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Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders

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ABSTRACT

Both observational and experimental studies have documented drastic reductions in salamanders after forest harvesting. Yet, the amount of time until salamander populations rebound and the factors limiting recovery after harvesting are unknown. We compared the effects of six oak regeneration practices to a control, representing a disturbance gradient from no treatment to silvicultural clearcut, on the relative abundance and reproductive demography of terrestrial salamanders through 13-years post-harvest. Following the experimental disturbance, relative abundance of terrestrial salamanders in treatments that opened the canopy were significantly and persistently lower than in either untreated control stands or midstory herbicide treatments. In general, this trend persisted through 9–13 years after treatment. Changes to demography of commonly captured salamanders varied by species, but *Plethodon cinereus* had a greater proportion of juveniles in unharvested treatments 7–13-years post-harvest, and *Desmognathus ochrophaeus* had a greater proportion of juveniles and a greater number of eggs/female in unharvested treatments 1–6-years post-harvest. Population modeling of *P. cinereus* indicated that adult survival had the greatest elasticity of the vital rates. Further, >60 years may be needed before *P. cinereus* reduced by the observed decline could reach pre-harvest levels of abundance. Of the treatments with canopy disturbance, the group selection harvest had the greatest abundances of salamanders 7–13-years post-harvest, but when coupled with future stand entries, the volume of wood fiber extracted, costs of harvesting, reduced sprouting of oaks, and soil disturbances, this method may not have the best balance of ecological and economic sustainability in central Appalachian hardwood forest.

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1. Introduction

Understanding how forest harvesting affects the structure of ecosystems, ecological processes, diversity of species, and viability of populations is integral for management of forests for ecological and economic sustainability. Within both private commercial and public (state and national) forests within the United States, forest management and silvicultural

systems are subject to review for alleged effects on ecological sustainability in addition to achieving economic, social, recreational, and aesthetic objectives. Despite these complex and often conflicting management goals, little research has compared effects on ecological communities from clearcut harvesting to a range of silvicultural alternatives. Even rarer are experiments that investigate long-term responses (>5 years) of plant and animal populations exposed to a gradient of

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silvicultural disturbances (deMaynadier and Hunter, 1995; DeStefano, 2002), which may represent alternative forest management practices.

In forests of eastern North America, salamanders are one of the most abundant and diverse vertebrate taxa (Burton and Likens, 1975) and are considered by some as indicators of forest biodiversity (Welsh and Droege, 2001) and of ecosystem health and integrity (Davic and Welsh, 2004). Terrestrial salamanders may influence ecosystem processes as apex predators of invertebrates in the detrital ecosystem (Wyman, 1998; Walton, 2005; Walton and Steckler, 2005), as high-quality prey for numerous taxa (Pough et al., 1987), and as regulators of leaf litter decomposition (Hairston, 1987; Wyman, 1998). Plethodontid salamanders are excellent study animals in forested ecosystems because of their physiological ties to microhabitat and microclimate, the relative ease of sampling populations, and the low variation in abundance estimates (Welsh and Droege, 2001).

Although researchers generally agree that terrestrial salamanders play important roles in ecosystem processes, the strength and persistence of effects from forest harvesting on salamander populations has been more controversial. Across 16 research projects, control stands had about 4.3× more captures of salamanders than clearcut stands (deMaynadier and Hunter, 1995), yet the length of time for populations to return to pre-harvest levels and comparisons of clearcut harvesting to other silvicultural regimes have not been well-documented. Recovery times of salamander populations following clearcut timber harvest reportedly range from 20 to 70 years in southern Appalachian forests, but these estimates represent extrapolated salamander captures through time (Ash, 1997) or are from chronosequence studies without randomization (Petranka et al., 1993). Likewise, the effects of timber harvesting on demography of salamanders remains largely unstudied over long time periods and across large spatial scales (deMaynadier and Hunter, 1995). Even a single disturbance to a population of salamanders with low reproductive rates may contribute to the lengthy recovery period that seems to outlast microclimatic or structural changes to managed stands (Dupuis and Bunnell, 1999; Semlitsch et al., 2007). Thus, understanding how anthropogenic disturbances influence vital rates of salamanders could be important to prioritize conservation and management efforts by identifying mechanisms of population changes (Biek et al., 2002) associated with forestry practices.

We examined changes in the relative abundance and reproductive demography of plethodontid salamanders following the experimental application of a suite of forest management prescriptions designed to facilitate oak (*Quercus* spp.) regeneration in a randomized design replicated across central Appalachian hardwood forests over a 13-year post-treatment period. Based on prior research on these sites, relative abundances of salamanders decreased immediately following treatment (Harpole and Haas, 1999; Knapp et al., 2003). However, we predicted that relative abundances of salamanders would increase as harvested treatments gained vertical structure and entered the stem exclusion stage (Smith et al., 1997). We further predicted that if habitat quality for salamanders remained suppressed, then demographics associated with

reproduction (e.g., number of eggs/gravid female, number of gravid females) would be greater in unharvested treatments through the study period. Finally, we evaluated the relative importance of demographic parameters to the population growth rate with a sensitivity/elasticity analysis and modeled population growth of the most common salamander species in our study. These data contribute to a growing body of research documenting that human-caused disturbances to forested habitats may have lasting consequences to salamander population size and dynamics.

2. Materials and methods

2.1. Study sites

Our research encompassed six study areas across Virginia and West Virginia, spanning ≈300 km north to south and 200 km east to west. Study sites (blocks) were established within the Ridge and Valley and the Cumberland Plateau physiographic provinces in the Jefferson National Forest, Virginia (BB1, BB2, CL1, and CL2), and the Mead-Westvaco Corporation's Wildlife and Ecosystem Research Forest (MWERF), West Virginia (WV1 and WV2) (Belote et al., 2008). Sites were selected to be south-facing with moderate slopes (10–40%), and relatively uniform stocking of merchantable trees (Hammond, 1997; Wender, 2000). They were dominated by moderately productive mixed-hardwoods forest type with stand ages of 62–100 years. Oaks (*Quercus* spp.) dominated the overstory of study sites, and red maple (*Acer rubrum*), yellow poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), Fraser magnolia (*Magnolia fraseri*), and sourwood (*Oxydendron arboretum*) were present (Wender, 2000). At each site, seven 2-ha experimental units (EU) were established adjacent to one another.

