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Effects of timber harvesting on terrestrial survival of pond-breeding amphibians

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ABSTRACT

Successful forest management for multiple uses requires balancing extractive practices with maintaining biodiversity, among other important goals. Amphibians comprise an important and abundant part of the biodiversity of many forests. Previous studies have documented declines in the abundance and diversity of amphibians in harvested forests. However, only recently have studies begun to elucidate the mechanisms that underlie such declines. Here, we studied the effects of timber harvesting on survival of geographically widespread ambystomatid salamanders in three forest regions of North America. We used terrestrial enclosures in the Northeast, Midwest, and Southeast to compare amphibian survival in unharvested controls, partially harvested stands (~25% canopy reduction), and clearcuts with coarse woody debris either retained or removed. In all regions, patterns of amphibian survival were similar, with both juvenile and adult salamanders generally having significantly lower survival in clearcuts compared with unharvested controls. Survival of juvenile salamanders in partially harvested stands was also low, but adult salamanders survived as well or better in partially harvested stands as in controls. Larger body size in juveniles was significantly correlated with recapture, irrespective of treatment, in both the Northeast and Southeast, but not in the Midwest or for adults in any region. Relatively heavier adults were more likely to be captured again in the Southeast, but relative mass was not correlated with recapture in any other regions or for juveniles. Our results suggest that increased amphibian mortality may contribute to declines of amphibian abundance and richness after forest clearcutting for the regions evaluated here. Although our results indicate that partial harvesting is compatible with survival of adult salamanders, retention of intact forest around breeding ponds would benefit all terrestrial stages of pond-breeding salamanders and represents a best management practice for the maintenance of amphibian biodiversity.

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1. Introduction

Alteration of terrestrial habitat from deforestation or harvesting is a leading cause of global species declines and population extinctions (Mace et al., 2005). Although harvesting of primary forest remains a major concern (Gardner et al., 2007), industrial silviculture and logging of second-growth forests are more prevalent in developed countries and continue to have ecological consequences to biodiversity and ecosystem processes (Coates and Burton, 1997). For example, 6.1 million ha of a total 734 million ha forest area is estimated to be affected by harvest each year in North America, with an additional 1 million ha converted to other land uses (Masek et al., 2011). Because of the large scale of forestry and its global reach, there has long been interest in understanding the effects of harvesting practices such as clearcutting on plant and animal populations, particularly where such knowledge can inform management and reduce negative effects. In some cases, this has led to improvements in land management that benefit threatened species (e.g., uneven-aged stand management for Red-cockaded woodpeckers, *Picoides borealis*; Hedrick et al., 1998) or that restore ecosystem integrity (e.g., retention of riparian buffer zones; Lowrance et al., 1997), demonstrating a valuable role for solution-based research on forestry impacts.

Applied ecological research on amphibians has lagged behind that of other vertebrates (Clark and May, 2002), but growing appreciation for the current plight of amphibians has generated greater interest in mechanisms of amphibian decline (Wake and Vredenburg, 2008). As with many fauna, habitat loss is a major factor in global amphibian declines (Alford and Richards, 1999; Stuart et al., 2004). However, unlike nearly all other vertebrates, many amphibians have complex life histories that require them to live

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in both aquatic and terrestrial habitats at different stages in their lives. This aspect of their ecology makes them especially sensitive to habitat loss or alteration and may contribute to their high level of imperilment among vertebrates (Stuart et al., 2004; Bielby et al., 2008; Murray et al., 2011). Over 80% of amphibians are forest-dependent (Stuart et al., 2004), and in some studies, amphibians have been found to comprise more forest biomass than all other vertebrate groups combined (Burton and Likens, 1975; Peterman et al., 2008), playing an important role in ecosystem dynamics (e.g., Wyman, 1998). Thus, there is an urgent need to understand the degree to which structural changes in forests after harvesting affect amphibian biodiversity.

Past studies of forestry effects on amphibians have focused on evaluating changes in amphibian abundance and diversity after clearcutting (Kroll, 2009). Generally, these studies have found reduced amphibian abundance and richness in clearcuts (reviewed in deMaynadier and Hunter, 1995; Tilghman et al., 2012). Such studies identify declines in abundance and richness that can result from forest harvesting but provide little insight into the processes that underlie such declines. Moreover, due to high inter-annual variation in amphibian abundance (Pechmann et al., 1991), it is often difficult to anticipate long-term consequences of forest harvesting on amphibian populations based solely on changes in abundance. Consequently, there is an increasing need to understand demographic responses of amphibians to forest harvesting. Population models have also found that post-metamorphic, terrestrial stages of amphibians typically have the greatest impact on population persistence compared with aquatic stages (Biek et al., 2002; Vonesh and De la Cruz, 2002). It is therefore important to determine how forest harvesting and other activities affect demographic processes such as survival or growth (i.e., vital rates; Todd and Rothermel, 2006). Understanding such demographic responses is an important step in improving forest management for amphibians and will also inform future modeling efforts aimed at understanding the long-term demographic consequences of forest alteration. There are currently few studies that provide estimates of vital rates in amphibians, especially in response to factors expected to alter survival or reproduction. Moreover, studies of forestry impacts on amphibians have typically focused on woodland salamanders (i.e., plethodontids), excluding a broad range of pond-breeding amphibians whose primary terrestrial habitat is forest.

The primary goal of our study was to examine the effects of forest harvesting on patterns of survival of ambystomatid salamanders in multiple regions of North America. We focused on the Northeast, Midwest, and Southeast, three economically important timber-producing regions with closely related amphibian species, but with widespread variation in other factors such as climate, topography, and land ownership, among others. By examining amphibian responses across multiple regions, our results should offer broad management applicability. We examined salamander survival using replicated field enclosures in forest habitats harvested at varying intensities, including unharvested controls, partially harvested forests (~25% canopy reduction), and clearcuts with coarse woody debris either retained or removed. Previous studies have shown at least short-term decreases in the abundance of many amphibians following forest harvesting, often simultaneously with increases in temperature and a loss of refuge that may be associated with lower survival of these species (deMaynadier and Hunter, 1995; Rothermel and Luhring, 2005; Tilghman et al., 2012). Thus, we predicted that salamanders would exhibit decreasing rates of survival as the degree of forest harvesting increased and conditions presumably became less favorable for many amphibians. Also, because body size in amphibians is often correlated with survival (Semlitsch et al., 1988), we predicted that larger animals would be more likely to survive and be recaptured irrespective of treatment.

2. Methods

2.1. Study sites

We conducted our study in three regions of the United States, the Northeast, the Midwest, and the Southeast (Table 1), as part of the LEAP study (Semlitsch et al., 2009). Our study site in the Northeast was located in the University of Maine Demeritt and Penobscot Experimental Forests, Penobscot County, Maine. The forests were predominately mixed coniferous-deciduous forests with dominant tree species of balsam fir (*Abies balsamea*), eastern white pine (*Pinus strobus*), northern white cedar (*Thuja occidentalis*), red maple (*Acer rubrum*), eastern hemlock (*Tsuga canadensis*), red oak (*Quercus rubra*), and paper birch (*Betula papyrifera*). Understory included American beech (*Fagus grandifolia*), bigtooth aspen (*Populus grandidentata*), quaking aspen (*P. tremuloides*), and balsam poplar (*P. balsamifera*) (see also Patrick et al., 2006).

