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Post-disturbance effects of even-aged timber harvest on stream salamanders in southern Appalachian forests

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Abstract

Habitat degradation and fragmentation has received increased attention in the past 15 years as a primary factor responsible for the decline of many species of wildlife including amphibians. In the eastern USA many of the studies have focused on fully terrestrial plethodontid salamanders, while information on stream-breeding plethodontids remains relatively lacking. Using two different survey methods (area-constrained daytime searches and night-time visual encounter searches), we estimated terrestrial habitat use and abundance for stream-breeding salamanders in three different tree stand age-classes in southern Appalachian streams from May to August 2005. We found that overall stream salamander abundance and terrestrial habitat use was reduced in stands < 40 years of age compared with stands 41–80 years old, and > 81 years old. The decreased abundance and terrestrial habitat use was accompanied by a decrease in leaf litter depth, soil moisture and canopy cover. The Blue Ridge two-lined salamander *Eurycea wilderae* was the most affected salamander in the assemblage and we conservatively estimate at least a 40-year recovery period for the assemblage to return to pre-disturbance levels. To protect stream amphibians, alternative silvicultural practices such as uneven-aged timber harvest (e.g. selective harvesting) must be considered.

Introduction

Habitat loss and degradation can result from a number of processes (e.g. land development, agriculture), with amphibians being especially sensitive to these disturbances (Cushman, 2006). Amphibians are sensitive to loss and degradation of habitat due to their unique life history requirements (i.e. most amphibians require both aquatic and terrestrial resources to complete their life cycle; Semlitsch, 2000). Within the past decade a number of studies have examined the impacts of timber harvesting on wildlife populations (e.g. Gram *et al.*, 2003; Constantine *et al.*, 2004; Goldstein, Wilkins & Lacher, 2005) and on ecosystem processes (e.g. Ash, 1995; Swank, Vose & Elliot, 2001; Wilkerson *et al.*, 2006) in the USA. In Pacific Northwest redwood forests, Ashton, Marks & Welsh (2006) found that species richness and relative abundance of stream amphibians were significantly greater in the late-seral forests (unharvested) compared with mid-seral forests (37–60 years post-harvest). Karraker & Welsh (2006) also found that body condition was lower in thinned versus unthinned forests. In the Ozark region of the Midwest, Herbeck & Larsen (1999) found that terrestrial salamander density was lowest in recently harvested forests (≤5 years post-harvest) and highest in old-growth forests (>120 years). Comparison of recently harvested forests (≤5 years) with second growth mature forests (>70 years post-harvest) showed that terrestrial salamanders were reduced to very low numbers when mature forests were harvested (Herbeck & Larsen, 1999). Both studies indicate that it could take at least 60 years for amphibian assemblages to return to pre-harvest levels.

In the eastern part of the USA, the effects of timber harvesting have focused on a specific family of salamanders (Plethodontidae). Plethodontid salamanders make up an important ecological component of many forested ecosystems (Davic & Welsh, 2004) and often exceed the combined biomass of other terrestrial vertebrates throughout the Appalachian Mountain region (Burton & Likens, 1975; Petranka & Murray, 2001; Peterman, Crawford & Semlitsch, 2008). There has been considerable debate as to the long-term impacts and recovery of plethodontid salamander populations as a result of even-aged timber harvesting in the southern Appalachian Mountain region (Ash & Pollock, 1999). Petranka, Eldridge & Haley (1993) found that mean abundance of salamanders was approximately five times higher in mature forests (>50 years old) versus forests that were recently clear-cut (<10 years old). They estimated that it would take 50–70 years for salamander populations to return to pre-disturbance levels. In contrast, Ash (1997) found that abundance of salamanders on clear-cut plots decreased to *c.* 30–50% of forested plots in the first year after timber harvest and were almost zero after the second year. However, he found that salamanders returned to clear-cut plots 4–6 years post-disturbance and estimated that it

