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# Impact of forestry practices at a landscape scale on the dynamics of amphibian populations

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**Abstract.** Forest loss is a primary cause of worldwide amphibian decline. Timber harvesting in the United States has caused dramatic changes in quality and extent of forest ecosystems, and intensive forest management still occurs. Although numerous studies have documented substantial reductions in amphibian densities related to timber harvest, subsequent extinctions are rare. To better understand the population dynamics that have allowed so many amphibian species to persist in the face of widespread forest disturbance, we developed spatially explicit metapopulation models for four forest-dependent amphibian species (*Lithobates sylvaticus*, *Ambystoma opacum*, *A. talpoideum*, and *A. maculatum*) that incorporated demographic and habitat selection data derived from experiments conducted as part of the Land Use Effects on Amphibian Populations Project (LEAP). We projected local and landscape-scale population persistence under 108 different forestry practice scenarios, varying treatment (partial cut, clear-cut with coarse woody debris [CWD] removed, and clear-cut with CWD retained), cut patch size (1, 10, or 50 ha), total area cut (10, 20, or 30%), and initial amphibian population size (5, 50, or 500 adult females per local breeding population). Under these scenarios, landscape-scale extinction was highly unlikely, occurring in <1% of model runs and for only 2 of the 4 species, because landscape-scale populations were able to persist via dispersal even despite frequent local extinctions. Yet for all species, population sizes were reduced to ~50% in all clear-cut scenarios, regardless of the size of harvested patches. These findings suggest that debate over timber harvesting on pool-breeding amphibian populations in the United States should focus not on questions of landscape-scale extinction but on the ecological consequences of dramatic reductions in amphibian biomass, including changes in trophic interactions, nutrient cycling, and energy transfer. Additionally, we conclude that amphibian declines and extinctions are far more likely to occur as a result of permanent habitat loss resulting from development than from the temporary degradation of habitat caused by current forestry practices.

**Key words:** *Ambystoma*; amphibian decline; clearcut; forestry; habitat degradation; *Lithobates*; metapopulation; population dynamics.

## INTRODUCTION

Habitat loss and degradation are the primary drivers of amphibian declines worldwide (Sodhi et al. 2008). With >80% of amphibian species occurring in forested habitat (Stuart et al. 2004), forest loss and degradation are of particular concern.

Numerous studies have documented reductions in amphibian abundance following forest clear-cutting (e.g., Enge and Marion 1986, Petranka et al. 1994, Ash 1997, DeMaynadier and Hunter 1999, Harpole and Haas 1999, Duguay and Wood 2002, Renken et al. 2004, Homyack and Hass 2009; but see Russell et al. 2002).

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Within the United States, forests have undergone dramatic changes in recent history, including extensive forest clearing in the 1800s (Lorimer and White 2003, Foster and Aber 2004). Given the sensitivity of forest-dependent amphibians to forest disturbance, and the fact that forest cover was reduced to as low as 25% in regions of New England in the late 1800s (Foster and Aber 2004), it seems paradoxical that amphibian populations were able to persist in these regions. Of the nearly 300 amphibian species in the United States, just two have undergone recent extinction, and only one, *Plethodon ainsworthi*, may have been forest dependent (Lazell 1998) or may never have existed (Himes and Beckett 2013).

Whereas many studies of the effects of forestry practices on amphibians have documented changes in abundance and diversity (reviewed in DeMaynadier and Hunter 1995), understanding the ecological drivers that lead to these demographic outcomes for forest amphibians has been challenging. Reductions in amphibian

numbers following forestry practices can result from multiple and potentially interacting factors including mortality, changes in behavior that alter detectability, and/or temporary movements away from unsuitable habitat (Van Horne 1983, DeMaynadier and Hunter 1998, Rothermel and Semlitsch 2002, Semlitsch et al. 2008, Welsh et al. 2008). Each potential cause has very different implications for landscape-scale population dynamics (Van Horne 1983, Petranka et al. 1993, Ash and Bruce 1994, Johnson 2005, Semlitsch et al. 2008). For example, temporary movement away from unsuitable habitat may reduce local abundance, but have little effect on the size of a landscape-scale population (Semlitsch et al. 2008), whereas mortality may result not only in a smaller local population, but also in reduced dispersal, which could limit recolonization within a metapopulation and affect landscape-scale population sizes (Hanski 1991).

Understanding the effects of forest disturbance on amphibian population dynamics at larger spatial scales requires an understanding of the interactions among habitat selection in a heterogeneous landscape, the subsequent changes in vital rates and dispersal rates, and the metapopulation dynamics of local and landscape-scale populations (Pulliam and Danielson 1991). These responses to forest disturbance are likely mediated by a host of factors including: (1) differences among forestry practices (DeMaynadier and Hunter 1995), including clear-cut vs. partial cut, whether coarse woody debris is retained or removed, the size of cuts, and the total area of the landscape that is cut; (2) differences among amphibian life histories, including dispersal ability, fecundity, and longevity (Harper et al. 2008); (3) spatial and temporal environmental variation including climate and pre-disturbance habitat quality (Semlitsch et al. 2009); and (4) stochasticity inherent in amphibian population dynamics, such as frequent boom and bust cycles related to weather conditions and breeding site hydroperiod (Berven 1990).

To both understand how amphibian populations have persisted in landscapes across the eastern United States despite widespread forest disturbance, and to understand the consequences of current forest management practices for amphibians, we developed spatially explicit, landscape-scale population models that incorporate all of these factors. To parameterize our models, we used data from experiments conducted as part of the Land Use Effects on Amphibian Populations (LEAP) project, a landscape-scale experimental manipulation designed to determine the effects of three different forestry practices on amphibian populations in three geographic regions of the United States: Maine, Missouri, and South Carolina (Semlitsch et al. 2009). These experiments quantified the effects of each forestry treatment on the survival and behavior of multiple amphibian species to identify the mechanisms by which forestry practices affect amphibian populations (Rothermel and Luhring 2005, Patrick et al. 2006, 2008, Todd and

Rothermel 2006, Rittenhouse et al. 2008, 2009, Semlitsch et al. 2008, 2009, Todd et al. 2008, 2009). We synthesized data from these experiments in a population-modeling framework to determine the landscape-scale response of amphibian populations to forestry practices including: partial harvest, clear-cut with coarse woody debris (CWD) retained, and clear-cut with CWD removed. We developed separate models for four forest-associated pool-breeding amphibian species to better understand these effects on species with different life history strategies and population dynamics: spotted salamander (*Ambystoma maculatum*), marbled salamander (*A. opacum*), mole salamander (*A. talpoideum*), and wood frog (*Lithobates sylvaticus*). These four species were chosen because there were sufficient data available in the literature to parameterize baseline population models. We tested a wide range of scenarios (108 scenarios per species) that included different forestry practices and varied in the size of cuts, the proportion of the total area of forest cut, and the initial size of each local population. For each scenario we tracked local and landscape-scale population size, local population turnover rate (extinction/recolonization frequency), the probability of landscape-scale persistence, and the proportion of pools occupied over a 100-year timescale.