A suite of silvicultural systems, ranging from no management (control) to silvicultural clearcut, was applied randomly to EUs within each site using the following prescriptions (in order of increasing overstory removal) during 1994–1998: (1) Control: no silvicultural activity occurred, (2) Midstory herbicide treatment: basal application of herbicide (triclopyr and imazapyr) applied to individual stems to reduce competition for oak seedlings and saplings. Woody stems were individually treated on the lower 15–30 cm with an oil/herbicide solution, (3) Group selection: all stems >2.5 cm dbh removed from 2 to 3 small openings (0.5 ha total) and the residual stand was selectively harvested to improve tree growth and quality. The group selection plots are intended to have additional groups harvested at 20 years following the initial treatment (approximately 2014–2018), (4) Shelterwood: partial harvest, with a 41% reduction in basal area, and the residual stems were dominant or co-dominant stems with dbh of 25–40 cm that will be removed 13–15 years after the initial entry, (5) Leave-tree harvest: partial harvest with 25–45 high-quality trees/ha retained through the rotation, (6) Commercial clearcut: partial overstory removal without regard to future values and unmerchantable trees left on site, and (7) Silvicultural clearcut: all stems >5 cm dbh cut, except for scattered wildlife trees (<10 stems/ha). Treatments were applied randomly within sites. WV1 had

only five of seven treatments; the midstory herbicide treatment and commercial clearcut were not applied. Additional details regarding study sites were reported by Belote et al. (2008) and Knapp et al. (2003). This study included those sites used by Knapp et al. (2003) but include an additional 9-years of post-harvest data and an additional 6th site.

2.2. Field methods

We applied the methods of previous investigations to quantify the relative abundances of terrestrial salamanders among treatments (Harpole and Haas, 1999; Knapp et al., 2003). We sampled salamanders using night-time, area-constrained searches of 2 m × 15 m transects to non-destructively estimate relative abundance of salamanders. Nine sampling transects per 2-ha EU were established in each study site in a 3 × 3 grid ($n = 360$ transects). Transects were >30 m from any edge of EUs, but in some instances, transect locations had to be shifted slightly to avoid slash piles or skid trails that made salamander sampling ineffective.

For each sampling night, one randomly selected transect per treatment was sampled. Each night, we rotated the order in which transects were sampled to avoid potential biases with changing activity levels of salamanders as the night progressed. Individual transects were not searched >1 time/sampling year. Transects were searched nights (>1 h after sunset) during or after rain events when temperatures exceeded 7 °C and the leaf litter and/or soil surface were moist, April–November. Two to three observers hand-captured surface-active salamanders and marked capture locations within transects. Salamanders were measured in the lab and individuals were returned to the point of capture the following day. Salamanders active on surface habitats represent only a portion of the total superpopulation both of surface and subsurface individuals (Bailey et al., 2004). Captures or counts of individuals are a measure of relative abundance only, having a presumably positive and linear relationship to the true population size (Hairston, 1983; Welsh and Droege, 2001; Williams and Berkson, 2004; Reichenbach and Sattler, 2007). We continued to utilize relative abundance indices to provide continuity with prior data collection on EUs (Harpole and Haas, 1999; Knapp et al., 2003), and we assume that expected capture probabilities were approximately equal across all EUs, years, and species complexes (Yoccoz et al., 2001; Pollock et al., 2002; Mazerolle et al., 2007). For a field experiment of this geographic scale, the use of relative abundance estimates from a standardized, non-destructive sampling scheme rather than mark-recapture of uniquely marked salamanders had both logistical and financial benefits.

Densities of forest-dwelling wildlife populations do not always correlate positively with habitat quality (Van Horne, 1983; Todd and Rothermel, 2006), and additional information regarding species demographics or vital rates may strengthen inferences made from relative abundances (Welsh et al., 2008). To develop relationships among salamander relative abundances, habitat quality, and demography, we identified stage-classes (juvenile or adult) from published ranges of snout-vent lengths (SVL) (Sayler, 1966; Petranka, 1998), and counted eggs in gravid females of light-colored salamander species (*Plethodon cinereus*, *Desmognathus ochrophaeus*) by can-

dling (Gillette and Peterson, 2001). We followed Knapp et al. (2003) and pooled members of the slimy salamander semispecies complex (*Plethodon glutinosus* and *P. cylindraceus*) into *P. glutinosus*.

2.3. Statistical analyses for relative abundances

We averaged data from individual transects across sampling nights within a year and EU to the mean number of salamander captures/transect/EU. The study site was the unit of replication and was blocked in analyses. We used a repeated-measure Analysis of Covariance (ANCOVA) to determine effects of the silvicultural treatment, site, year of sampling, and treatment × year interaction on relative abundances of salamanders using SAS 9.1 (SAS Institute, Cary, North Carolina, USA). EUs within study sites had 1–2-years of pre-harvest abundances, which was used as a covariate to account for spatial variation in abundances among treatment plots. We averaged across years to develop the covariate for sites with >1-year of preharvest data. Prior to analyses, data were examined for normality and homoscedasticity, and all non-normal data and data with inconstant variance were square-root transformed to meet the assumptions of analysis of covariance (ANCOVA) (Neter et al., 1996). We used the autoregressive heterogeneous option in SAS to structure the covariance matrices.

Whereas BB1, BB2, WV1, and WV2 were sampled nearly every year since the initial harvest, CL1 was sampled during years 1, 8, and 9 post-harvest and CL2 was sampled years 1, 2, 9, and 10 post-harvest. The large number of missing cells from CL1 precluded its use in an analysis of all post-harvest sampling years. Therefore, we conducted two separate repeated-measures ANCOVAs for the relative abundance of all terrestrial salamanders combined: (1) from years 1 to 13 post-treatment, excluding the CL1 site, and (2) using years 1–2, and 8–9 post-treatment, which included all six study sites. Differences among silvicultural treatments were examined after adjusting p -values with the Tukey–Kramer adjustment. We considered statistical significance at $\alpha = 0.05$.