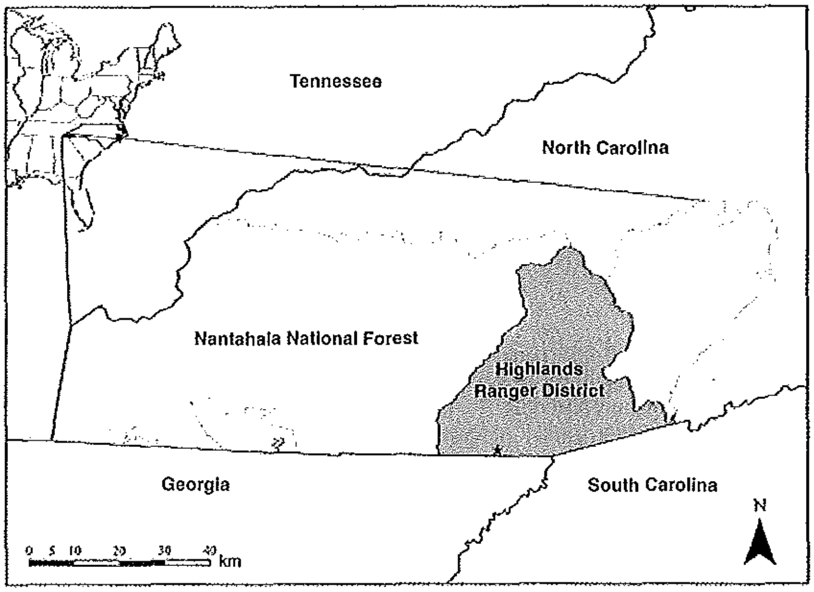

Figure 1 Location of study sites in the Nantahala National Forest, North Carolina, USA.

would take 20–24 years for salamander populations to return to pre-disturbance levels. Despite this considerable work in the eastern USA, the majority of this research has focused on woodland salamanders (genus *Plethodon*; e.g. Petranka *et al.*, 1993; Ash, 1997; Harper & Guynn, 1999). However, all woodland salamanders are completely terrestrial, have direct development, and do not require water for reproduction, which means they are not constrained to terrestrial areas near streams. Yet, many species of the Plethodontidae require streams for reproduction and larval development and the riparian areas surrounding streams are known to be important for various life history functions of stream-breeding salamanders (Petranka & Smith, 2005; Crawford & Semlitsch, 2007). While some stream-breeding species have been captured in studies that dealt with timber harvesting in the southern Appalachians, research to date has not specifically addressed the effects of logging on streamside assemblages.

We sampled stream salamanders in three different stand age-classes to determine the effects of post-disturbance timber harvest and estimate recovery time of salamander populations. Specifically, we compared terrestrial habitat use and salamander abundance in riparian areas found in three stand age-classes. Based on previous studies of plethodontids, we hypothesized that terrestrial habitat use and salamander abundance would be significantly lower in stands <40 years old compared with stands between the ages 41 and 80 years and stands >81 years.

Methods

Study area

To estimate terrestrial habitat use (which was defined as distance from the streams) and stream salamander abundance, we sampled riparian forests adjacent to 12 headwater streams in the southern Appalachian Mountains, Nantahala National Forest, Macon County, NC, USA (Fig. 1). All sites were located between 771 and 1221 m in elevation and were located at least 1 km apart. Four streams were located in stands between 0 and 40 years since last timber harvest (average 27 years, range 25–31 years), four streams were located in stands between 41 and 80 years since last timber harvest (average 68 years, range 62–78 years) and four streams were located in stands that had not been harvested for ≥ 81 years (average 96 years, range 84–108 years). To assign age categories of each stand, compartment maps were consulted at the Highlands Ranger District office in Highlands, NC. At the time of harvest, each stand had at least 70% of the trees logged. To ensure maximum capture success and detection of rare species (Hyde & Simons, 2001), we used two different sampling techniques. Sites were sampled six times each (three-day transects, three-night transects) from May to August of 2005.

Daytime sampling

During daytime transect searches, we sampled along a paired transect that was separated by 1 m (to increase sample sizes of salamanders; data for each plot were combined) and extended perpendicular from the stream bank into the adjacent forest. Monitoring stations were established at 1, 3, 7, 10, 15, 25, 50 and 100 m from the stream bank, based on the home range sizes and potential distances traveled by the target species of stream-breeding salamanders (Crawford & Semlitsch, 2007). Three different transect lines were sampled during the season, each separated by 25 m (transect lines were also at least 25 m away from the nearest road to reduce any potential edge effects). Surveys of streams and transect lines at each stream were performed randomly. At each stream, we sampled along the daytime transect by using area-constrained searches of each plot (2×2.25 or $4.5\,m^2$ per station) by sifting through leaf litter and coarse woody debris at each monitoring station for an average of 10 min. At each plot, data were collected on four environmental variables: (1) leaf litter depth – measured three times in each plot (six times per station) using a hand ruler for an average leaf litter depth value; (2) soil temperature – measured three times in each plot on bare soil after the leaf litter was removed (six times per station) using an infrared Raytek® MT4 temperature gun (Raytek, Santa Cruz, CA, USA) for an average temperature value; (3) soil moisture – measured three times in each plot (six times per station) at a depth of 6 cm using an Aquaterr® M300 soil moisture meter (Aquaterr Instruments and Automation, Costa Mesa, CA, USA) for an average soil moisture value; (4) canopy cover – measured one time in each plot (two times per station) using a spherical crown densiometer for an average canopy cover value.

