood frog survival was found to decrease with increasing temperature variability. Similarly, American toad growth rates decreased with increasing soil moisture variability. However, for wood frog and leopard frog growth, we found a positive relationship with temperature variability. Wood frog growth also increased with soil moisture variability. The temperature variance can have a positive or negative effect on population growth rate depending on how close the mean temperature was to the species' thermal optimum (García-Carrerras and Reuman 2013, Vasseur et al. 2014). It is likely that there is a similar effect for individual growth rates. Further, effects of temperature on organisms depend greatly on their dehydration status (Preest and Pough 1989), potentially causing complex interactions between temperature and moisture means and variation. It would be easier to address such interactions with laboratory experiments than field manipulations, such as our study.

Microhabitat features were only important to juvenile survival from metamorphosis to September and not from September to May. Downed wood is an important resource for amphibians (Otto et al. 2013). We found that juvenile wood frog survival increased with the number of logs. Similarly, adult wood frogs tend to choose habitats with more coarse woody debris (Blomquist and Hunter 2010), and brushpiles in clearcuts can mitigate water loss for wood frogs and other amphibians species (Rittenhouse et al. 2008). Downed wood provides a thermal and hydric refuge for individuals (deMaynadier and

Hunter 1995, Fritts et al. 2015) due to high levels of water storage even in dry periods (Fraver et al. 2002). It has been hypothesized that new downed wood in younger forest stands may not be of a sufficient decay class to provide benefits to amphibians. Most logs in our enclosures were of decay class 3, which are logs that are still round but faded, twig-less, and only slightly covered in bark (Maser et al. 1979). Our results suggest that this level of log decay is sufficient for use by juvenile wood frogs, though there have been no studies on amphibian preferences for different log decay classes or comparing the effect log decay class on survival, growth or water loss (Otto et al. 2013).

Canopy cover is also important for amphibian survival. We found that American toad survival had a positive relationship with canopy cover. This is consistent with other studies showing that American toad juveniles prefer forested habitat over fields (Rothermel and Semlitsch 2002), and other toad species have higher survival in forested habitat than clearcuts (Todd and Rothermel 2006). Furthermore, population persistence of American toads is associated with increased forest cover (Gibbs et al. 2005). Although leaf litter was not a key habitat feature for survival, greater leaf litter depth led to increased growth rates for American toads and southern leopard frogs from September to May. Leaf litter is an important source of invertebrate prey (Gist and Crossley 1975), which increase with increasing amounts of leaf litter (Haskell 2000, Walton 2005). Also, by providing a refuge, greater leaf litter depth may allow amphibians to spend more time foraging under leaf litter with lower risk of predation and dehydration (Heatwole 1962, Jaeger 1980, Seebacher and Alford 2002), leading to higher growth rates (Walsh and Downie 2005, Walton 2005).

Microhabitat variables were strongly affected by forestry practices, but microclimate variables were not. Our study took place four to six years post-harvest, and the clearcut areas had grown into early successional forest. This regrowth likely mitigates many of the harsher aspects found in more recent clearcuts (Earl and Semlitsch 2013) and alters microhabitat and microclimate. As such, successional

processes likely affected our results. However, microclimate has been shown to be more influenced by topography, aspect, and microhabitats than forestry practices (Brooks and Kyker-Snowman 2008), though these effects may depend on regional context and the amount of variability in topography on the landscape. In the same area as our study, Peterman et al. (2013) found that amphibian water loss was greater on southwest than northeast facing slopes and on ridges relative to ravines within forest habitat during the daytime, but there was no effect of aspect or landscape position at nighttime. Amphibians are typically active at night, but many anurans are still present above ground under leaf litter or cover objects. Rittenhouse et al. (2008) compared water loss and survival of American toads and wood frogs in different microhabitats and microclimates. American toads had less variability in water loss among microhabitats due to burrowing behavior. Wood frogs, alternatively, had much greater water loss in drier habitats (clearcut open and forest ridge) than moister habitats (clearcut brushpile and forest drainage). Thus, it would be useful to conduct more complex experiments examining the interaction of forestry practices with topography and aspect. Maintaining favorable microhabitats in areas of naturally favorable microclimates such as northeast facing slopes and in drainages may enhance amphibian survival and growth.