2.4. Demography

We determined the proportion of sampled populations that were juveniles, the proportion of light-vented adult females that were gravid during the pre-brooding season, and the mean number of yolked eggs of gravid females of light-vented species as metrics of demography. We addressed small sample sizes by pooling salamanders from non-harvested treatments (i.e., control and herbicide EUs) and comparing estimates to pooled harvested treatments (i.e., group selection, shelterwood, leave tree, commercial clearcut, and silvicultural clearcut), which all had decreased relative abundances up to 4-years post-harvest (Knapp et al., 2003). Further, we pooled data across years into three time periods to examine how long potential changes to demography persisted after treatment. We examined demographics within year 0, the preharvest sampling period, and divided the post-harvest periods into two, approximately equal time periods. We examined demographics from 1 to 6-years post-harvest, which we termed “early,” and from 7 to 13-years post-harvest, which we termed “late.”

To estimate the reproductive status of females, we only considered adult female salamanders captured prior to June 15 of each year, after which gravid females could be expected to be brooding eggs, and thus unavailable for capture. We separated adult salamanders from juveniles using maximum SVLs for juveniles reported in Petranka (1998): 34 mm for *P. cinereus*, 38 mm for *P. richmondi*, 58 mm for *P. glutinosus*, and 30 mm for *D. ochrophaeus*. Demographics of less commonly captured species were not compared.

We used two-tailed binomial proportions tests to compare differences between the proportion of gravid to non-gravid females of light-vented species (i.e., *P. cinereus* and *D. ochrophaeus*) and the proportion of juveniles to adults between harvested and unharvested treatments for commonly captured species (Zar, 1996). We compared the mean number of eggs/gravid female between harvested and unharvested treatments within a time period with two-tailed t-tests (Zar, 1996). The number of eggs in gravid salamanders was not recorded consistently prior to treatment application, so we did not compare the mean number of eggs/female for the preharvest time period.

2.5. Population matrices and projections

Vital rates of *P. cinereus*, the most commonly captured species in our study, were examined for their influence on population growth rates and to determine the potential influence of vital rates on the long-term reduction in relative abundances in harvested treatments. We predicted that relatively low fecundity and high survival of *P. cinereus* would result in a low population growth rate and an extended recovery period. We used a pre-hatching pulse female-based, Lefkovitch three-stage population matrix with pre-juvenile (egg), juveniles, and adults as life-stages based on sizes of individuals (Crouse et al., 1987; Biek et al., 2002) (Fig. 1). *P. cinereus* are direct developers without a larval stage. Thus, we considered females <34 mm SVL as non-reproductive juveniles, and considered females ≥34 mm SVL adults.

We estimated the number of eggs laid/female (i.e., fecundity, F_i) from our estimates of yolked ova during the pre-brooding periods and assumed a 1:1 sex ratio of hatchlings.

Egg survival is thought to be high based on a laboratory study (Highton and Savage, 1961, but see Yurewicz and Wilbur, 2004), and our estimates of eggs/gravid *P. cinereus* ($\bar{X} = 7.03$) matched closely with an estimate of hatchlings/nest ($\bar{X} = 7.17$) from a wild population near our BB1 and BB2 sites (Angleberger and Chinnici, 1975). Based on this information, we estimated egg survival as 0.9 to account for some egg mortality. Across the 13-years of post-harvest sampling, we never captured a gravid female *P. cinereus* with a SVL < 34 mm, and Sayler's (1966) sampling of *P. cinereus* in Maryland only reported gravid females ≥34 mm. Therefore, we assumed that the probability of animals classified as juveniles laying eggs was zero, and based on the literature, females may only reproduce biennially so that the adult probability of laying eggs was 0.5 (Sayler, 1966). Annual survival rates for specific stages of plethodontid salamanders have not been well-documented, but those estimates that are available range from 0.626 to 0.743 for adult *D. ochrophaeus* (Tilley, 1980), 0.155–0.229 for *D. fuscus* (Danstedt, 1975) and 0.81 for *P. jordani* (Hairston, 1983). Because published juvenile survival and adult survival rates for *P. cinereus* were unavailable, we incorporated estimates from a life table analysis of the species with the most similar life history, *P. jordani* (Hairston, 1983). Using demographic parameters from a congener is a commonly used technique for population modeling (Biek et al., 2002; Heppell et al., 2000). Although life tables rely on the often untenable assumptions of a stable age distribution and equal probability of being sampled among individuals (Gaillard et al., 1998), these survival estimates represented the best available information. From Hairston (1983), we estimated annual adult survival as 0.81 and annual juvenile survival as 0.574 and incorporated these values into the population matrix (Fig. 1). We followed Crouse et al. (1987) to estimate stage-specific probabilities of surviving and remaining a juvenile (P_i) and of surviving and entering the adult stage (G_i).

We used analytical sensitivity and elasticity analysis (Caswell, 2001) to determine the influence of individual vital rates on proportional changes in the population growth rate (λ) (Biek et al., 2002). Sensitivity refers to the change in λ from an infinitesimal change in an individual vital rate, and elastic-

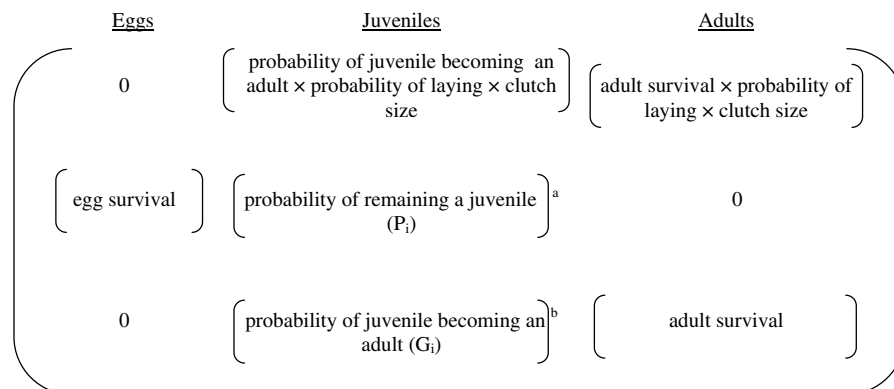


Fig. 1 – Female-based Lefkovitch population matrix for eastern red-backed salamanders, *Plethodon cinereus*. (a) We calculated P_i as $\left((1 - p_i^{d_i-1}) / (1 - p_i^{d_i}) * p_i \right)$ following Crouse et al. (1987) where p_i is the annual survival estimate of a juvenile and d_i is the number of years spent as a juvenile. (b) We calculated G_i as $\left(p_i^{d_i} * (1 - p_i) / (1 - p_i^{d_i}) \right)$ following Crouse et al. (1987) where p_i is the annual survival estimate of a juvenile and d_i is the number of years spent as a juvenile.

ity simply rescales sensitivity to a proportional change in λ with a proportional change in a single vital rate (Caswell, 2001). Sensitivity and elasticity analyses are useful for estimating changes in λ when changes to survival or reproduction occur; thus, these results can be used to predict how salamander populations may respond to perturbations in survival or reproduction (Biek et al., 2002).