#### METHODS

##### *Incorporation of forestry effects data from the LEAP project*

We summarized data from experiments conducted as part of LEAP (see Semlitsch et al. 2009). This research was conducted in replicated experimental arrays (four arrays in three regions; Maine, Missouri, and South Carolina), each consisting of an amphibian breeding pool surrounded by a 164-m radius area (8.4 ha) of experimentally manipulated forest habitat. Experimental treatments included clearcuts with coarse woody debris (CWD) retained, clearcuts with coarse woody debris removed, partial harvests with 50–60% reduction of canopy cover, and control forests that were not manipulated. (For additional details see Rothermel and Luhring [2005], Patrick et al. [2006], and Rittenhouse et al. [2008]; details of study site characteristics can be found in Appendix A.) To summarize the results of the LEAP experiments, data were categorized as quantifying either habitat selection or survival. We focused on the species for which the most data were available, which included wood frogs (*L. sylvaticus*) and four salamander species (*Ambystoma annulatum*, *A. maculatum*, *A. opacum*, and *A. talpoideum*). We grouped data on habitat selection and change in survival for all ambystomatid salamanders because they responded similarly to the forestry treatments in the LEAP arrays across the three sites (Semlitsch et al. 2009, Todd et al. 2014), and by pooling the data we were able to more precisely estimate model parameters. To quantify habitat choice, we calculated the mean proportion of adults and juveniles selecting cut habitat (partial cut or either type

TABLE 1. Habitat selection parameter estimates incorporated in demographic models predicting forestry impacts on amphibian populations.

Amphibian	Partial cut		Clear-cut (CWD retained)		Clear-cut (CWD removed)	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
Ambystomatid salamanders						
Juveniles†	0.24	...	0.15	...	0.10	...
Adults‡	0.41 (0.04)	0.38–0.44	0.31 (0.08)	0.21–0.39	0.25 (0.10)	0.15–0.39
<i>L. sylvaticus</i>						
Juveniles§	0.44	...	0.26	...	0.17 (0.08)	0.09–0.26
Adults¶	0.46 (0.10)	0.35–0.53	0.31 (0.12)	0.18–0.42	0.30 (0.12)	0.18–0.42

Notes: Estimates are for proportion of individuals selecting cut habitat (partial cut, clear-cut with CWD [coarse woody debris] retained, or clear-cut with CWD removed) relative to control (i.e., uncut) habitat. Data are compiled from experiments conducted within LEAP arrays in Maine, Missouri, and South Carolina and include data from radio-tracking, drift-fences, powder-tracking, and terrestrial enclosures. These means were used in model simulations in conjunction with data describing the available amount of cut and uncut habitat, to determine the proportion of individuals in each local population that selected cut habitat.

† Patrick et al. 2006

‡ Patrick et al. 2006, Semlitsch et al. 2008, Todd et al. 2014

§ Patrick et al. 2006, 2008

¶ Patrick et al. 2006, Blomquist 2008, Rittenhouse et al. 2008

of clearcut) when given an equal opportunity to enter cut or uncut forest (Tables 1 and 2). These data came from studies using radio-tracking (Blomquist 2008, Rittenhouse et al. 2009), powder-tracking (Graeter et al. 2008), enclosures (Patrick et al. 2008), and drift-fences (Patrick et al. 2006, Semlitsch et al. 2008, Todd et al. 2009). To quantify habitat-specific survival (i.e., the consequences of habitat choice) we calculated the average proportion of adults and juveniles surviving in each forestry treatment relative to the control (Table 3). These data came from experiments in which individuals were confined to enclosures within specific forestry treatments (Rothermel and Luhring 2005, Todd and Rothermel 2006, Harper 2007, Rittenhouse and Semlitsch 2007a, Blomquist 2008, Rittenhouse et al. 2008, Todd et al. 2008) and from survival estimates of radio-tracked adults (Blomquist 2008, Rittenhouse et al. 2009). We incorporated these data in our landscape-scale population simulations (see *Demographic models*) to quantify the effects of forest harvesting on adult and juvenile *L. sylvaticus* and three species of ambystomatid salamanders including *A. maculatum*, *A. talpoideum*, and *A. opacum*. We did not include simulations of *A. annulatum* because we lacked sufficient published data to parameterize a baseline population model. We did, however, use data from LEAP experiments on *A. annulatum* to improve our estimates of habitat choice and habitat-specific survival of Ambystomatid salamanders under the four forestry scenarios.

#### Demographic models

Although the ambystomatid salamanders at each site exhibited similar behavioral and demographic responses to the forestry treatments, each species differs in its life history strategy (e.g., clutch size, dispersal rates, hydro-period requirements, dispersal distances). Therefore to determine the effects of the forestry treatments on landscape-scale population dynamics, we developed

species-specific population models for four species: *A. maculatum*, *A. opacum*, *A. talpoideum*, and *L. sylvaticus*. Focal species were chosen if sufficient published life history data were available to construct a robust demographic model and LEAP data were available to quantify changes in both survival and habitat selection resulting from forestry practices.

We developed a baseline population model for each species using published demographic data (Table 3). The models were spatially explicit, stochastic, matrix meta-population models, with local populations defined as the populations associated with each breeding site in the landscape. When multiple estimates of a parameter were available, we used the average or midpoint (Table 3). When standard deviations or standard errors were available, we calculated the coefficient of variation and used the mean coefficient of variation to estimate the standard deviation of the mean value used in the stochastic simulations. This variance was calculated from estimates reflecting variation in vital rates among years rather than among study sites, thereby reflecting temporal variability rather than spatial variation. During each year of the simulation, vital rates for each local population were drawn randomly from a normal distribution defined by the mean and estimated SD. We assumed a normal distribution for all parameters except larval survival to metamorphosis, for which estimates are consistently right skewed (typically low, but with infrequent boom years [e.g., Shoop 1974, Berven 1990]); therefore, we used a power function to define a probability density curve that fit the larval survival data. Within each local population, survival rates of adults and juveniles were correlated within years. Demographic rates were not correlated among local populations (i.e., parameter values varied independently among local populations within years), with the exception of larval survival to metamorphosis, which is largely dependent on annual rainfall and therefore



TABLE 2. Annual survival estimates incorporated into demographic models predicting forestry effects on amphibian populations.