Our study site in the Midwest was located in the Daniel Boone Conservation Area, Warren County, Missouri. The Daniel Boone Conservation Area is a 1424 ha oak-hickory forest managed by the Missouri Department of Conservation. The canopy is dominated by second-growth oak (*Quercus spp.*) and hickory (*Carya spp.*) and the understory was predominantly sugar maple (*Acer saccharum*) (see also Semlitsch et al., 2008).

Our study site in the Southeast was located on the Department of Energy's Savannah River Site (SRS) in Barnwell County, South Carolina. The Savannah River Site is a 770 km^2 restricted-access site with forests managed by the US Forest Service – Savannah River. The areas used in this study were composed of second-growth planted loblolly pine (*Pinus taeda*) with a few interspersed, naturally-occurring hardwoods (oaks [*Quercus* spp.], red maple [*Acer rubrum*], hickories [*Carya* spp.], dogwood [*Cornus florida*], and sweetgum [*Liquidambar styraciflua*]). Understory consisted of sweetgum (*Liquidambar styraciflua*), wax myrtle (*Morella cerifera*), and holly (*Ilex opaca*) (see also Rothermel and Luhring, 2005; Todd and Rothermel, 2006).

2.2. Experimental arrays

In each of the three regions, we centered replicated circular experimental arrays on four separate, isolated seasonal wetlands (Northeast and Southeast) or 40+ year old wildlife ponds (Midwest) that serve as reproduction sites for local amphibians. The experimental arrays extended 165 m from the wetland edges. We divided each circular array into four quadrants via two perpendicular transects that intersected at the center of each wetland (e.g., Todd et al., 2009). Each quadrant was randomized to receive one of four of the following treatments with the stipulation that clearcut plots were always opposite from each other. The four treatments included: an unharvested control (>30 years old, hereafter 'control'); a partially harvested stand in which the canopy was thinned by approximately 25% (hereafter 'partial'); a clearcut with coarse woody debris retained (hereafter 'CC-retained'); and a clearcut with coarse woody debris removed (hereafter 'CC-removed'). Not all coarse woody debris (CWD) could be removed in the Northeast, but enough was removed to make CWD comparatively lower in the CC-removed than in CC-retained (13.8 m^3 per ha versus 55.2 m^3 per ha; Table 2). Logging was completed in 2004 in all regions. We did not perform any subsequent site manipulation such as replanting, harrowing, burning, or biocide application after harvesting.

Our treatments were chosen and applied in close consultation with site foresters and the applicable forest stewards. The treatments were designed to encompass a range of practices represented by forest harvesting methods in North America, which

Table 1

Summary of the locations and details of the study design in each region. 'Control' denotes unharvested control treatment, 'partial' denotes partially harvested treatment, 'CC-retained' denotes clearcut with coarse woody debris retained, and 'CC-removed' denotes clearcut with coarse woody debris removed.

	Northeast	Midwest	Southeast
Location	Penobscot Co., ME	Warren Co., MO	Barnwell Co., SC
Enclosure material	Steel hardware cloth	Steel hardware cloth	Aluminum flashing
Enclosure size	14.5 m^2	9 m^2	16 m^2
Juvenile study species	*A. maculatum*	*A. maculatum*	*A. opacum*
Juvenile stocking density	1.72 per m^2	2 per m^2	1.8 per m^2
Juvenile mean snout-to-vent length	22.9 mm	30.1 mm	38.4 mm
Juvenile release date	August 2005	June 2006	May 2005
Juvenile end date	June 2006	June 2007	December 2005
Number of sites used	4	4	4
Treatments	Control, Partial, CC-retained, CC-removed	Control, CC-removed	Control, Partial, CC-retained, CC-removed
Replicates per treatment	8	4	8
Adult study species	Not tested	*A. maculatum*	*A. opacum*
Adult stocking density	Not tested	0.6 per m^2	1 per m^2
Adult mean snout-to-vent length	Not tested	89.3 mm	58.1 mm
Adult release date	Not tested	April 2006	January 2006
Adult end date	Not tested	June 2007	November 2006
Number of sites used	Not tested	2	4
Treatments	Not tested	Control, Partial, CC-retained, CC-removed	Control, Partial, CC-removed
Replicates per treatment	Not tested	2	3

Table 2

Summary of post-harvesting mean habitat characteristics (±1 SE) at the start of the study in 2005–2006 inside the terrestrial enclosures from each treatment in Maine (Northeast), Missouri (Midwest), and the South Carolina (Southeast). 'Control' denotes unharvested control treatment, 'partial' denotes partially harvested treatment, 'CC-retained' denotes clearcut with coarse woody debris retained, and 'CC-removed' denotes clearcut with coarse woody debris removed.

	Northeast			
	Control	Partial	CC-retained	CC-removed
Mean canopy density (%)	70.6 (7.2)	49.1 (8.4)	0 (0)	0 (0)
Mean litter depth (cm)	6.0 (1.5)	9.3 (2.2)	3.9 (1.5)	1.8 (0.6)
Mean volume of coarse woody debris (m^3 per ha)	20.7 (5.1)	34.5 (6.2)	55.2 (7.1)	13.8 (4.9)
	Midwest			
	Control	Partial	CC-retained	CC-removed
Mean canopy density (%)	89.5 (2.4)	83.9 (8.3)	4.4 (1.3)	2.7 (1.3)
Mean litter depth (cm)	1.3 (0.3)	0.2 (0.1)	2.1 (0.8)	1.4 (0.4)
Mean volume of coarse woody debris (m^3 per ha)	44.4 (6.9)	100.0 (8.8)	177.8 (12.2)	0 (0)
	Southeast			
	Control	Partial	CC-retained	CC-removed
Mean canopy density (%)	91.0 (2.3)	80.1 (2.3)	10.9 (2.5)	11.7 (2.6)
Mean litter depth (cm)	4.8 (0.3)	3.0 (0.2)	3.0 (0.2)	2.4 (0.2)
Mean volume of coarse woody debris (m^3 per ha)	35.3 (9.3)	44.2 (7.2)	61.8 (10.1)	12.5 (6.5)

vary depending on region and land ownership, among other factors. The partial harvest treatment was designed to be representative of the types of incomplete canopy reduction represented in many different regional management methods such as group selection, single tree selection, and pre-commercial or commercial thinning that reduces forest stand density (USDA, 2005). Our clearcut treatment with retained coarse woody debris was meant to be representative of the types of clearcuts often prescribed as best management practices by forest councils and some state conservation programs. For example, the Forest Stewardship Council prescribes as part of its certification program that ecological functions should be maintained, including retaining well-distributed coarse down and dead woody material during harvesting (FCS-US Forest Management Standard v1.0 2010). Both the Missouri Department of Conservation and the Maine Forest Service similarly counsel against removing all CWD and instead recommend retaining well-distributed dead wood on the site as part of their best management practices (Missouri Woody Biomass Harvesting: Best Management Practices Manual 2008; A Review of Biomass harvesting Best Management Guidelines – North East Foresters Association 2012). In contrast, South Carolina makes no specific recommendations about retaining CWD for biodiversity in its