Our use of enclosures in this study restricted the movement of individuals and did not allow them to display any habitat selection at a scale of 9 m² or larger. Our results may represent the survival and growth for individuals with only one type of forestry practice around their natal pond. Alternatively, they may also represent individuals that move into poor habitat due to difficulties detecting suitable habitat. For example, juvenile spotted salamanders (*Ambystoma maculatum*) will preferentially orient towards forest where habitat edges are easily detected, but they exhibit random orientation relative to forest when in ESF, where habitat edges are less obvious (Pittman and Semlitsch 2013). Thus, juveniles may prefer habitats that will result in higher survival, but they may not always be able to detect favorable habitat and move towards it. Additionally, our use of enclosures prevents individuals from choosing different habitats

during different seasons. Southern leopard frogs likely had lowered survival from September to May due to lack of suitable overwintering sites in enclosures. Adult southern leopard frogs overwinter in permanent water bodies (Butterfield et al. 2005), while wood frogs and American toads overwinter terrestrially (Green 2005, Redmer and Trauth 2005).

Another factor potentially affecting our study was the variation in aquatic habitats that individuals experienced prior to placement in terrestrial enclosures (Earl and Semlitsch 2013). This likely created greater initial variability among individuals than would typically occur and may have reduced our ability to detect effects of the terrestrial environment. One other limitation was the combination of low sample sizes due to low survival and the higher number of parameters in the forestry treatment model, which likely contributed to the low ranking of the forestry treatment model. Repeating this type of study with the same species at different times post harvest would provide useful information on the potential changing mechanisms for the effects of forestry practices on juvenile amphibians with forest regrowth. A longitudinal study would also inform management as to the ability of creating favorable microclimates or microhabitats in mitigating negative effects of certain forestry practices, such as clearcutting.

5. Conclusions

Forestry practices, microclimate, and microhabitat are groups of variables affecting amphibian population dynamics and performance. Determining which variable type and the specific parameters within each type will potentially help managers establish management practices that balance the competing needs of timber harvest, forest management, and species conservation. Our study found that microsite conditions were best for predicting juvenile survival and growth. Many of our effects varied with the species/year and season. However, amphibians will benefit from maintaining some areas with higher amounts of downed wood, canopy cover, leaf litter, and microsites that buffer against extreme

temperatures within managed forests. Including a variety of microhabitats and microclimates within habitats will likely allow the persistence of a diverse community of amphibians.

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638

Table 1. Important dates for terrestrial enclosure experiments involving the placement of individuals in enclosures and the collection of amphibian, microhabitat, and microclimate data.

	Wood Frogs: 2008	American Toads: 2009	Leopard Frogs: 2010
1 st Metamorph Emergence	30 May	11 June	9 June
Last Metamorph Emergence	10 July	22 July	8 September
September Census	26, 27 September	12, 13 September	18, 19, 21 September
May Census*	20, 28 May, 4 June	23, 24 May	18, 19, 27, 31 May, 11 June
Habitat Sampling	8, 10 July	16 July	21, 22, 23 July
Soil Moisture Measurements [§]	30 August, 5 September, 24 April, 15 May	28 June, 5 July, 22, 28 April, 11 May	14, 21 July, 5, 18 September, 2 April, 4, 16 May
iButton Deployment	26 August – 15 May	5 July – 11 May	15 July – 16 May

*May censuses occurred the following year.

[§]Soil moisture measurements were taken during at least one wet and one dry period per survival period (metamorphosis to September census and between census periods).

659 Table 2. Model set used to determine the importance of forestry treatment, microhabitat and microclimate
660 to juvenile anuran survival and growth. K indicates the number of parameters and trt is an abbreviation for
661 treatment. The three parameters for the null model include the intercept, the variance, and a random
662 blocking variable. All parameters are continuous except forestry trt.

663

Model	K	Parameters
Null Model	3	Intercept only
Forestry Treatment	6	Intercept, forestry trt
Density	4	Intercept, initial anuran density
Microhabitat: Forestry	5	Intercept, canopy cover, number of logs
Microhabitat: Cover	5	Intercept, leaf litter depth, number of logs
Microclimate: Average	5	Intercept, average daily temperature, soil moisture minimum
Microclimate: Variation	5	Intercept, average daily temperature standard deviation, soil moisture range
Microclimate: Average, Variation ^a	7	Intercept, average daily temperature, soil moisture minimum, average daily temperature standard deviation, soil moisture range

664

665 ^a For the wood frog (2008) September models and American toad models, soil moisture minimum was
666 removed due to high collinearity (VIF = 6+) between soil moisture minimum and range.