Amphibian	Partial cut		Clear-cut (CWD retained)		Clear-cut (CWD removed)	
	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)	Range
<i>Ambystoma</i> spp.						
Juveniles†	0.70 (0.40)	0–1	0.42 (0.18)	0.14–0.58	0.38 (0.22)	0–0.64
Adults‡	1.60 (0.56)	1.2–2	0.33 (0.47)	0–0.67	0§	0–0
<i>L. sylvaticus</i>						
Juveniles¶	1.7 (1.5)	0.66–2.8	0.53 (0.18)	0.32–0.67	0.34 (0.02)	0.32–0.35
Adults#		...	0.43	...	0.43	...

Notes: Survival estimates are for forest-dependent amphibians in cut habitat relative to control (i.e., uncut) habitat. Data are compiled from studies of amphibians confined to enclosures in experimental forest arrays in Maine, Missouri, and South Carolina.

† Rothermel and Luhring 2005, Todd et al. 2008, Todd et al. 2014

‡ Todd et al. 2014

§ Enclosure experiments with adult ambystomatid salamanders in clearcuts with CWD (coarse woody debris) removed resulted in zero survival; however, drift fence data suggest that some adult ambystomatid salamanders are able to persist in this treatment (Patrick et al. 2006). Therefore, in model simulations we used a survival value of 0.22 relative to the control, a value that represents the minimum detection threshold given the sample sizes used in the enclosure experiments.

¶ Harper 2007, Blomquist 2008, Rittenhouse et al. 2008, Todd et al. 2014

# Rittenhouse et al. 2009

|| Because there were no data available to determine the effects of partial cuts on adult wood frog survival, we did not alter adult wood frog survival in these simulations.

expected to be correlated within a landscape (Shoop 1974, Berven 1990). To enable comparisons among species, we began simulations for each species with transition matrices that yielded a stochastic logarithmic growth rate of  $0.12 \pm 0.01$  in uncut forest. This uniformity was achieved by multiplying each element of the transition matrices by a constant value (0.02 for *L. sylvaticus*, 0.02 for *A. maculatum*, 0.19 for *A. opacum*, and 0.07 for *A. talpoideum*).

#### Landscape scenarios

We generated hypothetical landscapes with the density and degree of clustering of pools based on data from wetland surveys (summarized in Gibbs and Reed 2007), which resulted in 23 pools within a  $10 \times 10$  km landscape (Fig. 1). Each pool was considered to be a local population within the landscape-scale population. For each species we created a range of forestry scenarios in which we varied type of cut (control, partial cut, clearcut with CWD retained, and clearcut with CWD removed), cut size (1, 10, and 50 ha), and proportion of forest cut (10, 20, and 30% of the landscape), as well as initial population size (5, 50, 500 adult females per local population). We chose the range of cut size and proportion of forest cut based on forestry practices commonly used over the past 50 years (Hunter 1999). We randomly applied the forestry practices to the landscapes in ArcGIS. For each scenario we calculated: (1) the total distance between each pair of pools; (2) the distance of each potential dispersal path that fell within a forest cut; (3) the proportion of core terrestrial habitat area within a forest cut. Core habitat was defined as the area expected to contain 95% of individuals in a local population based on kernel density estimates of space use for radio-tracked individuals (Rittenhouse and Semlitsch 2007b). Based on these estimates, core habitat was defined as the area within 245 m of each breeding

pool for ambystomatid salamanders and within 703 m of each breeding pool for *L. sylvaticus*. Forest succession was not explicitly included in the model due to data limitations; however, we assumed that throughout the simulation a consistent proportion of the total landscape (i.e., 10, 20, or 30%) was cut, with the remainder of the habitat uncut, meaning that although succession occurs over a 100-year time frame, forestry practices would continue to occur as well, so the model assumes that a constant proportion of the landscape is affected at any point in time during the simulation.

#### Hydroperiod

We assigned each of the 23 breeding pools an average hydroperiod that varied spatially and temporally (see Appendix B for additional details). In our simulations, hydroperiod determined the frequency with which each pool dried before metamorphs emerged (i.e., frequency of years with no recruitment). We assumed a high degree of spatial autocorrelation within the  $10 \times 10$  km landscape, so that within a year, each pool was either above or below its assigned average hydroperiod by the same proportion of the coefficient of variation.

#### Population simulations

All population simulations were carried out using MATLAB (R2009b). The combination of 4 species, 3 initial population sizes, 4 forestry treatments, 3 cut sizes, and 3 different proportions of area cut resulted in a total of 432 different scenarios. Thirty stochastic simulations were run for each scenario for 100 years, resulting in a total of 12960 simulations. Populations reached stochastic equilibrium within this time frame (Fig. 2). We varied the initial landscape-scale population sizes by orders of magnitude in different simulations to ensure that starting population size did not skew our results and to make our results more generalizable, since

TABLE 3. Summary of vital rate estimates (mean with estimated SD in parentheses) used in simulations of landscape-scale population dynamics for four pool-breeding amphibian species.

Population parameters	<i>Ambystoma maculatum</i> †	<i>A. opacum</i> ‡	<i>A. talpoideum</i> §	<i>Lithobates sylvaticus</i> ¶
Clutch size	215 (75)	102 (29)	407 (77)	690 (179)
Survival from egg to metamorphosis#	0.069 (0.056)	0.13 (0.11)	0.023 (0.025)	0.0305 (0.021)
Survival from metamorphosis to 1 year	0.32 (0.12)	0.39 (0.10)	0.35 (0.11)	0.579 (0.12)
Survival from year 1 to year 2	0.78 (0.06)	0.60 (0.08)	0.73 (0.14)	0.33 (0.13)
Annual adult survival (2nd to 3rd year and beyond)	0.78 (0.06)	0.60 (0.08)	0.73 (0.14)	0.216 (0.084)
Probability of reaching maturity in year 1	0	0.02	0.67	0.02
Probability of reaching maturity in year 2††	0.5	0.32	0.60	0.75
Annual probability of reaching maturity in subsequent years	0.5	0.56	0.60	1
Annual breeding frequency	0.91	0.60	0.49	1
Minimum larval period (days)	112	215	133	78