best management practices (http://www.state.sc.us/forest/refbmp. htm accessed October 25, 2013). None of the three states in question have regulations requiring retention of CWD beyond consideration of possible impacts to stream and water quality. Thus, our CC-retained treatment here is intended to be both representative of some best management practices and to test for beneficial effects of CWD retention for amphibians (deMaynadier and Hunter, 1995; Herbeck and Larsen, 1999; Otto et al., 2013). Our clearcut treatment with no intentionally retained CWD is representative of whole-tree harvesting that does not meet best management practices and may also represent complete biomass harvest in instances where as much biomass is removed as possible, such as for use in cellulosic ethanol production, or where landowners may choose not to follow best management practices. The removal of all CWD after clearcutting leaves a landscape similar to that left after forest clearing in preparation for conversion to other land use and was intended to represent a 'worst-case' scenario of forest clearing in our study. We acknowledge that in many partial harvesting applications there will be multiple stand entries over time and our study only included stand entries at the beginning of the study. Further, many harvesting regimes will use herbicide application, managed fires, and replanting or harrowing as additional

site preparation or stand management. However, our study was intended to test the effects of the fundamental stand structure changes on amphibian survival and did not include these additional site management applications or temporal components that may also affect amphibian survival.

2.3. Terrestrial enclosures

We constructed enclosures in each treatment at each site after logging was completed. To avoid trampling vegetation and compacting soil within the enclosures, we worked on enclosures from the outside during installation. Enclosure designs were similar among regions; however, they varied slightly by region depending on the availability of construction materials and institutional restrictions. All enclosures were square in shape, were buried ∼30 cm into the soil to prevent escape by burrowing, and were flanged at the top or made of material that would eliminate climbing and escape by animals contained within (e.g., Pechmann, 1995; Chazal and Niewiarowski, 1998; Rothermel and Semlitsch, 2006; Harper et al., 2010). Minor differences among regions in our study underscore the broader applicability of findings. Details of the enclosure designs in our three regions can be found in Table 1.

Enclosures in the Northeast were constructed of galvanized steel hardware cloth (3.2 mm square mesh; TWP Inc., Berkeley, California) supported with wooden garden stakes. The enclosures were buried 40 cm deep and stood 80 cm tall. Enclosures in the Midwest were constructed similarly, but of slightly smaller dimensions (Table 1). Enclosures in the Southeast were made of aluminum flashing and were buried 30 cm deep and stood 65 cm tall. We buried metal coffee can pitfall traps (15.5 cm diameter by 17 cm height) in each corner of all enclosures and midway along the interior of each wall at all regions and left them closed when not sampling occupants.

We measured canopy density at enclosures using hemispherical photographs in the Northeast (Nikon Coolpix 995 digital camera with FC-E8 fisheye converter lens on a 35-cm tripod) combined with the Gap Light Analyzer program (Version 2.0, Simon Fraser University, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York) or by using a hemispherical densiometer in the Midwest and Southeast. We measured litter depth to the nearest cm to the top of the duff layer (the Oi horizon) at 5 random points inside each enclosure and calculated a mean for each enclosure. Finally, we made sure that the volume of CWD was comparable inside each enclosure relative to the overall treatment where it was located (unpublished data). The resulting enclosure habitat characteristics are summarized in Table 2.

2.4. Terrestrial amphibian survival

In each region, we acquired terrestrial animals primarily from local wild populations. However, where local populations could not accommodate removal, we raised animals to metamorphosis in cattle tanks from eggs collected at breeding ponds. We kept methods similar among the three regions. However, there was some variation in methodology among regions due to logistic constraints, the timing of rainfall (which facilitates amphibian movement and capture; Todd and Winne, 2006), the duration of above-ground amphibian activity that varies with latitude and onset of winter, and the availability of study animals. Nevertheless, differences among regions serve to underscore the broader applicability of our findings. Details on amphibian species, initial body sizes, and stocking densities are summarized in Table 1.

In the Northeast, recently metamorphosed spotted salamanders, *Ambystoma maculatum*, were obtained from both nearby ponds and cattle tanks in August 2005. We weighed, measured, and individually marked all juveniles with visible implant elasto-

mer. We randomly assigned groups of 25 juveniles to enclosures so that two enclosures in each of the four treatments at all four sites contained juvenile salamanders at a density of 1.72 per m². We conducted daily sampling of the enclosures for approximately three weeks in October 2005 and again in June 2006 when the study was terminated. Sampling periods included both clear and rainy nights and warm and cool temperatures, and were intended to coincide with maximal activity of the salamanders (i.e., encompassing typical migration or movement periods). We used two techniques to recapture animals within enclosures: we conducted active searching consisting of at least three 20-min, time-constrained searches every 5–7 days, and we checked pitfall traps daily during sampling. Upon capture, we identified each animal and measured their mass and snout-to-vent length (SVL) and immediately returned them to their enclosures except during the final sampling interval when animals were removed. Too few adults were available to study adult survival in the Northeast.

In the Midwest, we collected recently metamorphosed spotted salamanders, *A. maculatum*, as they emerged from natal ponds or cattle tanks in June 2006. We weighed, measured, and individually marked each salamander using visible implant elastomer. We randomly assigned groups of 18 juveniles to enclosures so that one enclosure in each control and each CC-removed treatment at all four sites contained juvenile salamanders at a density of 2 per m². The other two treatments were not used for juveniles at any of the sites due to a limited supply of juvenile salamanders and the desire to at least examine the two management extremes in our study. We captured post-reproductive adult female *A. maculatum* in pitfall traps as they emigrated from breeding ponds in April 2006 and we placed them in enclosures on their day of capture. Before releasing animals into enclosures, we weighed each salamander, measured its SVL, and photographed each animal to individually identify them at recapture since they can be identified by their unique spot patterns (e.g., Grant and Nanjappa, 2006). We randomly assigned groups of five females to enclosures (separate from those used in the juvenile study) so that one enclosure in each of the four treatments at two sites contained adult salamanders at a density of 0.55 per m². We opened pitfall traps in both juvenile and adult enclosures on nights when rain was expected for at least two consecutive nights. Traps were opened in juvenile enclosures on 3–6 August, 19–20 August, and 5–6 September 2006. Traps were opened in the enclosures containing the adult female salamanders on these same dates and earlier on 23–26 April 2006. We also actively searched leaf litter and beneath CWD to locate any additional animals when we checked pitfall traps. When animals were captured, they were individually identified, measured, weighed, and returned to their enclosures. In the spring we conducted continuous removal sampling of all enclosures from 17 April–25 June 2007.