667

668 Table 3. Average ($\pm$ standard deviation) survival and growth for metamorphosis (meta.) to September and
 669 September to May in all three species/years.

670

Species (Year)	Survival (%)		Growth (mg/d)	
	Meta. – Sept.	Sept. – May	Meta. – Sept.	Sept. – May
Wood frogs (2008/2009)	12.04 $\pm$ 17.36	41.16 $\pm$ 41.36	6.0 $\pm$ 6.6	4.2 $\pm$ 2.6
American toads (2009/2010)	21.13 $\pm$ 22.09	42.42 $\pm$ 43.86	12.4 $\pm$ 3.4	5.6 $\pm$ 3.2
Leopard frogs (2010/2011)	52.35 $\pm$ 33.06	28.33 $\pm$ 37.30	27.1 $\pm$ 20.0	7.1 $\pm$ 4.5

676

677 Table 4. AIC_c tables for survival, where K is the number of parameters and N is the sample size (number of enclosures). All models
 678 include a random variable for treatment plot except for wood frogs in May.

679

680	Species/Time Period	Model	K	-2log(L)	AIC_c	Δ_i	ω_i
681	Wood Frog						
682	September 2008 (N = 24)	Microhabitat: Forestry	5	2.3	12.4	0	0.26
683		Microhabitat: Cover	5	2.6	12.7	0.3	0.23
684		Null	3	8.4	12.9	0.5	0.21
685		Microclimate: Variation	5	3.4	13.6	1.2	0.14
686		Density	4	8.1	15.3	2.9	0.06
687		Microclimate: Average	5	6.3	16.4	4.0	0.04
688		Microclimate: Average, Variation	7	3.4	16.7	4.3	0.03
689		Forestry Treatment	6	3.5	16.8	4.4	0.03
690							
691	May 2009 (N = 11)	Null	2	19.6	25.1	0	0.58
692		Density	3	17.0	26.5	1.4	0.29
693		Microhabitat: Forestry	4	15.2	29.9	4.8	0.05

694		Microhabitat: Cover	4	15.9	30.6	5.5	0.04
695							
696		Microclimate: Variation	4	17.0	31.6	6.5	0.02
697		Microclimate: Average	5	17.4	32.0	6.9	0.02
698		Forestry Treatment	5	14.4	36.5	11.4	0.002
699		Microclimate: Average,					
700		Variation	6	13.5	46.5	21.4	< 0.001
701	American Toad						
702	September 2009	Microhabitat: Forestry	5	10.5	20.0	0	0.71
703	(N = 32)	Microhabitat: Cover	5	14.4	23.8	3.8	0.11
704		Density	4	18.1	24.9	4.9	0.06
705		Null	3	18.3	25.2	5.2	0.05
706		Forestry Treatment	6	13.8	26.1	6.1	0.03
707		Microclimate: Variation	5	17.0	26.4	6.4	0.03
708		Microclimate: Average,					
709		Variation	7	16.4	28.7	8.7	0.009
710		Microclimate: Average	5	18.0	30.3	10.3	0.004

711	May 2010	Density	4	39.8	50.2	0	0.48
712	(N = 22)	Null	3	44.0	51.3	1.1	0.28
713		Microclimate: Average	5	38.4	52.2	2.0	0.18
714		Microhabitat: Cover	5	42.1	55.8	5.6	0.03
715		Microhabitat: Forestry	5	43.2	56.9	6.7	0.02
716		Microclimate: Variation	5	43.9	57.6	7.4	0.01
717		Microclimate: Average,					
718		Variation	7	36.5	58.5	8.3	0.008
719		Forestry Treatment	6	42.0	59.6	9.4	0.004
720	Southern Leopard Frog						
721	September 2010	Null	3	35.7	42.6	0	0.36
722	(N = 30)	Microclimate: Average,					
723		Variation	7	31.0	43.5	0.9	0.23
724		Density	4	34.6	44.2	1.6	0.16
725		Microclimate: Average	5	32.1	44.6	2.0	0.13
726		Microhabitat: Cover	5	34.5	47.0	4.4	0.04
727		Microhabitat: Forestry	5	35.2	47.7	5.1	0.03

728		Microclimate: Variation	5	35.5	48.0	5.4	0.02
729		Forestry Treatment	6	32.8	48.5	5.9	0.02
730	May 2011	Density	4	27.0	36.9	0	0.88
731	(N = 26)	Null	3	35.4	42.5	5.6	0.05
732		Microclimate: Average	5	29.6	42.6	5.7	0.05
733		Microclimate: Variation	5	33.1	46.1	9.2	0.009
734		Microhabitat: Forestry	5	34.3	47.3	10.4	0.005
735		Microhabitat: Cover	5	34.8	47.8	10.9	0.004
736		Forestry Treatment	6	32.9	49.4	12.5	0.002
737		Microclimate: Average,					
738		Variation	7	29.6	49.8	12.9	0.001
739							
740							

Table 5. Parameter estimates for models predicting juvenile survival (arcsine square-root transformed).