† Bishop 1941, Husting 1965, Whitford and Vinegar 1966, Minton 1972, Shoop 1974, Wilbur 1977, Woodward 1982, Ireland 1989, Flageole and Leclair 1992, Rothermel and Semlitsch 2006, Kinkead and Otis 2007, Hocking et al. 2008; E. Harper, unpublished data

‡ McAtee 1907, Noble and Brady 1933, King 1939, Green 1955, Petranka and Petranka 1980, Scott 1990, 1994, Palis 1996, Semlitsch et al. 1996, Paton and Crouch 2002, Rothermel and Semlitsch 2006, Taylor et al. 2006, McGarigal et al. 2008, Gamble et al. 2009

§ Shoop 1960, Semlitsch 1987, Semlitsch et al. 1988, 1996, Raymond and Hardy 1990, Pechmann 1995

¶ Bellis 1961, Herreid and Kinney 1966, Meeks and Nagel 1973, Berven 1982, 1988, 1990, 1995, Corn and Livo 1989, Riha and Berven 1991, Bastien and LeClair 1992, Sagor et al. 1998, Redmer 2002

# These mean values for survival from egg to metamorphosis include only non-zero values. In the simulations the frequency of years without successful recruitment was determined by the hydroperiod of individual pools.

|| Survival from year 1 to year 2 for ambystomatid salamanders is set equal to adult survival because survival data for individuals in natural populations were unavailable for this age class.

†† Probabilities of reaching maturity represent the proportion of individuals that mature at a given age if they have not yet reached maturity by that point.

amphibian population sizes are extremely variable (Pechmann and Wilbur 1994). In each model run, local populations began with 5, 50, or 500 adult females (i.e., 115, 1150, or 11500 total adult females in the landscape). Carrying capacity was included in all models as a ceiling on the number of adult females in each local population and was set at twice the initial population size (i.e., 10, 100, or 1000 adult females). A local population was considered quasi-extinct when only two or fewer adult females remained in the population, and the landscape-scale population was considered extinct when all local populations reached quasi-extinction (Morris and Doak 2002).

Individuals were able to move among local populations and to recolonize extinct pools. The relative probability of individuals moving between each pair of pools was based on the extremely limited published dispersal data available for ambystomatid salamanders and ranid frogs, including the California tiger salamander *Ambystoma californiense* (Trenham et al. 2001), *A. opacum* (Gamble et al. 2007), and *L. sylvaticus* (Berven and Grudzien 1990) (see Appendix B for additional details). We applied a survival cost to emigration that increased linearly with distance for individuals dispersing beyond the core habitat area. Individuals dispersing to pools within the core habitat area (245 m for ambystomatids and 703 m for *L. sylvaticus*) experienced no additional mortality, but the probability of survival declined linearly after that distance, so that mortality reached 100% at 2600 m for dispersing ambystomatids and at 5000 m for *L. sylvaticus*. To our knowledge there

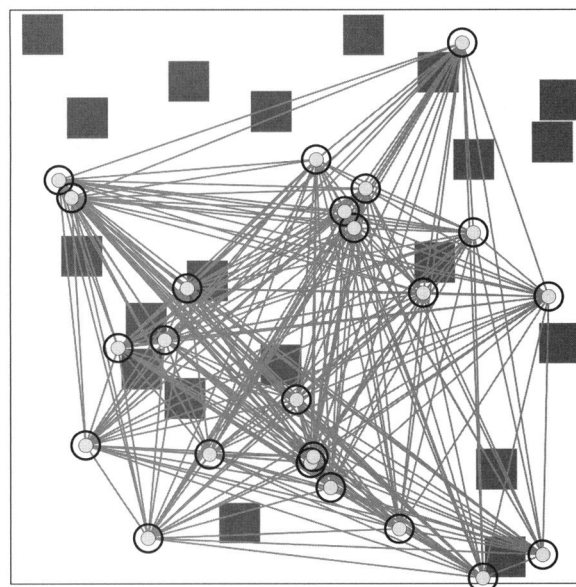


FIG. 1. An example of the 10 × 10 km hypothetical forested landscapes used as the basis for landscape-scale population simulations of forestry impacts on amphibian populations. Solid circles represent amphibian breeding pools. Black circles define the core terrestrial habitat (245 m for ambystomatid salamanders). Gray lines indicate potential dispersal paths between pairs of pools. Dark gray squares indicate the application of forestry practices. In this example, each forest cut is 50 ha and cuts have been applied to a total of 10% of the landscape.