Secondly, to qualitatively evaluate whether observed changes to relative abundance from forest harvesting impeded population recovery to pre-harvest levels, we projected our population matrix for 15 time steps, the approximate length of this study. First, we multiplied our female-based projection matrix by a hypothetical population-vector representing the number of individuals in the stage classes at time zero (PM1). Our vector was based on the number of juveniles: adults observed during years 1–6 post-treatment across all treatments (14:37). We assumed 1/2 of females produced seven eggs, and 1/2 of the eggs were female, so that 64 eggs were in the population at $t = 0$. We selected our starting numbers of individuals to sum to a population size close to 100 to simplify interpretation. However, we were not interested in absolute numbers of salamanders, but rather in determining the dynamics of the population over time so that any number of eggs: juveniles: adults in the aforementioned proportions would produce the same conclusions.

From our field data, 24% of the pre-harvest abundance of *P. cinereus* was present in the silvicultural treatments with canopy disturbance by 3-years post-harvest. Assuming this reduction in relative abundance of salamanders represented the decline in the population size of *P. cinereus*, or at least of surface-active salamanders, we estimated whether a simultaneous reduction of all stage-classes by 76% would prevent populations from rebounding to pre-harvest levels of abundance within 15 years (PM2). We considered PM1 to be a baseline population unaffected by disturbance and qualitatively compared PM2 to the population structure. We projected the population prior to reaching the stable age distribution because we were interested in the initial dynamics, which represented the disruption of population age structure from forest harvesting. Population projections and associated computations were calculated with the PopTools 2.7.5 (G.M. Hood, CSIRO Corporation) add-in to Microsoft Excel 2003 (Microsoft Corporation).

3. Results

3.1. Overstory basal area

Overstory basal area of EUs prior to treatment, 2 years after treatment and 9–11 years after treatment averaged 29 m²/ha, 30 m²/ha, and 32 m²/ha for the control EUs, 32 m²/ha, 32 m²/ha, and 33 m²/ha for the midstory herbicide treatment EUs, 32 m²/ha, 18 m²/ha, and 20 m²/ha for the group selection EUs, 32 m²/ha, 14 m²/ha, and 16 m²/ha for the shelterwood EUs, 31 m²/ha, 8 m²/ha, and 10 m²/ha for the leave tree EUs, 34 m²/ha, 6 m²/ha, and 10 m²/ha for the commercial clearcut EUs, and 33 m²/ha, 1 m²/ha, and 2 m²/ha for the silvicultural clearcut EUs, respectively (C. Atwood, Virginia Tech, Department of Forestry, unpublished data).

3.2. Total salamander abundance

Across the 14 years of sampling, we attained >10,000 captures of plethodontid salamanders across 263 sampling nights. Data were square-root transformed prior to analyses to meet the parametric assumptions of normally distributed residuals and homogeneity of errors. Following transformation, residuals were normally distributed and variances were homogeneous ($P > 0.55$). Pre-treatment estimates of abundance differed ($F_{1,21} = 17.01$, $P < 0.001$) and were incorporated in analyses as a covariate. For the analysis up to 13-years post-treatment, there were significant differences among years post-harvest ($F_{12,179} = 9.74$, $P < 0.001$) and treatments ($F_{6,21} = 9.71$, $P < 0.001$), but no significant treatment \times year interaction ($F_{72,179} = 0.62$, $P = 0.989$). In general, silvicultural treatments with canopy disturbance had lower relative abun-

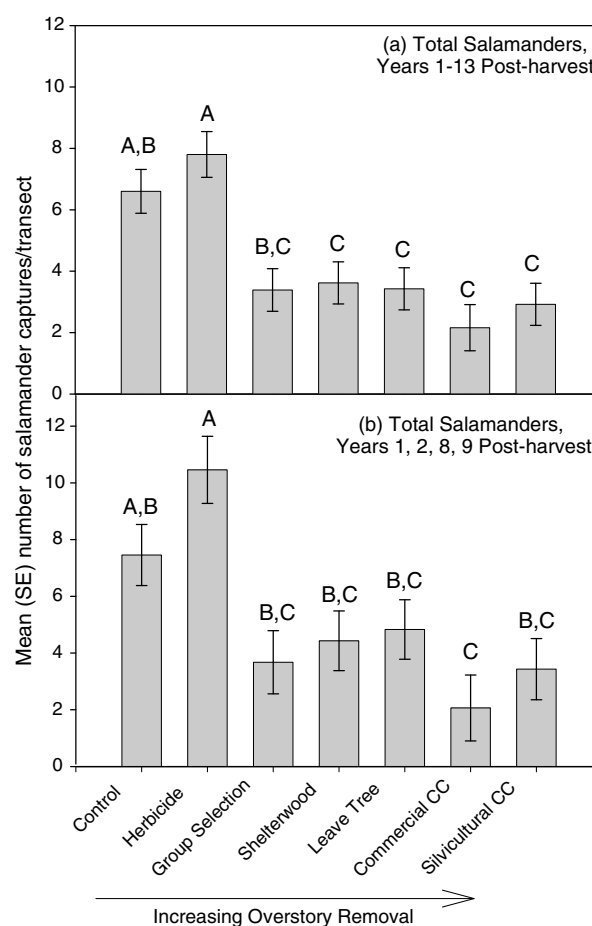


Fig. 2 – Effects of six experimental forest harvests and an untreated control on the relative abundances of (a) total salamander captures from 1 to 13-years post-harvest on five of six study sites (b) total salamander captures during years 1, 2, 8, 9 post-harvest on six of six study sites. Data were analyzed with repeated-measures Analysis of Covariance so that presented means are adjusted by preharvest abundances. Different letters indicate statistical differences among treatments ($P < 0.05$). Non-transformed data are presented, but analyses were conducted on square-root transformed abundances.

dances of salamanders than treatments without canopy disturbance (i.e., control and herbicide) (Figs. 2 and 3). Relative abundance of salamanders in the group selection harvest was lower than the herbicide treatment, but not significantly different than any other treatment.