In the Southeast, we collected recently metamorphosed marbled salamanders, *A. opacum*, as they emerged from a nearby natal wetland in May 2005. We individually marked all animals using an equal number of toe-clips and we recorded SVL and mass of each animal. We randomly assigned groups of 30 juvenile salamanders to enclosures so that two enclosures in each of the four treatments at all four sites contained juvenile salamanders at a density of 1.8 per m². We released animals into enclosures on rainy nights in May 2005. We opened pitfall traps and captured animals in enclosures for 3–6 day periods during rainfall in June and August 2005, releasing them after handling. From November to December 2005, we sampled enclosures with open pitfall traps for 25 continuous days to remove all animals. We also searched leaf litter and cover objects by hand at that time to recover any additional uncaptured salamanders. In January 2006, we collected post-reproductive adult marbled salamanders as they emigrated from a breeding pond located near our study sites. We again individually marked all

animals using an equal number of toe-clips and we recorded SVL and mass of each animal. We randomly assigned groups of 16 adults to enclosures (separate from those used in the juvenile study) so that one enclosure in a control, a partial, and a CC-removed at three sites contained adult salamanders at a density of 1 per m². We released animals into enclosures at night following rain in January 2006. We opened pitfall traps and captured animals in enclosures for 3–6 day periods during rainfall in April, May, and July 2006. Animals were identified, measured, weighed, and released under moist cover in the interior of the enclosure the following morning. In November 2006, we sampled the enclosures continuously with open pitfall traps for 20 days and removed all animals captured. We also searched leaf litter and cover objects by hand to recover any additional uncaptured salamanders.

Densities of salamanders in the enclosures reflected a tradeoff in the availability of study animals with the desire to have sufficient individuals from which to make inferences about treatment effects. Densities were intended to remain with 0.5 individuals per m² across the regions for a given age class. Juveniles were stocked at greater densities than adults because we expected them to have lower survival and wanted to ensure some chance of recovering individuals for treatment comparisons. There are no data available on actual densities of ambystomatid salamanders in the wild but previous studies have used densities that varied from 0.28 to 10.76 individuals per m² in enclosures (see Table 12.1 in Harper et al., 2010). We kept our densities toward the lower end of this spectrum where Harper and Semlitsch (2007) found little evidence for density dependent survival or growth in two amphibians over 1 year.

2.5. Data analysis

In general, very few individuals were captured at later intervals that had been missed during previous sampling (<3%). Also, animals that were captured once were likely to be captured again. However, recapture rates tended to be low overall (<20%). We had trouble obtaining model convergence in Program MARK when treating each replicate enclosure as an independent population, presumably because starting populations were small in each enclosure (5–30 animals) and recapture rates insufficiently low. In model iterations where we combined all encounters within a treatment, age class, and region, we were able to obtain model convergence. Model selection processes identified unequivocal support for treatment effects in the same cases where the analyses below also identified significant treatment effects. Moreover, in the only instance where model selection unambiguously supported different detectability among treatments (juveniles in the Southeast), the models estimated slightly higher detection probabilities (and lower survival) in clearcuts than in forested treatments. However, given that combining encounter histories of all individuals within treatments ignored replication, spatial stratification, and the randomized block design of treatments, we felt these analyses were less statistically defensible and we opted instead to use the minimum number of salamanders known alive (MKNA) at each census for statistical analyses. We calculated MKNA during each census by reading individual marks of captured animals. This allowed us to determine whether any animals captured in later censuses had been missed in previous censuses so that the MNKA in previous censuses could be adjusted upward if necessary (e.g., Rothermel and Semlitsch, 2006; Todd and Rothermel, 2006). We discuss possible limitations of the use of MNKA as a proxy for survival in the Discussion section but we reiterate here that results from MNKA analyses were supported by the combined mark-recapture analyses that do account for potential variation in detectability.

To test for effects of treatment on survival, we used a repeated measures multivariate analyses of variance (MANOVA) with MKNA at initial release and each subsequent census as a repeated measure in a profile analysis General Linear Model (Scheiner and Gurevitch, 2001). Because MNKA were count data, we square-root transformed them to normalize data prior to analysis. We performed separate analyses for juveniles, for adults, and for each region, testing within regions and age classes for effects of harvest treatment on survival to the first fall (all regions) or next spring (Northeast and Midwest only). In cases where multiple enclosures were in the same physical treatment at a study site (i.e., where we had two enclosures in a treatment at the same site in a region), we accounted for nestedness in the model structure to avoid errors of pseudoreplication by blocking nested pens by site within a treatment (Hurlbert, 1984). Because there was no variance in the initial release interval (that is, all populations had the same known MNKA in the first interval in a given MANOVA), this violated an assumption of normality. However, this violation should only be problematic for interpretations of time effects or interactions of forest treatment with time (Scheiner and Gurevitch, 2001), both of which were not responses of primary interest compared with our predominant interest in the effect of treatment (forest management practice) on survival. Because each region and age class represented an independent test, we used Fisher's combined probability test and Stouffer's weighted Z-method to combine P-values and test the overall null hypothesis that forest treatment had no effect on survival of ambystomatid salamanders (Whitlock, 2005).

We used logistic regression to determine whether initial SVL or relative mass of salamanders affected the likelihood of recapture during the course of the study, irrespective of treatment or enclosure. Relative mass was calculated as $[(mass/SVL^3) \times 10{,}000]$ and regressions were run separately for age classes (juvenile or adult) and regions to test for effects of body size (SVL) and relative mass separately. Animals that were never recaptured were scored as a '0' and animals that were recaptured at least once during the study were scored as '1'. We ran additional logistic regressions for the Northeast and Midwest to determine whether body size or relative mass affected likelihood of survival over winter.

3. Results

3.1. Effects of forest harvesting treatment on minimum number known alive

The minimum number of juvenile salamanders known alive declined rapidly in all regions and treatments (P-values < 0.001; Table 3). The mean number of juveniles known alive by the first fall differed significantly among treatments in the Northeast and Southeast (Northeast: $F_{3,25} = 7.2$, $P = 0.001$; Southeast: $F_{3,25} = 3.6$, $P = 0.03$; Table 3). We found a similar pattern, but no significant effect, in the Midwest where fewer treatments and replicates were used ($F_{1,3} = 1.9$, $P = 0.26$; Table 3). By fall, survival was typically greatest in controls, lower in the partials, and lowest in the two clearcuts (Table 3). There was a significant time-by-treatment interaction in the Northeast ($F_{3,25} = 7.2$, $P = 0.001$), but not in the Midwest ($F_{3,9} = 0.8$, $P = 0.51$) or the Southeast ($F_{9,75} = 1.6$, $P = 0.12$).

The mean number of juveniles known alive after winter (Northeast and Midwest only) differed significantly among harvesting treatments in the Northeast ($F_{3,25} = 5.9$; $P = 0.003$), with survival being greatest in controls, lower in the partials, and lowest in the two clearcuts (Table 3). In the Midwest, there was no significant effect of treatment on survival over winter ($F_{1,3} = 3.3$; $P = 0.17$). There was a significant time-by-treatment interaction in the Northeast ($F_{6,50} = 3.0$, $P = 0.01$), but not in the Midwest ($F_{4,12} = 0.5$, $P = 0.71$).

Table 3
Proportion of minimum number known alive (MNKA) for each species and age class in Maine (Northeast), Missouri (Midwest), and the South Carolina (Southeast) and P-values from statistical tests of treatment and treatment-by-time interactions. Means are listed with 95% confidence intervals shown parenthetically. Bold values denote significant effects at the $\alpha = 0.05$ level. 'Control' denotes unharvested control treatment, 'partial' denotes partially harvested treatment, 'CC-retained' denotes clearcut with coarse woody debris retained, and 'CC-removed' denotes clearcut with coarse woody debris removed.