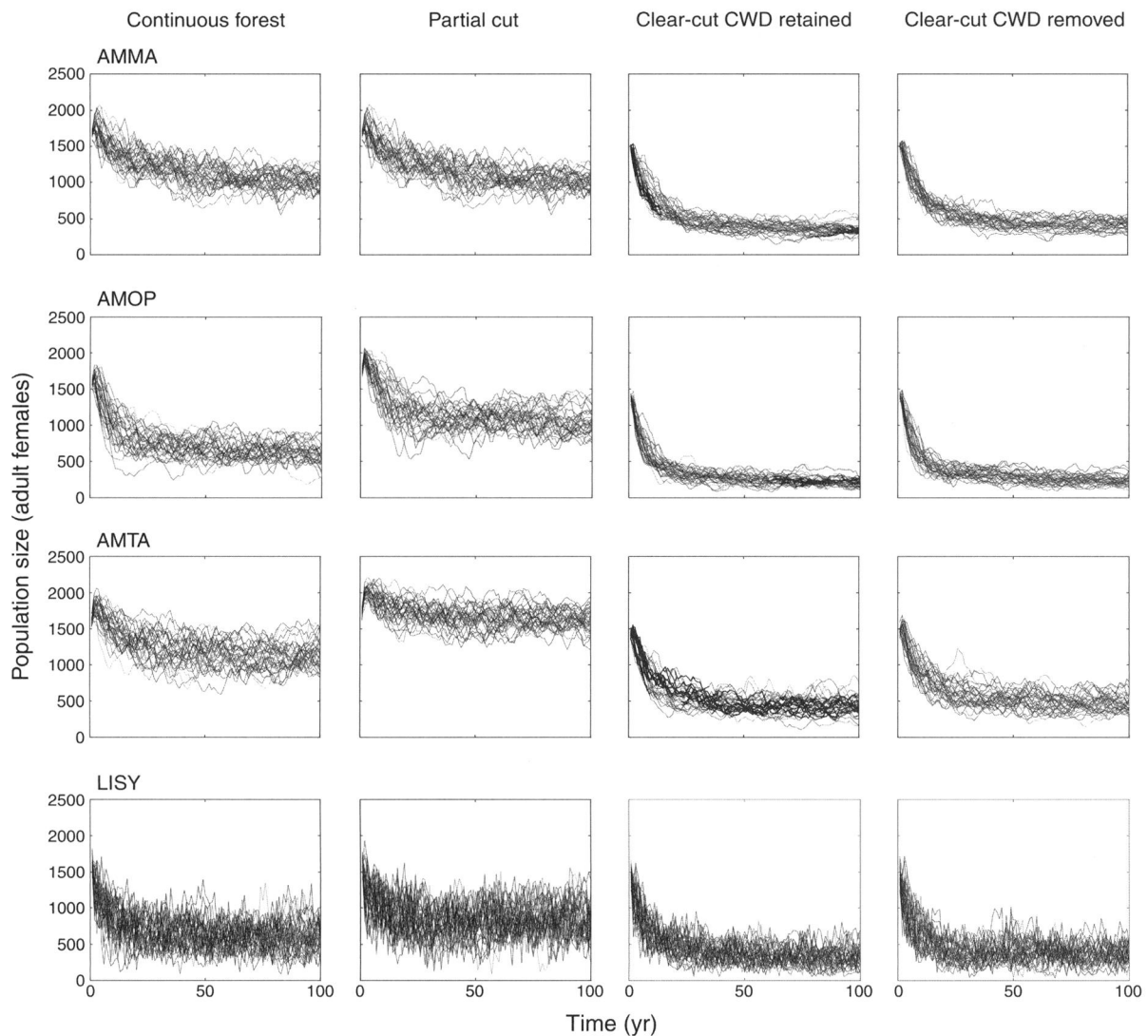


FIG. 2. Changes in landscape-scale population size of four amphibian species over a 100-year stochastic simulation of four different forestry practice scenarios (AMMA, *Ambystoma maculatum*; AMO, *A. opacum*; AMTA, *A. talpoideum*; LISY, *Lithobates sylvaticus*). In the scenarios shown here, 10-ha cuts were applied to 30% of the landscape, and the landscape-scale population began with 1150 adult females (50 adult females in each of 23 breeding pools). Within each graph, each line represents one of 30 individual stochastic iterations of the same scenario. All models reached stochastic equilibrium within the first 50 years of the simulation. CWD is coarse woody debris.

are no published amphibian studies quantifying the survival cost of dispersing specific distances, but we considered it more conservative to assume that there is a cost and that the cost increases with distance (Koenig et al. 1996).

We based the number of individuals in each local population on: (1) the proportion of the core habitat area that was cut; and (2) the proportion of individuals expected to select cut habitat. Within this core habitat, data from experiments in the LEAP arrays determined the proportion of individuals in the population that chose cut habitat as opposed to uncut habitat, and the associated effects on survival (Table 1). The survival of

dispersers was also reduced based on the proportion of their dispersal path that occurred in cut habitat.

#### Synthesis

For each landscape scenario, model outputs included the probability of landscape-scale persistence, landscape-scale population size, population turnover rate (the frequency of recolonization), and the proportion of local populations that existed at the end of the simulation. To determine which components of the model (species, forestry practice, cut size, and total area cut) contributed most to the variation in each of these output metrics, we ran a fully factorial four-way fixed effects ANOVA in program R (R Development Core



Team 2009). From this output, we summed the total error explained by each model component and its interactions with all other components. This allowed us to quantify the relative contributions of management practice, size of cuts, and the total area cut to each output metric. To illustrate the role of interactions among model components in determining changes in amphibian population size, we used a pruned regression tree model to estimate the proportion of the initial population remaining at the end of each simulation (R package rpart 3.1-45 [Therneau and Atkinson 2009]).

## RESULTS

Landscape-scale population extinction was extremely rare within the range of forest disturbance scenarios explored in our simulations, whereas local extinctions were common, particularly in clear-cut scenarios. Extinction of populations in all 23 pools occurred only in clear-cut simulations of *L. sylvaticus* and *A. opacum*, and even within these scenarios, landscape-scale extinction occurred in <1% of model iterations. For all species, however, clearcuts reduced landscape-scale population sizes to nearly half of those in continuous forest or partial-cut simulations (Figs. 2 and 3a). Across species, the models predicted slightly larger landscape-scale populations in partial-cut scenarios than in continuous forest, and slightly larger landscape-scale populations in clearcuts with CWD removed than with CWD retained (Figs. 2 and 3a). The proportion of pools occupied at the end of each simulation was typically high (>95%) in continuous forest simulations and slightly greater for partial-cut scenarios across species (Fig. 3b). The effect of clearcuts on pool occupancy varied among species, with *A. opacum* occupying on average 65% of pools, compared to 86–92% occupancy among the other species (Fig. 3b). The population turnover rate (i.e., the average annual number of extinction and recolonization events per pool) was consistently higher for *L. sylvaticus* than for salamander species (Fig. 3c). Among ambystomatid salamanders, *A. opacum* had the highest rates of turnover (Fig. 3c). For all species, extinction and recolonization events were most frequent in clear-cut simulations.

In terms of the relative effects of the four primary factors (species, forestry practice, cut size, and area cut), forestry practice had the greatest effect on both landscape-scale population size and the proportion of pools occupied, whereas species had the greatest effect on recolonization rate as measured by parsing variance components of the ANOVA model (Fig. 4). In general, the total area of forest cut influenced model predictions more than the size of individual cuts (Fig. 4). Regression tree analysis of amphibian abundance outputs identified forestry practice, followed by species and initial population size, as the primary factors determining landscape-scale population size (Fig. 5). Population sizes increased from their initial size only in control and partial-cut scenarios and only for the longer-lived

species: *A. talpoideum* and *A. maculatum* (Fig. 5). Some clear-cut scenarios resulted in average final population sizes representing 95% of the initial population size for *A. maculatum*, *A. talpoideum*, or *L. sylvaticus*, but only when initial population sizes were small ( $N = 115$  or 1150) and no more than 10% of the forested area was cut (Fig. 5). Population sizes averaging <50% of the initial population size resulted only from clear-cut scenarios, and included all *A. opacum* scenarios, *L. sylvaticus* scenarios in which the initial population size was high ( $N = 11500$ ), and *A. maculatum* and *A. talpoideum* scenarios in which the initial population size was high and 30% of the forested area was cut (Fig. 5).