For the ANCOVA that included all six study sites, but only years 1, 2, 8, and 9 post-harvest, there were significant differences among pre-treatment estimates of abundance ($F_{1,27} = 10.11, P < 0.004$), treatments ($F_{6,27} = 6.36, P < 0.001$), but no significant effect of year ($F_{3,78} = 1.04, P < 0.379$), or

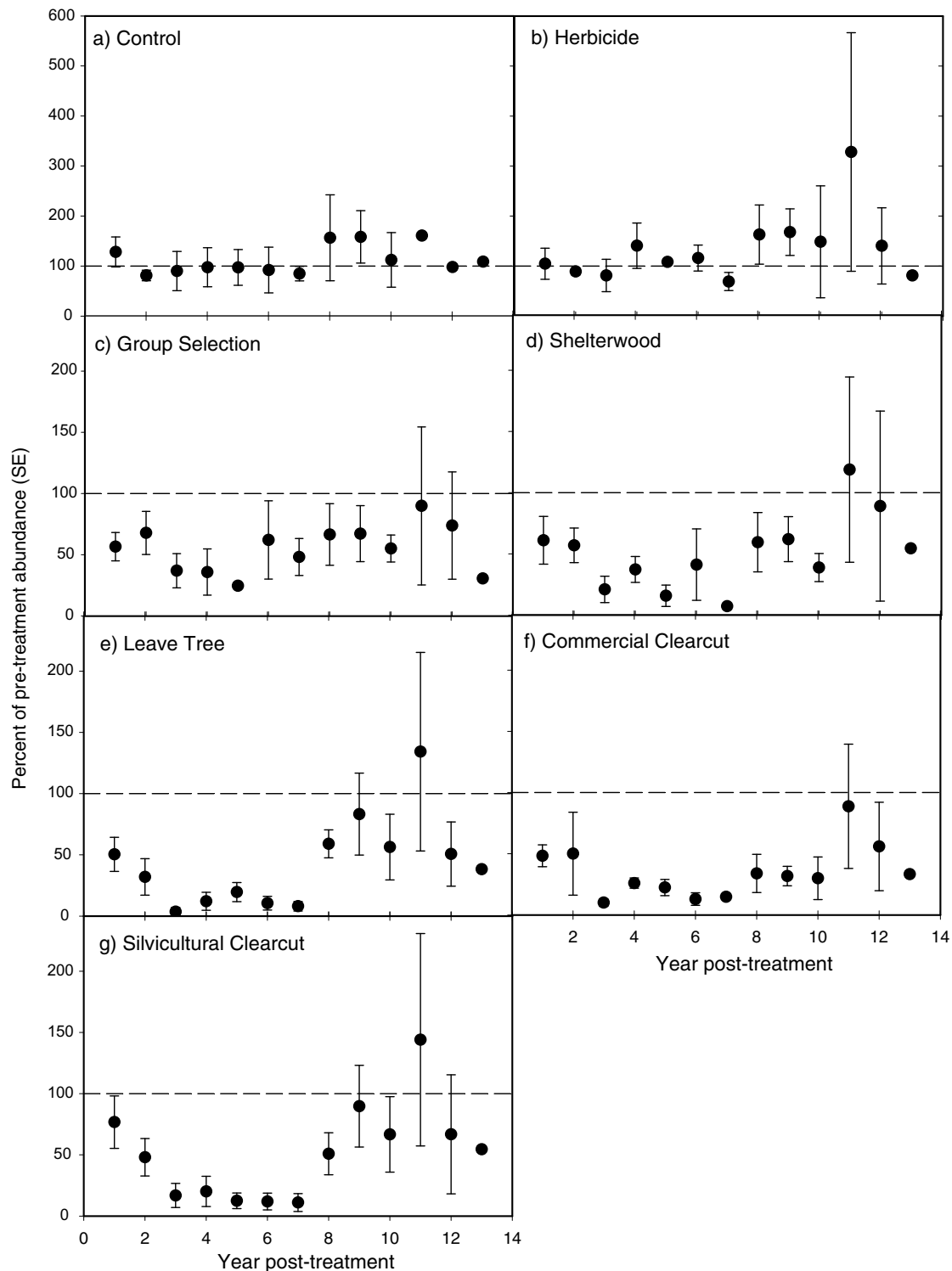


Fig. 3 – Percent of pre-treatment abundance (SE) of terrestrial salamanders across seven silvicultural treatments in experimentally manipulated forested sites in Virginia ($n = 4$) and West Virginia ($n = 2$), USA to 13-years post-harvest. Sites were harvested in different years, so not every site was sampled yearly or to 13-years post-harvest, which contribute to variation in standard errors across years. Dashed line indicates recovery to pre-treatment abundance (100%).

year \times treatment interaction ($F_{18,78} = 0.53$, $P = 0.934$). Relative abundance of terrestrial salamanders was greatest in the control and herbicide treatments, which were similar to each other ($P = 0.820$). Whereas the control EUs did not differ ($P > 0.05$) from any treatment with canopy disturbance except for the commercial clearcut ($P = 0.014$), the herbicide treatment had greater salamander abundances than all silvicultural treatments other than control EUs (Fig. 2).

3.3. Demographic differences in treatments

No consistent patterns emerged for demographics across the four species of salamanders examined. The proportion of juvenile salamanders captured varied among the four most common species, ranging from 22% of *P. cinereus* in the harvested treatments, during the late period, to 75% of *P. glutinosus* in the harvested treatments during the late period (Table 1). The proportion of juvenile *P. cinereus* was greater in the unharvested than harvested treatments during the late time period and for *D. ochrophaeus* during the early period ($P < 0.05$) (Table 1). For *P. richmondi*, the proportion of juveniles was greater in harvested treatments during the pre-treatment period ($P = 0.039$), but this did not persist through later periods. The proportion of juvenile *P. glutinosus* did not differ between treatment classes in any time period ($P > 0.05$).