Region	Species	Age class	Proportion MNKA in fall in each forest treatment – mean (95% CI)				Treatment effect	Time-by-treatment interaction
			Control	Partial	CC-retained	CC-removed		
Northeast	A. maculatum	Juvenile	0.49 (0.38–0.59)	0.41 (0.32–0.49)	0.23 (0.12–0.33)	0.27 (0.21–0.32)	**0.001**	**0.001**
Midwest	A. maculatum	Juvenile	0.17 (0.13–0.21)	Not tested	Not tested	0.10 (0.07–0.13)	0.26	0.51
Southeast	A. opacum	Juvenile	0.07 (0.00–0.14)	0 (0.00–0.00)	0.01 (0.00–0.02)	0 (0.00–0.00)	**0.03**	0.12
Midwest	A. maculatum	Adult	0.5 (0.08–0.92)	0.6 (0.60–0.60)	0.2 (0.20–0.20)	0.2 (−0.08-0.48)	0.07	0.46
Southeast	A. opacum	Adult	0.19 (0.06–0.31)	0.23 (−0.05–0.51)	Not tested	0 (0.00–0.00)	**0.02**	0.36
			Proportion MNKA next spring in each forest treatment – mean (95% CI)					
Northeast	A. maculatum	Juvenile	0.05 (−0.03–0.13)	0.02 (−0.01–0.05)	0 (0.00–0.00)	0.02 (−0.01–0.04)	**0.003**	**0.01**
Midwest	A. maculatum	Juvenile	0.11 (0.09–0.13)	Not tested	Not tested	0.07 (0.03–0.11)	0.17	0.71
Midwest	A. maculatum	Adult	0.3 (0.16–0.44)	0.6 (0.60–0.60)	0.2 (0.20–0.20)	0 (0.00–0.00)	**0.02**	0.08

Table 4
Results of logistic regressions testing effect of snout-to-vent length (SVL) or body condition index (BCI) on likelihood of recapture during the study in Maine (Northeast), Missouri (Midwest), and South Carolina (Southeast). Odds ratios are presented with 95% confidence intervals shown parenthetically. Bold values denote significant effects at the $\alpha = 0.05$ level.

Region	Species	Age class	Odds ratio for likelihood of recapture by first fall			
			SVL	P-value	BCI	P-value
Northeast	A. maculatum	Juvenile	1.08 (1.01–1.15)	**0.02**	1.00 (0.99–1.02)	0.29
Midwest	A. maculatum	Juvenile	1.05 (0.89–1.24)	0.57	1.03 (0.95–1.11)	0.50
Southeast	A. opacum	Juvenile	1.16 (1.07–1.27)	**<0.001**	1.08 (1.01–1.16)	**0.04**
Midwest	A. maculatum	Adult	1.15 (0.97–1.36)	0.08	0.84 (0.59–1.21)	0.34
Southeast	A. opacum	Adult	1.07 (0.96–1.18)	0.21	1.05 (1.02–1.07)	**<0.001**
			Odds ratio for likelihood of recapture by next spring			
			SVL	P-value	BCI	P-value
Northeast	A. maculatum	Juvenile	1.14 (0.95–1.39)	0.19	0.98 (0.93–1.03)	0.41
Midwest	A. maculatum	Juvenile	0.94 (0.73–1.22)	0.63	1.10 (0.98–1.24)	0.09
Midwest	A. maculatum	Adult	0.98 (0.83–1.14)	0.76	1.10 (0.76–1.60)	0.61

Adult salamanders (Midwest and Southeast only) had survivorship curves superficially similar to those of juveniles, with a significant time effect on the number known alive in both regions (P-values < 0.001). However, adult survivorship was greater overall than that of juveniles and plateaued earlier. Although there was a trend toward lower survivorship in clearcut treatments, there was no significant effect of harvest treatment on the mean number of adults known alive to the first fall in the Midwest ($F_{3,3} = 7.3$, $P = 0.07$; Table 3) and no significant time-by-treatment interaction ($F_{6,6} = 1.1$, $P = 0.46$; Table 3). However, there was a significant effect in the Midwest through overwintering ($F_{3,3} = 17.6$, $P = 0.02$; Table 3), but no significant time-by-treatment interaction ($F_{9,9} = 2.7$, $P = 0.08$; Table 3). In the Southeast, the mean number of adults known alive in enclosures in the first fall also differed significantly among forest harvesting treatments ($F_{2,4} = 11.3$; $P = 0.02$; Table 3), but there was no significant time-by-treatment interaction ($F_{8,16} = 1.2$, $P = 0.36$; Table 3). Adult survival in the Southeast was similar in the control and partial treatments, but lower in the CC-removed (Table 3).

Overall, the weight of evidence indicated that forest treatment had a significant effect on survival to the first fall from the five combined tests using both Fisher's combined probability (P < 0.0001) and Stouffer's weighted Z-method (P < 0.0001). Similarly, the weight of evidence indicated that forest treatment had a significant effect on survival to the next spring from the three combined tests using both Fisher's combined probability (P = 0.0009) and Stouffer's weighted Z-method (P = 0.0007). In all cases, survival of ambystomatid salamanders was lowest in the CC-removed and CC-retained treatments compared to the controls and partial harvests.

3.2. Effects of initial body size on likelihood of recapture

The likelihood of recapturing a juvenile salamander at least once during the study was significantly correlated with its initial SVL in the Northeast ($\chi^2 = 5.8$, df = 1, $P = 0.02$) and Southeast (SVL: $\chi^2 = 10.9$, df = 1, $P < 0.001$) but not in the Midwest ($\chi^2 = 0.3$, df = 1, $P = 0.57$; Table 4). A 1 mm increase in initial SVL increased the odds of a juvenile being recaptured alive by 8% and 16% in the Northeast and Southeast respectively. Relatively heavier juveniles were more likely to be recaptured alive at some point in the Southeast ($\chi^2 = 4.4$, df = 1, $P = 0.03$), but there was no effect in the other two regions (P-values > 0.2; Table 4). Neither SVL nor relative mass of juveniles was correlated with recapture after winter in the Northeast or Midwest (P-values $\geqslant$ 0.1; Table 4).

Among adults, there was no significant effect of SVL on the likelihood of recapture in either the Midwest ($\chi^2 = 3.0$, df = 1, $P = 0.08$; Table 4) or Southeast ($\chi^2 = 1.6$, df = 1, $P = 0.21$; Table 4). There was no significant effect of relative mass of adults on recapture likelihood in the Midwest ($\chi^2 = 0.9$, df = 1, $P = 0.34$; Table 4). However, in the Southeast, relatively heavier individuals were more likely to be recaptured alive at some point ($\chi^2 = 12.1$, df = 1, $P < 0.001$; Table 4). Neither initial size nor relative mass of adults was correlated with recapture after winter in the Midwest (P-values > 0.6; Table 4).