## DISCUSSION

Our model results suggest that landscape-scale extinctions of amphibians in predominantly forested landscapes are unlikely to occur in the eastern United States as the result of current forestry practices. This generalization is based on simulations that incorporated changes in habitat selection and survival for four pool-breeding amphibian species under a range of forestry practice scenarios based on experiments carried out in three geographic regions (citations in Table 2). Simulations included forestry scenarios that affected up to 30% of the canopy cover in the landscape. Historically, these landscape-scale amphibian populations survived forest clearing of >80% in some eastern U.S. states during the 1800s (Foster 1992, Drummond and Loveland 2010). While extinction of local amphibian populations (i.e., those associated with individual pools) were common in our simulations, and particularly high in clear-cut scenarios, landscape-scale extinction occurred in <0.1% of model iterations.

While landscape-scale extinction was extremely rare in our simulations, clearcuts reduced landscape-scale population sizes by ~50%. Population declines of similar magnitude (29–62% reductions) have been documented at local scales for a wide range of terrestrial salamander species following timber harvests (reviewed in Tilgman et al. 2012). While reductions in population size may not result in regional extinction, such declines would be expected to have ecosystem-level effects (Pough et al. 1987, Petranka et al. 1994, Davic and Welsh 2004, Whiles et al. 2013). Amphibians comprise a large proportion of the vertebrate biomass in many forested and freshwater ecosystems (Petranka and Murray 2001, Gibbons et al. 2006). They consume a wide range of taxa (Regester et al. 2008) and are consumed by a diverse suite of predators (e.g., Rittenhouse et al. 2009). Ectothermy allows amphibians to efficiently convert prey to biomass, and thereby allows pool-breeding amphibians to be particularly effective in transferring nutrients from the aquatic to the terrestrial environment (Regester et al. 2005). Therefore, reductions in ecosystem function and the provisioning of ecosystem services may be of greater concern than landscape-scale extinc-



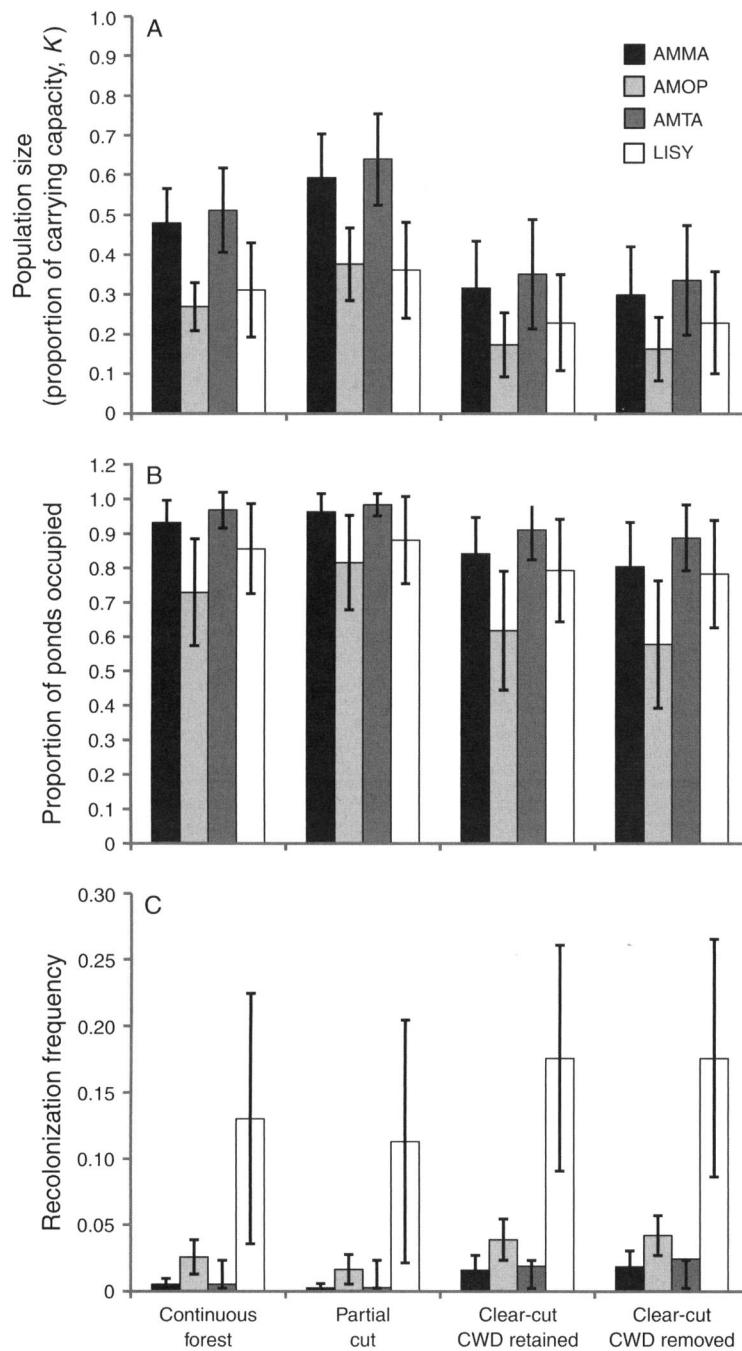


FIG. 3. Results of 12 960 stochastic landscape-scale population simulations of four amphibian species (*Ambystoma maculatum*, *A. opacum*, *A. talpoideum*, and *Lithobates sylvaticus*) in four forestry treatments, with variation in carrying capacity, size of cuts, and the total area of the landscape cut. Error bars represent  $\pm$ SD. (A) Average landscape-scale population sizes (as proportion of carrying capacity) of four amphibian species at the end of population simulations. (B) Proportion of the 23 pools in the landscape occupied at the end of population simulations. (C) Mean annual recolonization frequency for individual pools in each year of the simulations. CWD is coarse woody debris.

tion in the discussion of the effects of forestry practices on amphibian populations.