Across the entire study, we captured 512 gravid *P. cinereus* and 170 gravid *D. ochrophaeus* prior to June 15 (Table 1). The proportion of gravid female *P. cinereus* or *D. ochrophaeus* did not differ between harvested or unharvested treatments during any time period ($P > 0.09$) (Table 1). However, the proportion of gravid female *P. cinereus* did appear to decline through time since harvest. Further, the number of yolked eggs/gravid female *P. cinereus* did not differ between harvested and unharvested treatments ($P > 0.17$) (Table 1). During years 1–6 post-harvest, the average number of eggs/gravid female *D. ochrophaeus* was 13.8 in unharvested treatments and 11.3 in harvested treatments, which differed statistically ($t_1 = 2.64$, $P = 0.01$).

3.4. Population projections of *P. cinereus*

Based on the population matrix derived from estimated vital rates of *P. cinereus*, the probability of surviving and remaining a juvenile (P_i) was 0.475 and the probability of surviving and entering the adult stage class (G_i) was 0.099. Further, we estimated λ as 1.03 indicating the population was increasing by 3%. The sensitivity and elasticity analyses revealed an infinitesimally small perturbation in adult survival would result in the greatest change of λ . Elasticity of adult survival (0.487) was 3.7–4.3 \times other elements of the population matrix. Therefore,

Table 1 – Demographic characteristics of common salamander species following experimental forest harvests in central Appalachian oak forests, 1994–2007. Data were divided into three time periods: (1) preharvest, which included sampling years prior to application of silvicultural treatments, (2) early, which included estimates from years 1 to 6 post-harvest, and (3) late, which included estimates from years 7 to 13 post-harvest.

Species	% Juvenile ^b		% Gravid ^c		Mean eggs/female	
	Unharvested	Harvested	Unharvested	Harvested	Unharvested	Harvested
<i>Plethodon cinereus</i>						
Preharvest, year 0	38 (62/165)	46 (210/453)	65 (22/34)	81 (54/67)	n/a	n/a
Early, years 1–6	26 (250/978)	29 (231/802)	32 (103/321)	33 (86/261)	6.7	6.9
Late, years 7–13	28 (242/853) ^d	22 (168/751) ^d	52 (122/235)	55 (125/229)	7.1	7.3
<i>Desmognathus ochrophaeus</i>						
Preharvest, year 0	38 (203/539)	39 (437/1112)	56 (37/66)	66 (90/137)	n/a	n/a
Early, years 1–6	35 (74/209) ^d	23 (36/155) ^d	55 (17/31)	57 (17/30)	13.8 ^d	11.3 ^d
Late, years 7–13	44 (135/310)	45 (66/148)	45 (9/20)	0 (0/3)	12.0	n/a
<i>Plethodon glutinosus</i>						
Preharvest, year 0	71 (76/107)	74 (211/287)				
Early, years 1–6	39 (80/121)	55 (84/153)				
Late, years 7–13	71(102/143)	75 (182/244)				
<i>Plethodon richmondi</i>						
Preharvest, Year 0	44 (71/161) ^d	54 (211/391) ^d				
Early, years 1–6	51 (27/53)	40 (23/58)				
Late, years 7–13	64 (55/86)	68 (41/60)				

a Unharvested plots included control and herbicide plots and harvested plots included group selection, shelterwood, leave tree, commercial clearcut and silvicultural clearcut plots.

b Proportions of juvenile salamanders were calculated by dividing the number of *P. cinereus*, SVL < 34 mm, *D. ochrophaeus*, SVL < 30 mm, *P. glutinosus* SVL < 58 mm, or *P. richmondi* SVL < 38 mm by the total number of that species. Within a time period, the proportion juvenile was compared between harvested and unharvested treatments with a two-tailed binomial proportions test.

c Gravid females were totaled from all adult females (*P. cinereus*, SVL \geq 34 mm, *D. ochrophaeus*, SVL \geq 30 mm,) of light-vented species captured on or prior to June 15th of each year. Within a time period, the proportion of gravid females was compared between harvested and unharvested treatments with a two-tailed binomial proportions test. Due to the low samples sizes of female *D. ochrophaeus* during the late period, a statistical comparison was not made for proportion of gravid female *D. ochrophaeus* 7–13-years post-harvest.

d Statistically different at $P < 0.05$.

if adult survival decreased from 0.81 to 0.71, λ would be expected to decrease by 5% $[((0.71-0.81) * 0.487) = -0.05]$.

The two projection scenarios varied in the resulting population structure after 15 years (Fig. 4). The baseline projection (PM1) displayed a steadily increasing population. In contrast, after a 76% reduction across stage classes to represent observed declines in abundance (PM2), only the number of juveniles grew to “pre-harvest” levels after 15 time steps. Approximately 60 years would be necessary for all stage classes to recover under PM2. Scenarios required approximately 3–4 time steps to reach the stable age distribution (Fig. 4).