Species/Time Period	Parameter	Estimate	95% Confidence Interval
Wood Frog			
September 2008†	Intercept	0.41	-0.23, 1.05
	Canopy cover	0.02	-0.05, 0.09
	Logs	0.05	0.01, 0.08*
	Litter depth	0.001	-0.007, 0.009
	Soil moisture range	-0.0002	-0.0005, 0.0001
	Temperature sd	-0.03	-0.06, -0.003*
May 2009†	Intercept	0.89	0.18, 1.61*
	Density	-0.01	-0.03, 0.002
American Toad			
September 2009	Intercept	0.03	-0.25, 0.31
	Canopy cover	0.51	0.18, 0.85*
	Logs	0.004	-0.07, 0.07
May 2010†	Intercept	0.30	-0.85, 1.45
	Density	-0.35	-0.64, -0.07*
	Soil moisture average	0.0005	-0.0003, 0.001
	Temperature average	0.09	0.009, 0.18*
Southern Leopard Frog			

764	September 2010†	Intercept	2.36	0.76, 3.97*
765		Density	0.003	-0.002, 0.007
766		Soil moisture average	0.00009	-0.0003, 0.0005
767		Soil moisture range	0.0002	-0.0006, 0.001
768		Temperature average	-0.07	-0.13, -0.008*
769		Temperature sd	0.04	-0.03, 0.10
770	May 2011	Intercept	-0.17	-0.60, 0.26
771		Density	0.04	0.02, 0.06*

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773 †Parameter estimation via model-averaging.

774 *Confidence interval does not overlap zero.

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776 Table 6. AIC_c tables for growth in mass, where K is the number of parameters and N is the sample size (number of enclosures).
 777 Leopard frog models include a random variable for treatment plot.

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779	Species/Time Period	Model	K	-2log(L)	AIC_c	Δ_i	ω_i
780	Wood Frog						
781	September 2008	Null	2	71.8	77.3	0	0.55
782	(N = 11)	Microclimate: Average,					
783		Variation	5	57.7	79.7	2.4	0.16
784		Microclimate: Variation	4	65.6	80.3	3.0	0.12
785		Density	3	71.7	81.1	3.8	0.08
786		Microclimate: Average	4	66.6	81.3	4.0	0.07
787		Microhabitat: Cover	4	71.7	86.3	9.0	0.006
788		Microhabitat: Forestry	4	71.7	86.4	9.1	0.006
789		Forestry Treatment	5	71.4	93.4	16.1	< 0.001
790	May 2009	Null	2	32.2	39.2	0	0.80
791	(N = 7)	Density	3	28.0	42.0	2.8	0.20
792		Microclimate: Average	4	25.6	53.6	14.4	0.001

793		Microhabitat: Forestry	4	26.5	54.5	15.3	< 0.001
794		Microclimate: Variation	4	27.9	55.9	16.7	< 0.001
795		Microhabitat: Cover	4	28.2	56.2	17.0	< 0.001
796		Forestry Treatment	5	19.6	89.6	50.4	< 0.001
797	American Toad						
798	September 2009	Microclimate: Average	3	101.8	112.3	0	0.41
799	(N = 21)	Microclimate: Average,					
800		Variation	5	99.3	113.3	1.0	0.25
801		Microclimate: Variation	3	104.2	114.7	2.4	0.12
802		Null	1	110	114.7	2.4	0.12
803		Density	2	108.3	115.8	3.5	0.07
804		Microhabitat: Cover	3	108.7	119.2	6.9	0.01
805		Microhabitat: Forestry	3	109.4	119.9	7.6	0.009
806		Forestry Treatment	4	108.8	122.8	10.5	0.002
807	May 2010	Null	1	65.3	74.0	0	0.59
808	(N = 13)	Microhabitat: Cover	3	57.3	75.9	1.9	0.23
809		Density	2	65.2	78.2	4.2	0.07