Of the forestry-related factors that we varied in the model (forestry practice, cut size, and area cut), forestry practice had the greatest effect on landscape-scale

population sizes. Partial cuts resulted in slight population increases relative to simulations in continuous forest due to higher rates of survival in partial cuts compared to control habitat. This pattern was common among the results of the LEAP experiments at multiple

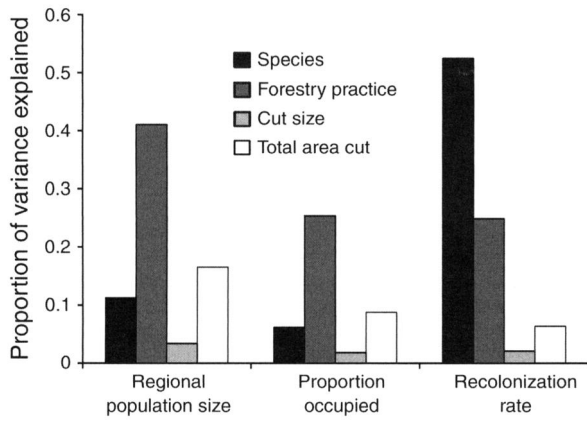


FIG. 4. The proportion of the total variance in three population metrics (landscape-scale population size, proportion of pools occupied, and mean annual recolonization rate) explained by four different factors (Species [nested in genus], *Ambystoma maculatum*, *A. opacum*, *A. talpoideum*, *Lithobates sylvaticus*; Forestry practice, Control forest, Partial cut, Clear-cut with coarse woody debris removed, and Clear-cut with coarse woody debris retained; Cut size, 1 ha, 10 ha, 50 ha; and Total area cut, 10%, 20%, 30%). Data were generated in 12 960 stochastic population simulations and the variance in model output metrics was partitioned using an ANOVA-based approach.

sites (Semlitsch et al. 2009). However, specific mechanisms driving increased survival were not determined (Harper 2007, Blomquist 2008). These cuts are thought to better mimic natural disturbance than do clearcuts; however, the implementation of partial harvests can vary substantially (Schuler 2004), and there may be some longer-term effects of partial harvests on forest ecosystems that were not accounted for in our model, such as increased mortality of unharvested trees in subsequent years (Thorpe et al. 2008). Partial harvests could potentially benefit amphibians by creating small patches of increased solar radiation, providing a wider range of microclimates within a small area, and thereby allowing for more efficient behavioral thermoregulation (Brattstrom 1963). This could result in increased foraging efficiency and growth rates, which can in turn affect survival and fecundity (Rome et al. 1992), ultimately increasing population sizes. Additional research is necessary to better understand the effects of partial harvests on amphibian demography.

In contrast to partial harvests, clearcuts resulted in dramatic reductions of landscape-scale population sizes, and in a small proportion of model iterations, caused landscape-scale extinctions. In these simulations, most but not all individuals in a population chose to migrate

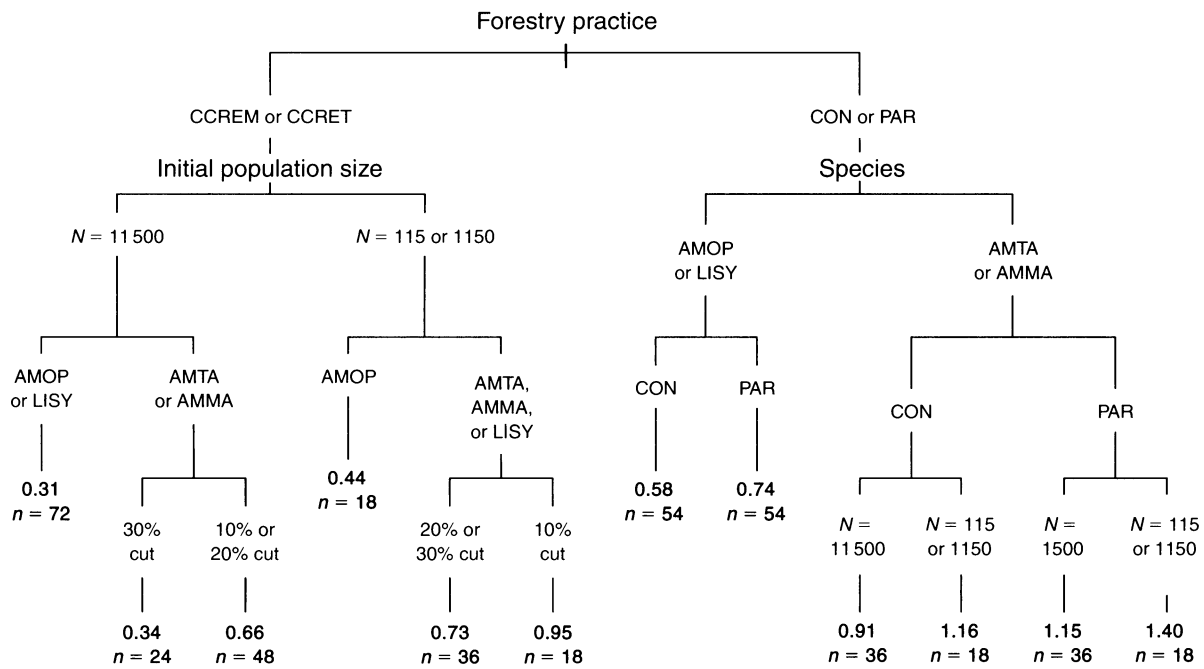


FIG. 5. Regression tree illustrating the combination of model parameters that resulted in differences in amphibian abundance (proportion of the initial population persisting) following the application of different forestry practices. The mean proportion of the initial population size represented by the final population size is labeled in boldface type at each terminal node along with the total number of model runs (*n*) in that category. Model parameters included: forestry practice (CCREM = clear-cut with coarse woody debris removed, CCRET = clear-cut with coarse woody debris retained, CON = control forest, PAR = partial cut), initial landscape-scale population size (*N* = 115, 1150, or 11 500 individuals), species (AMOP = *Ambystoma opacum*; LISY = *Lithobates sylvaticus*; AMTA = *Ambystoma talpoideum*; AMMA = *Ambystoma maculatum*), proportion of the total area of forest cut (10%, 20%, or 30%), and cut size (1 ha, 10 ha, or 50 ha). Forestry practice, followed by species and initial population size were the most influential parameters, whereas cut size was the least influential.

into forested rather than clear-cut habitat, but for the individuals that selected cut habitat, survival probabilities were extremely low. These interactions between habitat selection and the subsequent survival costs resulted in the unexpected pattern of lower population sizes in clear-cut simulations with CWD retained than with CWD removed. Field observations suggest that amphibians use coarse woody debris to aid in thermoregulation and to avoid desiccation (Whiles and Grubaugh 1993). The importance of CWD for plethodontid salamanders has been documented (Aubry et al. 1988, Hocking et al. 2013); however, little is known about the value of CWD for ambystomatid salamanders, which are fossorial (Pechmann 1995), or for *L. sylvaticus* which is typically associated with leaf litter (Constible et al. 2001). Our results suggest the possibility that CWD in clearcuts could create an ecological trap for pool-breeding amphibians (Schlaepfer et al. 2002). In this case, if a greater proportion of the population selects for cut habitat over forested habitat when CWD is present than when it is absent, but the probability of long-term survival in clearcuts, with or without CWD, is substantially lower than in forested habitat, the result may be lower population sizes for clear-cut scenarios with CWD retained than with CWD removed. Several studies have documented positive relationships between CWD and amphibian abundance; however, these studies have been short term and do not account for the likely increase in detection probability when CWD is present (reviewed in Otto et al. 2013). There are to our knowledge no field data to support or refute the long-term value of CWD for the population dynamics of pool-breeding amphibians.