We identified all salamanders to species, weighed and measured for snout–vent length and total length, determined sex and recorded the distance from the stream. We released all salamanders at the site of capture. We determined age class (adult or juvenile) by comparing measured snout–vent lengths of each individual to published size classes for each species (Petranka, 1998). Data on abundance and environmental parameters from each transect at a particular stream were pooled before analysis.

Night-time sampling

We used a visual encounter search during the three night-time transects (stream surveys were randomized to reduce bias related to seasonal activity) to capture surface-active salamanders. Two researchers walked a straight line that was perpendicular from the stream edge (defined as the edge of the streambed) out to 100 m and recorded distance from the stream edge for each salamander encountered. While walking the perpendicular transect, each researcher searched 2.5 m to the right and left of the transect line. The time it took to walk a transect line was dependent upon the number of salamanders captured. We processed salamanders in the night-time samples the same as detailed above for the daytime samples. Abundances from each transect at a particular stream were pooled before analysis.

Data analysis

We used a general linear model to test for treatment effects of stand age-classes on terrestrial habitat use and daytime and night-time salamander abundances (response variables) using the univariate ANCOVA model in SPSS (v. 15). Preliminary analyses revealed no significant differences between adults and juveniles of any of the study species with respect to abundance and terrestrial habitat use so data were pooled to increase sample size. Elevation was used as a covariate in all analyses because it can have strong effects on site parameters such as precipitation and temperature. Tukey's honestly significant difference test was used to test for differences among stand age-classes. Tests with $P < 0.05$ were considered significant. Data recorded in percentages were transformed with the arcsine transformation before analysis.

Results

Daytime salamander sampling

In 2005, 148 total salamanders were captured along the 12 different streams during daytime sampling. We captured 34 seal salamanders *Desmognathus monticola*, 66 Ocoee salamanders *Desmognathus ocoee* and 48 Blue Ridge two-lined salamanders *Eurycea wilderae*. Stream salamander abundance was 5.03 salamanders $transect^{-1}$ in stands ≥ 81 years of age, 5.08 salamanders $transect^{-1}$ in stands between 41 and 80 years of age and 2.17 salamanders $transect^{-1}$ in stands ≤ 40 years of age (Table 1). Stream salamander abundance was significantly reduced in stands ≤ 40 years of age compared with stands between the ages of 41–80 years, and stands ≥ 81 years old (Table 1). While there was no significant difference between stands of the three different age-classes for seal salamanders or Ocoee salamanders, the two-lined salamanders were significantly reduced in stands ≤ 40 years of age compared with stands between the ages of 41–80 years, and stands ≥ 81 years old (Table 1).

As monitoring distance increased from the stream edge, the abundance of stream salamanders decreased relatively rapidly in stands ≤ 40 years of age, while the decrease in abundance in stands between 41 and 80 years was much less severe, and abundance remained relatively stable in stands ≥ 81 years of age (Fig. 2). Leaf litter and soil temperature increased slightly with increasing distance from the stream, while canopy cover remained relatively constant, and soil moisture decreased (Fig. 3a–d). Average leaf litter depth, average soil moisture and average canopy cover in stands ≤ 40 years of age were all significantly lower compared with stands between the ages of 41–80 years, and stands ≥ 81 years (Table 2). There were no significant differences in average elevation or average soil temperature among the three different stand age-classes (Table 2). Overall, the only significant predictor of daytime stream salamander abundance was average leaf litter depth, although both elevation and moisture approached significance (Table 3).

Night-time salamander sampling

During the 2005 field season, 473 total salamanders were captured among the 12 different stands during night-time sampling. We captured 108 seal salamanders *D. monticola*, 167 Ocoee salamanders *D. ocoee* and 198 Blue Ridge two-lined salamanders *E. wilderae*. Stream salamander abundance was 17.9 salamanders $transect^{-1}$ in stands ≥ 81 years of age, 14.6 salamanders $transect^{-1}$ in stands between 41 and 80 years of age and 6.83 salamanders $transect^{-1}$ in stands ≤ 40 years of age (Table 1). Stream salamander abundance was significantly lower in stands ≤ 40 years of age compared

Table 1 Summary of daytime and night-time abundances[a] of a stream salamander assemblage in the southern Appalachian Mountains in three different stand age-classes[b]