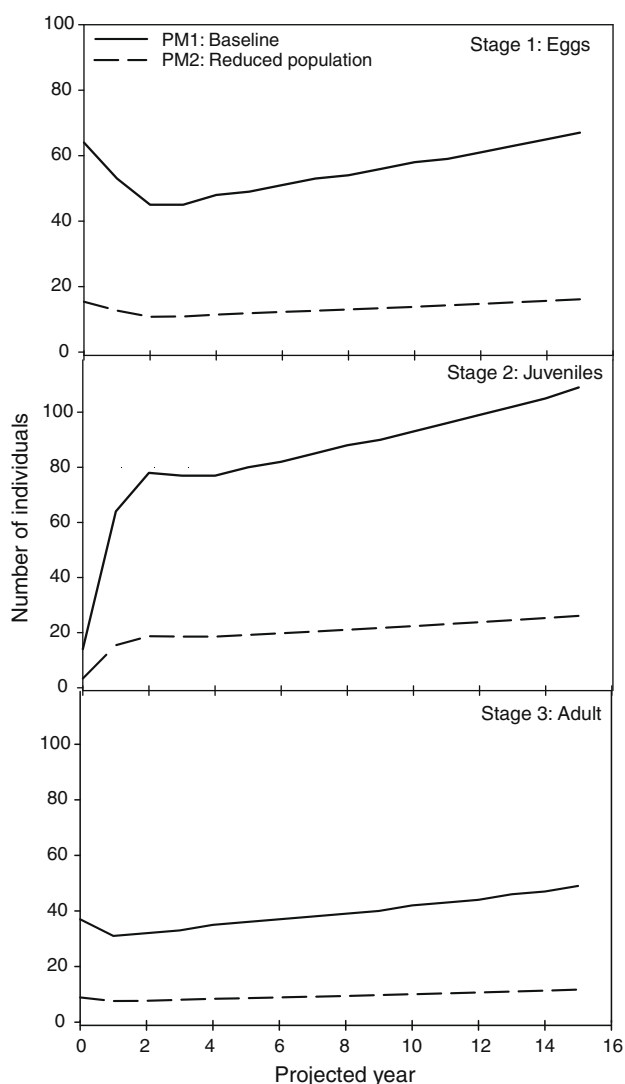


Fig. 4 – Number of individuals from a stage-based population matrix of vital rates of eastern red-backed salamanders (*Plethodon cinereus*) with egg, juvenile, and adult life-stages and projected to 15 years. We used our observed juvenile: adult ratio from years 1 to 6 post-harvest (14:37) and assumed 50% of females would produce 7 eggs with an equal sex ratio within a year. Two scenarios were projected: (PM1) a baseline projection, where the observed ratio of juveniles: adults from field studies was used, (PM2) where each stage was reduced by 76% to represent observed losses following silvicultural treatments.

4. Discussion

Silvicultural treatments that disturbed the canopy in Appalachian hardwood forests had long-term negative impacts on relative abundance of terrestrial salamanders. Contrary to our prediction, we detected significant treatment effects through 13-years post-harvest and failed to detect significant treatment \times time interactions, suggesting that the negative effects of the silvicultural techniques were persistent and consistent through our study period. Similar to Harpole and Haas (1999) and Knapp et al. (2003), we observed lower total numbers of salamander captures in most treatments with canopy disturbance as compared to both the control and herbicide EUs (Fig. 2). The exception was the group selection treatment, which only had significantly smaller numbers of salamander captures compared to the herbicide EUs.

As with worldwide losses in biodiversity, degradation of habitat has been implicated as one of a suite of factors causing global declines of amphibians (Alford and Richards, 1999; Beebee and Griffiths, 2005). Although North American plethodontid salamanders typically have not displayed the wide-scale population declines of other amphibians (but see Highton 2005), these species experience local declines after anthropogenic disturbances to their habitats, such as from forest harvesting. The short-term effects of forest harvesting to terrestrial salamanders (Pough et al., 1987; deMaynadier and Hunter, 1995) and longer-term consequences of clearcutting on forest amphibians (Petranka et al., 1993; Ash, 1997; Herbeck and Larsen, 1999; Ford et al., 2002) have been documented, but experimental comparisons of a broad range of forest regeneration techniques across broad spatial and temporal scales are lacking. Based on the results of our long-term experimental manipulation of mixed-hardwood forest, relative abundances of terrestrial salamanders showed long-term changes from the application of six oak regeneration techniques, and population vital rates indicate that life history characteristics may contribute to these observed patterns.

Results from our second analysis that included all six study sites, but only years 1, 2, 8, and 9 post-harvest were more ambiguous, presumably due in part to fewer degrees of freedom and subsequently lower power to detect differences. Further, strong declines in salamander abundances after harvesting were not evident in year 1 (Knapp et al., 2003), which also could have influenced the results. From this, only salamander abundances in the herbicide EUs were statistically greater than the other silvicultural treatments, and the control EUs could only be distinguished from the commercial clearcut (Fig. 2).

Although our results varied depending on whether all years of post-harvest data or all sites were included, it is clear that a wide range of oak regeneration treatments had lasting negative effects to salamanders in Appalachian hardwood forest. During years 8–9 post-harvest, only the control and herbicide EUs had abundances \geq the pretreatment period; the other treatments ranged from 33% of preharvest abundances for the commercial clearcut to 70% for the silvicultural clearcut (Fig. 3). Overall, the harvested treatments increased from a low of 18% at year 3 post-treatment to 67% at year 9. From the perspective of terrestrial salamanders, silvicultural alternatives to clearcutting may not be suitable for maintain-

ing abundances for an extended period of time following harvest.

During both the initial post-harvest period (Harpole and Haas, 1999; Knapp et al., 2003) and during our long-term study, the herbicide treatment supported either similar or greater abundances than control EUs. We are uncertain why salamanders may have increased their abundances following the understory herbicide treatment, especially given that the understory vegetation, microclimate, and leaf litter biomass were not substantially different from control EUs (Hammond et al., 1998; Harpole and Haas, 1999; Knapp, 1999). It is possible that subtle changes in understory vegetation structure in herbicide EUs led to increased foraging opportunities and success for salamanders (Jaeger, 1978), ultimately increasing fecundity or the proportion of juveniles surviving. Or, a slight decrease in basal area without a concurrent increase in canopy openness may have led to increased soil moisture from less evapo-transpiration through woody stems.

4.1. Demography of salamanders

If the long-term decreases in relative abundances of terrestrial salamanders were caused by reductions in habitat quality from oak regeneration treatments, then differences in reproduction of salamanders should be apparent between harvested and unharvested treatments. In agreement with our prediction, some demographics associated with fecundity were greater in unharvested treatments. Both *D. ochrophaeus* and *P. cinereus* had a greater proportion of juveniles in the unharvested treatments, but the difference was evident soon after harvesting (years 1–6 post-harvest) for *D. ochrophaeus* whereas the proportion of juveniles differed for *P. cinereus* 7–13-years post-harvest. *D. ochrophaeus* brood 8–37 eggs annually (Petranka, 1998) and female *P. cinereus* produce an average of 6–9 eggs every other year (Sayler, 1966; Petranka, 1998). Therefore, there may have been a greater time lag in the changes to demography caused by forest manipulations to *P. cinereus* as a result of lower fecundity.