While the type of forestry practice used in each simulation explained a large proportion of the variability in model predictions, differences among species' life history strategies were primarily responsible for the variation in predictions of population size, proportion of pools occupied, and recolonization rates. Life history strategy has been demonstrated to affect stream and terrestrially breeding amphibian responses to timber harvest (Connette and Semlitsch 2013). Of the four pool-breeding species that we modeled, only the two shortest-lived species, *L. sylvaticus* and *A. opacum*, experienced landscape-scale extinction in our simulations. These species reached extinction in all 23 pools in the simulations only very rarely, suggesting that while they were able to persist under the majority of circumstances, there were rare occasions when environmental stochasticity resulted in a convergence of consecutive "catastrophe" years (such as drought) with no recruitment, so that these short-lived species had no opportunity to recover. This circumstance, in which the consecutive number of years without successful recruitment is greater than the life span of the species, is far less likely to occur in long-lived species than in short-lived species (Harper et al. 2008). The life span of *L. sylvaticus* is particularly short, usually under 3 years, and most

individuals reproduce only once in their lifetime (Berven 1990). The life history strategy of *L. sylvaticus* is dependent on high fecundity, 500–2000 eggs per clutch (Berven 1990), and high rates of dispersal (Berven and Grudzien 1990). In the majority of scenarios in our model, landscape-scale wood frog populations persisted due to frequent recolonization of pools that had reached local extinction. Recolonization frequency was also high for *A. opacum*, which experienced more local extinctions than did the other salamander species, but not as high as in *L. sylvaticus*, which is capable of dispersing to far greater distances (Rittenhouse and Semlitsch 2007b). Despite interspecific variation in response to each forestry practice scenario, all four species exhibited the same general responses, with very low probabilities of landscape-scale extinction, slightly larger population sizes in partial cuts, and landscape-scale population size reductions of ~50% in the clear-cut scenarios.

Our conclusions apply to the range of scenarios included in our simulations. Circumstances in which >30% of the landscape is cut, or in which wetland densities are lower, or hydroperiods are shorter or more variable, would be more likely to result in landscape-scale extinction than the scenarios used in our models, which reflect current practices. Field studies have demonstrated that reduction in forest cover beyond 30% (50–70% open) results in the absence of some forest-dependent amphibians from the landscape, including *L. sylvaticus* and *A. maculatum* (Gibbs 1998, Porej et al. 2004). In our simulations we chose scenarios that represent practices commonly used in forestry today or in the past 50 years, in which 30% or less of the landscape is cut at any given time (Hunter 1999). The low probability of landscape-scale extinction under these scenarios is not surprising, because these species have persisted, even in areas that have experienced extensive forest degradation in the past. More significant ecologically is the reduction in landscape-scale population sizes and the potential effect of these reductions in amphibian biomass on ecosystem function, including nutrient cycling and nutrient transfer between aquatic and terrestrial environments. The low probability of landscape-scale extinction under the scenarios in our model also suggests that research focused on illuminating potential causes of landscape-scale extinction should focus on permanent loss of forested habitat, such as development, or on forestry practices that result in >30% loss of canopy cover at a landscape scale.

Limited understanding of dispersal processes in amphibians constrain modeling efforts such as ours. Data on maximum dispersal distances and the survival costs of dispersal are particularly scant for pool-breeding amphibians (but see Rittenhouse et al. 2009). We also lack information on the interactions of forest succession and pool-breeding amphibian population dynamics (DeMaynadier and Hunter 1995). The interactions of effects on the aquatic and terrestrial stages of pool-breeding amphibians, including carryover effects

and density-dependent population regulation are also not well understood (Pechmann 1994, Harper and Semlitsch 2007). Despite the limitations of existing data, the results of our model simulations are consistent with a broad range of field studies and historical observations. Many studies have shown that amphibian populations are resilient to small-scale forest disturbance, especially if natural succession occurs following the disturbance (Pough et al. 1987, Russell et al. 2002, Hicks and Pearson 2003, Renken et al. 2004). These studies and our model results are also consistent with the fact that these species have persisted in the landscape through times of extensive forest clearing, and are also consistent with the numerous observations that amphibian abundance typically declines following clear-cutting (e.g., Enge and Marion 1986, Pough et al. 1987, Petranka et al. 1994, Dupuis et al. 1995, Ash 1997, DeMaynadier and Hunter 1999, Harpole and Haas 1999, Renken et al. 2004, Homyack and Hass 2009; however, the majority of these references describe trends in terrestrial rather than pool-breeding amphibians).

The primary implication of our results is that on a landscape scale, pool-breeding amphibians are unlikely to reach extinction as the result of forestry practices as long as the following criteria (i.e., assumptions of our model) are met: (1) wetland densities are not reduced; (2) canopy cover is never reduced beyond 30% of the total landscape; (3) cuts do not completely surround wetlands (i.e., buffers allow juvenile amphibians to emerge from wetlands into continuous forest in at least one direction); (4) connectivity is maintained among pools to allow immigration and recolonization. If the management goal is to maintain or increase the biomass of amphibians occurring in continuous forest, rather than just preventing landscape-scale extinction, then partial harvests applied in a manner consistent with the LEAP experimental arrays would achieve this objective, whereas clear-cutting, regardless of the size of cuts or the area cut, should be expected to reduce amphibian biomass and alter the associated ecosystem functions. These conclusions are contingent on distinguishing between temporary habitat degradation and permanent habitat loss. Landscape-scale populations can recover from temporary habitat degradation such as partial or clear-cutting followed by forest succession, but not from large-scale permanent habitat loss as in development or wetland drainage (Delis et al. 1996, Knutson et al. 1999, Harper et al. 2008). Therefore our results pertain specifically to situations where forests have the opportunity to regenerate through natural succession.

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#### SUPPLEMENTAL MATERIAL

##### Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/14-0962.1.sm>

##### Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.rt1kg>