810		Forestry Treatment	4	60.7	79.3	5.3	0.04
811		Microclimate: Variation	3	61.0	79.6	5.6	0.04
812		Microhabitat: Forestry	3	61.4	80.0	6.0	0.03
813		Microclimate: Average	3	64.5	83.1	9.1	0.006
814	Southern Leopard Frog						
815	September 2010	Density	3	45.8	55.6	0	0.36
816	(N = 27)	Forestry Treatment	5	43.3	56.3	0.7	0.25
817		Microhabitat: Cover	4	47.0	56.8	1.2	0.20
818		Null	2	50.2	57.3	1.7	0.15
819		Microclimate: Average	4	48.1	60.9	5.3	0.03
820		Microhabitat: Forestry	4	49.3	62.1	6.5	0.01
821		Microclimate: Average,					
822		Variation	6	44.2	64.1	8.5	0.005
823		Microclimate: Variation	4	60.3	64.9	9.3	0.003
824	May 2011	Microclimate: Variation	4	71.2	83.6	0	0.44
825	(N = 14)	Microhabitat: Cover	4	72.4	84.8	1.2	0.24
826		Null	2	80.7	85.7	2.1	0.15

827	Microclimate: Average	4	74.0	86.5	2.9	0.10
828	Density	3	79.8	88.2	4.6	0.04
829	Microhabitat: Forestry	4	78.2	90.6	7.0	0.01
830	Forestry Treatment	5	77.2	94.7	11.1	0.002
831						
832						

Table 7. Parameter estimates for models predicting juvenile growth in mass.

Species/Time Period	Parameter	Estimate	95% Confidence Interval
Wood Frog			
September 2008†	Intercept	35.64	5.02, 66.26*
	Soil moisture range	0.04	0.01, 0.06*
	Temperature Avg.	-1.91	-3.20, -0.61*
	Temperature sd	1.92	0.15, 3.69*
May 2009†	Intercept	5.21	2.90, 7.53*
	Density	-0.07	-0.12, -0.01*
American Toad			
September 2009†	Intercept	-24.08	-56.14, 7.97
	Soil moisture average	0.006	-0.001, 0.01
	Soil moisture range	-0.009	-0.02, -0.0005*
	Temperature average	1.73	0.26, 3.20*
	Temperature sd	0.09	-0.67, 0.85
May 2010†	Intercept	4.91	2.91, 7.63*
	Leaf litter depth	0.19	0.10, 0.28*
	Logs	0.04	-0.25, 0.33
Southern Leopard Frog			
September 2010†,§	Intercept	3.33	2.66, 4.01*
	Density	-0.02	-0.03, -0.002*

856		Control forest	-0.10	-0.26, 0.05
857		Partial cut forest	0.07	-0.08, 0.23
858		ESF wood removed	0.07	-0.08, 0.22
859		ESF wood retained	.	.
860		Leaf litter depth	-0.03	-0.07, 0.001
861		Logs	0.0004	-0.03, 0.03
862	May 2011†	Intercept	-0.45	-9.47, 8.56
863		Leaf litter depth	0.48	0.19, 0.77*
864		Logs	-0.25	-0.54, 0.04
865		Soil moisture average	-0.004	-0.007, -0.001*
866		Soil moisture range	0.01	-0.002, 0.03
867		Temperature average	0.10	-0.40, 0.61
868		Temperature sd	2.41	0.98, 3.83*

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870

871 †Parameter estimation via model-averaging.

872 *Confidence interval does not overlap zero.

873 ‡Parameter estimate is not reliable due to only one replicate being represented in the data set.

874 §The response variable was log transformed for this analysis.

Figure Legends

Figure 1. Layout of circular, experimental forestry plots, forestry practice treatments, and terrestrial enclosures at Daniel Boone Conservation Area, Warren County, Missouri, USA. Note that terrestrial enclosures (3m x 3m) are not to scale, and site three consists of two half circles due to previous forest cutting nearby that prevented the placement of a full circular plot. ESF removed = Early Successional Forest (i.e. 4-6 year old clearcuts) with downed wood removed. ESF retained = ESF with downed wood retained.

Figure 2. Differences among forestry treatments in canopy cover (A), leaf litter depth (B), and log count (C). Error bars represent standard error (2008: N = 24; 2009: N = 32; 2010: N = 30).

888 Fig. 1

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892 Fig. 2

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