4. Discussion

Recent estimates indicate that about 1% of North America's forests are harvested or deforested each year (Masek et al., 2011). This represents a potentially sizable change in habitat for many forest-dependent species such as amphibians, a group that is both highly-imperiled and often forest-dependent for at least a part of their lives (Stuart et al., 2004). For this reason, there has been increased interest in finding ways to minimize the impacts of extractive forestry practices on biodiversity while supporting timber production. Studies that provide insights into the processes or mechanisms that underlie biodiversity declines following forest harvesting are especially helpful for refining forest management practices or for better understanding the consequences of current practices (Todd and Rothermel, 2006). The results of our study demonstrate that clearcutting negatively affects survival of the terrestrial stages of pond-breeding salamanders, but that some types of forest harvesting are compatible with amphibian survival during at least some portions of these species' life stages.

Forest harvesting practices vary across North America, but often include either complete harvesting (i.e., clearcutting) or partial harvesting, where intact canopy remains and only a proportion of timber is felled from a stand (Smith et al., 2009). In the US, approximately 40% of forest harvesting occurs via clearcutting, whereas much of the remainder is harvested via partial harvesting (Smith et al., 2009). In all three of our study regions, clearcutting had comparable negative impacts on the survival of the terrestrial stages of pond-breeding salamanders compared with survival in unharvested control forest plots. Because partial harvesting does not increase temperatures or reduce canopy to the degree that clearcutting does (Todd and Andrews, 2008), it has been proposed to be a more benign practice to minimize negative impacts to amphibians (deMaynadier and Hunter, 1995). Although temperatures may still rise as much as 2–5 °C in partially harvested stands relative to unharvested forests, some canopy structure and shade is retained and leaf litter is not completely removed (Todd and Andrews, 2008; Homyack et al., 2011). Similarly, retaining ∼50% canopy cover can result in winter low temperatures similar to those in unharvested forests (Boggs and McNulty, 2010). In a mark-recapture experiment at our Midwest experimental array, Osbourn (2012) reported the most recaptures of juvenile *A. maculatum* in the partially harvested treatment. Nevertheless, our results do not support the notion that partially harvested treatments benefit juvenile salamanders compared with clearcuts. However, survival of adults in partially harvested treatments was comparable to or exceeded that of adults in unharvested controls in the Midwest and Southeast. Also, the retention of some canopy cover in partially harvested stands appeared to mitigate at least partly some of the decreased survival over winter for both adults and juveniles. Our adult salamander survival results are consistent with the general trend observed in other studies at our experimental arrays, which indicate fewer negative effects and some positive short-term responses to partially harvested forests (Semlitsch et al., 2009). Ultimately, because less timber is derived from partial harvesting than from clearcutting, greater acreage must be disturbed to produce equivalent amounts of timber. Whether amphibian populations can withstand decreased juvenile survival in favor of increased adult survival could be investigated in the future using stage-based projection models that examine the sustainability of partial harvesting by altering parameters of each stage accordingly (e.g., Biek et al., 2002).

Most previous studies of the effects of forest harvesting on amphibians have examined changes in abundance or diversity in response to forestry practices (Ash and Bruce, 1994; deMaynadier and Hunter, 1995; Semlitsch et al., 2008). There are fewer studies

of the potential mechanisms that give rise to these changes, and several non-competing mechanisms may explain reductions in post-harvesting amphibian abundance and diversity, such as emigration from cleared forests, loss of breeding wetlands and failed recruitment, behavioral changes, or demographic changes. Whereas Knapp et al. (2003) found no significant effects of harvesting on the demography of terrestrial plethodontid salamanders, Homyack and Haas (2009) found that juveniles were more abundant in unharvested treatments. The results of Homyack and Haas (2009) suggest that lower adult survival and fecundity, or lower juvenile recruitment, may explain the lack of juveniles in harvested areas. Additionally, Peterman et al. (2011) and Semlitsch et al. (2008) both reported higher levels of emigration away from harvested forests by resident amphibians. Our study was designed to prevent emigration using enclosures to examine in isolation the degree to which survival is affected by forest harvesting, especially given that terrestrial survival can have the greatest consequences for population persistence in amphibians (Biek et al., 2002; Willson et al., 2012). Increased mortality reduces the regenerative capacity of a population by eliminating current (via adult mortality) and future (via juvenile mortality) reproductive output. Thus, our results identify some cause for concern over the effects of elevated mortality in the short-term after forest harvesting.

Amphibian mortality likely increases in harvested forests for several reasons. Harvested forests generally have elevated temperatures, greater rates of evaporative water loss, and less litter and coarse woody debris under which ground-dwelling fauna can find refuge (Zheng et al., 2000; Todd and Andrews, 2008). This in turn can lead to increased rates of body water loss in small vertebrates, a factor critical to many forest-dwelling salamanders (Spotila, 1972). For example, rates of body water loss in ambystomatid salamanders are significantly greater in harvested treatments than in unharvested controls, a factor that can lead to mortality in just days in clearcuts (Rothermel and Luhring, 2005; Todd et al., 2008). This is supported by the lower survival of juveniles than adults in the present study, given the greater surface area to volume ratios of juveniles and their greater rates of water loss than adults (Jørgensen, 1997). The idea that water loss affects salamander survival after forest harvesting is also supported by our finding that larger juveniles were more likely to be recaptured alive than were smaller individuals in two of the three forest regions. Size at metamorphosis is an important trait that is thought to be linked to survival to first reproduction and reproductive success in many pond-breeding amphibians (Semlitsch et al., 1988; Wilbur, 1980, 1997). Given the disparity in size between juveniles and adults, all else being equal, this factor may also partly explain lower survival of juveniles.

Because CWD serves as refuge to amphibians and can quickly ameliorate forest floor temperature increases in clearcuts (Homyack et al., 2011), it has been suggested as an important mitigating resource in harvested forests (deMaynadier and Hunter, 1995). We expected clearcuts with retained CWD to have greater salamander survival than those without it. Contrary to our expectations, there appeared to be only marginal benefit of CWD to survival of ambystomatid salamanders. Adult salamanders in the Midwest fared slightly better with CWD retained in clearcuts, but this trend did not extend to other age classes or regions. It is likely that CWD retention would be of greater benefit to woodland plethodontid salamanders, which do not rely on burrows to the degree that ambystomatids do, and which may therefore be more inclined to use CWD as refuge (Herbeck and Larsen, 1999). The utility of CWD retention for other amphibians remains an important area for future research (Otto et al., 2013).