Other research has noted differences in demographics of terrestrial salamanders when comparing uncut forest stands to recent clearcuts, including a smaller proportion of juvenile and fewer adult male *P. metcalfei* in reproductive condition in a 10-year-old clearcut (Ash et al., 2003). Conversely, a greater proportion of juvenile *P. cinereus* were reported in forest clearcuts harvested 2–11 years earlier than in mature stands (deMaynadier and Hunter, 1998) and a greater proportion of young *P. elongatus* in young forest compared to late seral forest (Welsh et al., 2008). A change in salamander reproductive demographics was not detected within the first 1–4 years following stand treatments on these study sites (Knapp et al., 2003), but the number of sites, years of post-treatment sampling, and number of salamander captures all have increased greatly in this study.

Adult salamanders in the unharvested EU's may have been more fecund and able to maintain the number of juveniles via higher reproductive values than salamanders in the harvested EU's with reduced reproduction. The greater number of *D. ochrophaeus* eggs/gravid female in unharvested stands supports the hypothesis that habitat quality for at least some

species of salamanders is altered by forest harvesting, although we did not detect differences in the proportion of gravid females for light-vented species. The mechanisms altering habitat quality of salamanders from forest harvesting are not known, but changes to invertebrate prey (Mitchell et al., 1996), increased energetic requirements (Brooks and Kyker-Snowman, 2008), or limits to cutaneous respiration (deMaynadier and Hunter, 1998) may negatively affect reproduction or survival of terrestrial salamanders.

4.2. Population modeling

Perturbations of vital rates and possibly λ may be a key mechanism causing reduced abundances of wildlife following a disturbance (Todd and Rothermel, 2006). Our elasticity analysis indicated that disturbances that affect survival of adult *P. cinereus* would have the greatest influence on the population growth rate (Biek et al., 2002). In fact, a decrease in adult survival of as little as 10% could cause the population to decline. However, PM2, which reduced numbers of juvenile and adult salamanders by a realistic 76% with no decrease in survival, closely approximated the reduction of salamanders we observed in our experimental treatments. At 9-years post-treatment the total number of salamanders in harvested EUs was at 67% of preharvest abundances, similar to the 62% of adult and juvenile salamanders predicted by the projection matrix at year 9. Our results suggest that increased mortality as a result of a single disturbance without long-term changes in survival of *P. cinereus* from forest harvesting could explain our observed patterns of abundance. Whether increased desiccation and/or temperatures had greater effects on juvenile salamanders is unknown, but plausible, given their higher surface area: volume ratios. We stress that survival estimates for this analysis were from a congener, that those estimates may differ based on skeletochronology (Ash et al. 2003), and currently no estimates of variability in this vital rate are available, so that our projections should be viewed cautiously. Additionally, we do not have information on movement of salamanders after harvesting, and recolonization of harvested EUs could have been facilitated by immigration of individuals from outside our sites (deMaynadier and Hunter, 1998; Ash et al., 2003).

With the observed reduction in salamanders and the low population growth rate (3%), >60 years would be needed for all life-stages of *P. cinereus* to reach predisturbance levels. In clearcut stands, recovery of salamanders has been estimated from 20 to 70 years in the Appalachians based on chronosequence and observational studies (Petranka et al., 1993; Ash, 1997), which encompasses this estimate. And, >80 years may be necessary for the negative effects of logging roads on terrestrial salamanders to dissipate, indicating that forest disturbances have long-lasting effects on salamanders (Semlitsch et al., 2007). Despite the potential benefits from population analyses to conservation and management of amphibians (Biek et al., 2002; Boyce et al., 2006; Todd and Rothermel, 2006), ours is the first study that we are aware of to use either a sensitivity/elasticity analysis or projection matrices to model the effects of forestry practices on dynamics of terrestrial salamanders. Although our population analyses were deterministic and density independent, these

results suggest that the return of salamander populations to harvested plots may not only be limited by long-term changes to habitat (deMaynadier and Hunter, 1995; Ash, 1997), but also by the life history characteristics and reproductive potential of salamander species.

4.3. Management implications

To evaluate the trade-offs between economic gain and ecological stability, forest managers need results from long-term experimental manipulations. Our research indicates that a range of forest management techniques may cause lasting reductions of terrestrial salamander populations likely due to both low population growth rates and changes to habitat. Future studies of the influence of silviculture on salamanders should estimate survival rates of salamanders before and after forest harvesting and determine whether movements occur in or out of harvested stands. In the past, long-term marking techniques for small amphibians were limited, but subcutaneous marking of *Plethodon* salamanders with elastomers can be a reliable method for mark-recapture studies (Davis and Ovaska, 2001; Heemeyer et al., 2007) to estimate survival as can individual pattern recognition (Tilley 1980; Church et al., 2007). Similarly, population reconstruction of salamanders from skeletochronology (Ash et al., 2003, but see Bruce and Castanet, 2006; Eden et al., 2007) or size distributions (Hairston, 1983) can provide estimates of age-specific survival for population modeling, but life table modeling relies on assumptions difficult to reach in wild populations and does not provide estimates of variability (Gaillard et al., 1998).

Although we provide some evidence that salamanders in group selection harvests may be recovering more quickly compared with other oak regeneration options, these EUs are scheduled for a second entry in 7–9 years (approximately 20 years after the first entry). The effects of multiple stand entries on terrestrial salamander populations are unknown, but are likely to have cumulative negative impacts. Further, managers must also consider the trade-offs between the amounts of wood fiber extracted, costs of harvesting, soil erosion, and number of re-entries required when evaluating silvicultural regimes. For example, combining loss of salamanders with the area of land required to extract a given amount of wood fiber, Knapp et al. (2003) determined that the group selection harvest has $1.8\times$ the landscape-scale effect on salamanders as the silvicultural clearcut. Additionally, the group selection harvest was estimated to have 10 tons/acre more soil loss than other treatments over a 100-year rotation (Hood et al., 2002) and may have less vigorous regeneration of oaks from stump sprouts than other silvicultural systems (Atwood, 2008). Thus, implementing silvicultural clearcuts, which could limit the spatial extent of habitat alteration, could provide a method to maintain populations of terrestrial salamanders at a larger scale, given that remaining forested habitats are not disturbed. Our study only examined the effect of a single stand entry on terrestrial salamanders on 2-ha EUs; repeated disturbances to the soil and vegetation from harvesting equipment and disturbances at a larger spatial scale may cause different effects on salamanders than what we observed.

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