In the present study, we used minimum number known alive as a proxy for survival. This carries with it the implicit assumption

that recapture probability (i.e., detectability) of salamanders does not vary among the various forest treatments and that recaptures reflect survival among treatments without systemic bias. Some authors have pointed out the importance of incorporating estimates of detectability into studies of amphibian responses to forest harvesting in order to differentiate true numerical decreases from simple behavioral changes (i.e., retreat from the surface) in study populations (e.g., Kroll, 2009). The size of our enclosures and the combination of active sampling and pitfall trapping should have contributed to high detections of live salamanders in our study in all treatments. Additionally, our pitfall trapping took place on rainy nights, which are conducive to surface activity of salamanders and which should have minimized any bias among the treatments in capture rates (Todd and Winne, 2006). Furthermore, previous studies have identified that clearcut habitats lead to greater movement and higher detection probabilities of ambystomatid salamanders in harvested plots. For example, Osbourn (2012) found that two ambystomatid species were less likely to settle in clearcut habitat compared to a closed canopy control and were caught more frequently after release into clearcuts. Similarly, Moseley et al. (2004) found in South Carolina that ambystomatid salamanders placed into enclosures similar to ours moved more frequently, for longer periods, and had greater surface activity when litter was removed. Based on this evidence, we would have expected that captures of salamanders in the CC-removed treatments should have been greater than those in other treatments where more litter was present, the opposite of what we found. Finally, we are encouraged that the mark-recapture models on combined encounter histories within treatments found congruent results with our MNKA analyses, as discussed in the Methods, because mark-recapture models do account for potential variation in detectability.

5. Conclusions

A primary strength of our study lies in the demonstration of similar forest harvesting effects on salamander survival across two species and age groups and in three regions. In general, we identified that for both juvenile and adult ambystomatid salamanders, clearcutting greatly reduced survival compared to that of salamanders in unharvested stands. Negative effects from partial harvesting were limited to juveniles in our study; adults fared equally well or better in partially harvested stands compared to unharvested stands. Given that nearly half of all clearcuts in the US are replanted and face additional soil and litter disturbance from site preparation (Masek et al., 2011), our results may under-represent the true extent to which terrestrial survival of amphibians is reduced in harvested forests in the short-term. However, replanting or rapid stand regeneration may limit the duration of any negative effects. The loss of amphibians from mortality carries with it greater negative implications for long-term persistence of populations than does emigration or underground retreat of amphibians from harvested forests due to the loss of future reproductive potential and reduced ability of local populations to quickly rebound.

One key recommendation for forest management emerges from the results of our study. In areas where rare or protected amphibians occur or where managers wish to otherwise maintain amphibian biodiversity, harvesting of upland forests, especially clearcutting, should be avoided close to breeding ponds. Previous studies have outlined recommendations for the distance at which core terrestrial habitat around breeding ponds should be maintained in order to preserve habitat (e.g., Semlitsch and Bodie, 2003; Rittenhouse and Semlitsch, 2007), and our study indicates that even partial harvesting may pose challenges to juvenile

amphibian survival in this core habitat. A similar, but more challenging strategy to implement could be to harvest just a portion of forest surrounding a breeding pond so that habitat is left intact around the remainder. Essential to success of such a strategy is a spatially explicit knowledge of dominant dispersal patterns of adults and juveniles from the breeding pond. Depending on local landscape features and the size of local populations, it is possible that long-term population viability may still be affected by removal of forest from even portions of habitat around wetlands.

References

Alford, R.A., Richards, S.J., 1999. Global amphibian declines: a problem in applied ecology. Annu. Rev. Ecol. Syst. 30, 133–165.
Ash, A.N., Bruce, R.C., 1994. Impacts of timber harvesting on salamanders. Conserv. Biol. 8, 300–301.
Biek, R., Funk, W.C., Maxell, B.A., Mills, L.S., 2002. What is missing in amphibian decline research: insights from ecological sensitivity analysis. Conserv. Biol. 16, 728–734.
Bielby, J., Cooper, N., Cunningham, A.A., Garner, T.W.J., Purvis, A., 2008. Predicting susceptibility to future declines in the world's frogs. Conserv. Lett. 1, 82–90.
Boggs, J.L., McNulty, S.G., 2010. Changes in canopy cover alter surface, air, and forest floor temperature in a high-elevation red spruce (*Picea rubens Sarg.*) forest. Pp. 13–21 In: Rentch, J.S., Schuler, T.M. (Eds.), Proceedings from the Conference on the Ecology and Management of High-Elevation Forests in the Central and Southern Appalachian Mountains. USDA Forest Service, GTR-P-NRS-64.
Burton, T.M., Likens, G.E., 1975. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia 1975, 541–546.
Chazal, A.C., Niewiarowski, P.H., 1998. Responses of mole salamanders to clearcutting: using field experiments in forest management. Ecol. Appl. 8, 1133–1143.
Clark, J.A., May, R.M., 2002. Taxonomic bias in conservation research. Science 297, 191b–192b.
Coates, K.D., Burton, P.J., 1997. A gap-based approach for development of silvicultural systems to address ecosystem management. For. Ecol. Manage. 99, 337–354.
deMaynadier, P.G., Hunter Jr., M.L., 1995. The relationship between forest management and amphibian ecology: a review of North American literature. Environ. Rev. 3, 230–261.
Gardner, T.A., Ribeiro-Junior, M.A., Barlow, J.O.S., Avila-Pires, T.C.S., Hoogmoed, M.S., Peres, C.A., 2007. The value of primary, secondary, and plantation forests for a neotropical herpetofauna. Conserv. Biol. 21, 775–787.

Grant, E.H.C., Nanjappa, P., 2006. Observer bias study: individual identification of spotted salamanders (Ambystoma maculatum) using spot patterns with recommendations for an improved method. Herpetol. Rev. 37, 57–60.

Harper, E.B., Semlitsch, R.D., 2007. Density dependence in the terrestrial life history stage of two anurans. Oecologia 153, 879–889.

Harper, E.B., Pechmann, J.H.K., Petranka, J.W., 2010. Field enclosures and terrestrial cages. In: Dodd, C.K., Jr. (Ed.), Amphibian Ecology and Conservation. Oxford University Press, New York, pp. 203–226.

Hedrick, L.D., Hooper, R.G., Krusac, D.L., Dabney, J.M., 1998. Silvicultural systems and red-cockaded woodpecker management: another perspective. Wildl. Soc. Bull. 26 (1), 138–147.

Herbeck, L.A., Larsen, D.R., 1999. Plethodontid salamander response to silvicultural practices in Missouri Ozark forests. Conserv. Biol. 13, 623–632.

Homyack, J.A., Haas, C.A., 2009. Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders. Biol. Conserv. 142, 110–121.

Homyack, J.A., Haas, C.A., Hopkins, W.A., 2011. Energetics of surface-active terrestrial salamanders in experimentally harvested forest. J. Wildl. Manage. 75, 1267–1278.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.

Jørgensen, C.B., 1997. 200 Years of amphibian water economy: from Robert Towson to the present. Biol. Rev. 72, 153–237.

Knapp, S.M., Haas, C.A., Harpole, D.N., Kirkpatrick, R.L., 2003. Initial effects of clearcutting and alternative silvicultural practices on terrestrial salamander abundance. Conserv. Biol. 17, 752–762.

Kroll, A.J., 2009. Sources of uncertainty in stream-associated amphibian ecology and responses to forest management in the Pacific Northwest, USA: a review. For. Ecol. Manage. 257, 1188–1199.

Lowrance, R., Altier, L.S., Newbold, J.D., Schnabel, R.R., Groffman, P.M., Denver, J.M., Correll, D.L., Gilliam, J.W., Robinson, J.L., Brinsfield, R.B., Staver, K.W., Lucas, W., Todd, A.H., 1997. Water quality functions of riparian forest buffers in Chesapeake Bay watersheds. Environ. Manage. 21, 687–712.

Mace, G., Masundire, H., Baillie, J., Ricketts, T., Brooks, T., Hoffman, M., 2005. Biodiversity. Chapter 4 in Millennium Ecosystem Assessment. Island Press, Washington, DC.

Masek, J.G., Cohen, W.B., Leckie, D., Wulder, M.A., Vargas, R., de Jong, B., Healey, S., Law, B., Birdsey, R., Houghton, R.A., Mildrexler, D., Goward, S., Smith, W.B., 2011. Recent rates of forest harvest and conversion in North America. Journal of Geophysical Research. Biogeosciences 116, G00K03.

Moseley, K.R., Castleberry, S.B., Ford, W.M., 2004. Coarse woody debris and pine litter manipulation effects on movement and microhabitat use of Ambystoma talpoideum in a Pinus taeda stand. For. Ecol. Manage. 191, 387–396.

Murray, K.A., Rosauer, D., McCallum, H., Skerratt, L.F., 2011. Integrating species traits with extrinsic threats: closing the gap between predicting and preventing species declines. Proc. R Soc. Biol. Sci. B 278, 1515–1523.

Osbourn, M.S., 2012. Initial juvenile movement of pond-breeding amphibians in altered forest habitats. Ph.D. dissertation. University of Missouri, Columbia, Missouri.

Otto, C.R.V., Kroll, A.J., McKenny, H.C., 2013. Amphibian response to downed wood retention in managed forests: a prospectus for future biomass harvest in North America. For. Ecol. Manage. 304, 275–285.

Patrick, D.A., Hunter, J.M.L., Calhoun, A.J.K., 2006. Effects of experimental forestry treatments on a Maine amphibian community. For. Ecol. Manage. 234, 323–332.

Pechmann, J.H.K., 1995. Use of large field enclosures to study the terrestrial ecology of pond-breeding amphibians. Herpetologica 51, 434–450.

Pechmann, J.H.K., Scott, D.E., Semlitsch, R.D., Caldwell, J.P., Vitt, L.J., Gibbons, J.W., 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. Science 253, 892–895.

Peterman, W.E., Crawford, J.A., Semlitsch, R.D., 2008. Productivity and significance of headwater streams: population structure and biomass of the black-bellied salamander (Desmognathus quadramaculatus). Freshwater Biol. 53, 347–357.

Peterman, W.E., Crawford, J.A., Semlitsch, R.D., 2011. Effects of even-aged timber harvest on stream salamanders: support for the evacuation hypothesis. For. Ecol. Manage. 262, 2344–2353.

Rittenhouse, T.A.G., Semlitsch, R.D., 2007. Distribution of amphibians in terrestrial habitat surrounding wetlands. Wetlands 27, 153–161.

Rothermel, B.B., Luhring, T.M., 2005. Burrow availability and desiccation risk of mole salamanders (Ambystoma talpoideum) in harvested versus unharvested forest stands. J. Herpetol. 39, 619–626.

Rothermel, B.B., Semlitsch, R.D., 2006. Consequences of forest fragmentation for juvenile survival in spotted (Ambystoma maculatum) and marbled (Ambystoma opacum) salamanders. Can. J. Zool. 84, 797–807.

Scheiner, S.M., Gurevitch, J., 2001. Design and Analysis of Ecological Experiments. Oxford University Press Inc., New York, NY.

Semlitsch, R.D., Bodie, J.R., 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conserv. Biol. 17, 1219–1228.

Semlitsch, R.D., Conner, C.A., Hocking, D.J., Rittenhouse, T.A.G., Harper, E.B., 2008. Effects of timber harvesting on pond-breeding amphibian persistence: testing the evacuation hypothesis. Ecol. Appl. 18, 283–289.

Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K., 1988. Time and size at metamorphosis related to adult fitness in Ambystoma talpoideum. Ecology 69, 184–192.

Semlitsch, R.D., Todd, B.D., Blomquist, S.M., Calhoun, A.J.K., Gibbons, J.W., Gibbs, J.P., Graeter, G.J., Harper, E.B., Hocking, D.J., Hunter, M.L., Patrick, D.A., Rittenhouse, T.A.G., Rothermel, B.B., 2009. Effects of timber harvest on amphibian populations: understanding mechanisms from forest experiments. Bioscience 59, 853–862.

Smith, W.B., Miles, P.D., Perry, C.H., Pugh, S.A. 2009. Forest resources of the United States, 2007, General Technical Report. WO-78, 336 pp., Forest Service, US Department of Agriculture, Washington, DC.

Spotila, J.R., 1972. Role of temperature and water in the ecology of lungless salamanders. Ecol. Monogr. 42, 95–125.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306, 1783–1786.

Tilghman, J.A., Ramee, S.W., Marsh, D.M., 2012. Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America. Biol. Conserv. 152, 1–9.

Todd, B.D., Andrews, K.M., 2008. Response of a reptile guild to forest harvesting. Conserv. Biol. 22, 753–761.

Todd, B.D., Luhring, T.M., Rothermel, B.B., Gibbons, J.W., 2009. Effects of forest removal on amphibian migrations: implications for habitat and landscape connectivity. J. Appl. Ecol. 46, 554–561.

Todd, B.D., Rothermel, B.B., 2006. Assessing quality of clearcut habitats for amphibians: effects on abundances versus vital rates in the southern toad (Bufo terrestris). Biol. Conserv. 133, 178–185.

Todd, B.D., Rothermel, B.B., Reed, R.N., Luhring, T.M., Schlatter, K., Trenkamp, L., Gibbons, J.W., 2008. Habitat alteration increases invasive fire ant abundance to the detriment of amphibians and reptiles. Biol. Invasions 10, 539–546.

Todd, B.D., Winne, C.T., 2006. Ontogenetic and interspecific variation in timing of movement and responses to climatic factors during migrations by pond-breeding amphibians. Can. J. Zool. 84, 715–722.

United States Department of Agriculture, 2005. 2005 Land and Resource Management Plan: 2005 Forest Plan. p. 234.

Vonesh, J.R., De la Cruz, O., 2002. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia 133, 325–333.

Whitlock, M.C., 2005. Combining probability from independent tests: the weighted Z-method is superior to Fisher's approach. J. Evol. Biol. 18, 1368–1373.

Wilbur, H.M., 1980. Complex life cycles. Annu. Rev. Ecol. Syst. 11, 67–93.

Wilbur, H.M., 1997. Experimental ecology of food webs: complex systems in temporary ponds. Ecology 78, 2279–2303.

Willson, J.D., Hopkins, W.A., Bergeron, C.M., Todd, B.D., 2012. Making leaps in amphibian ecotoxicology: translating individual-level effects of contaminants to population viability. Ecol. Appl. 22, 1791–1802.

Wyman, R.L., 1998. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition and the carbon cycle. Biodivers. Conserv. 7, 641–650.

Zheng, D., Chen, J., Song, B., Xu, M., Sneed, P., Jansen, R., 2000. Effects of silvicultural treatments on summer forest microclimate in southeastern Missouri Ozarks. Clim. Res. 15, 45–59.