	Stand age (years)			ANOVA	
Species[c]	0–40	41–80	80+	$F_{(2,11)}$	P
Stream day	2.17† (0.21) n=27	5.08* (0.43) n=61	5.03* (0.24) n=60	28.65	<0.001
Desmognathus monticola day	0.60 (0.10) n=7	1.03 (0.24) n=12	1.25 (0.28) n=15	2.28	0.158
Desmognathus ocoee day	1.10 (0.21) n=13	2.33 (0.42) n=28	2.08 (0.42) n=25	3.23	0.088
Eurycea wilderae day	0.58† (0.17) n=7	1.75* (0.17) n=21	1.68* (0.42) n=20	5.68	0.025
Stream night	6.83† (0.51) n=82	14.6* (1.09) n=176	17.9* (2.08) n=215	16.87	0.001
D. monticola night	1.48 (0.28) n=18	3.33 (0.84) n=40	4.18 (1.40) n=50	2.08	0.181
D. ocoee night	2.93 (0.65) n=35	4.98 (1.18) n=60	6.00 (1.35) n=72	2.02	0.188
E. wilderae night	2.40† (0.21) n=29	6.35* (0.20) n=76	7.77* (0.64) n=93	47.33	<0.001

[a]Mean and standard error values.
[b]Means with the same symbol within rows were not significantly different (Tukey's HSD multiple comparison, $P<0.05$).
[c]Stream denotes salamanders in the assemblage (*D. monticola*, *D. ocoee* and *E. wilderae*).

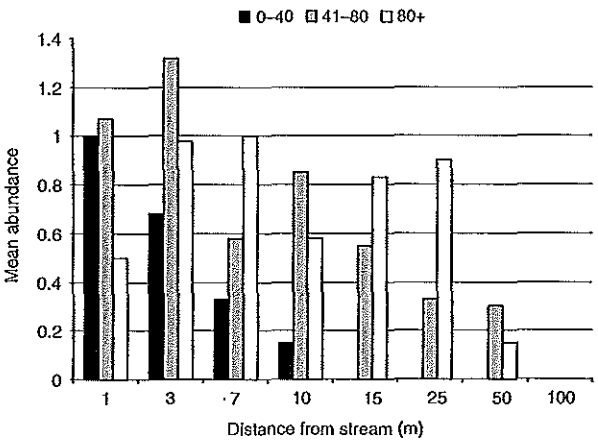

Figure 2 Stream salamander abundance from the edges of headwater streams in three different stand age-classes in the Nantahala National Forest, North Carolina (based on daytime transect searches).

with stands between the ages of 41–80 years, and stands ≥81 years old (Table 1). There was no significant difference between stands of the three different age-classes for seal salamanders or Ocoee salamanders; however, two-lined salamander abundance was significantly lower in stands ≤40 years of age compared with stands between the ages of 41–80 years, and stands ≥81 years old (Table 1).

Overall, stream salamanders were found an average of 9.5 m from the stream in stands ≤40 years of age, 21.2 m from the stream in stands between 41 and 80 years of age, and 21.8 m in stands ≥81 years of age (Table 4). Terrestrial habitat use was significantly reduced in stands ≤40 years old compared with stands between 41 and 80 years old, and stands ≥81 years old (Table 4). Terrestrial habitat use for seal salamanders, Ocoee salamanders and two-lined salamanders was also significantly reduced in stands ≤40 years of age compared with stands between the ages of 41–80 years, and stands ≥81 years old (Table 4).

Discussion

A number of studies have documented the importance of factors such as canopy cover, leaf litter availability and soil parameters in the abundance and distribution of plethodontid salamanders (Spotila, 1972; Ash, 1997; Hicks & Pearson, 2003; Crawford & Semlitsch, 2008). Lungless salamanders in the family Plethodontidae are even more dependent on moist habitats for dermal respiration than other families of amphibians (Petranka, 1998). In the southern Appalachian Mountains, clear-cutting of forests can result in reduced litter dry mass (amount of leaf litter), leaf litter depth and leaf litter moisture (Ash, 1995). Timber harvest can also degrade habitat for salamanders because the elimination of canopy cover can result in increased soil temperature and decreased surface soil moisture (Petranka *et al.*, 1994; Ash, 1997; Herbeck & Larsen, 1999; J. A. Crawford & R. D. Semlitsch, unpubl. data). We found that leaf litter depth, soil moisture and canopy cover were all significantly reduced in stands ≤40 years of age when compared with stands between the ages of 41–80 years, and stands ≥81 years of age. Leaf litter depth was the only significant predictor of salamander abundance, although soil moisture also approached significance (Table 2). In northern hardwoods, Covington (1981) found that 'forest floor organic matter'

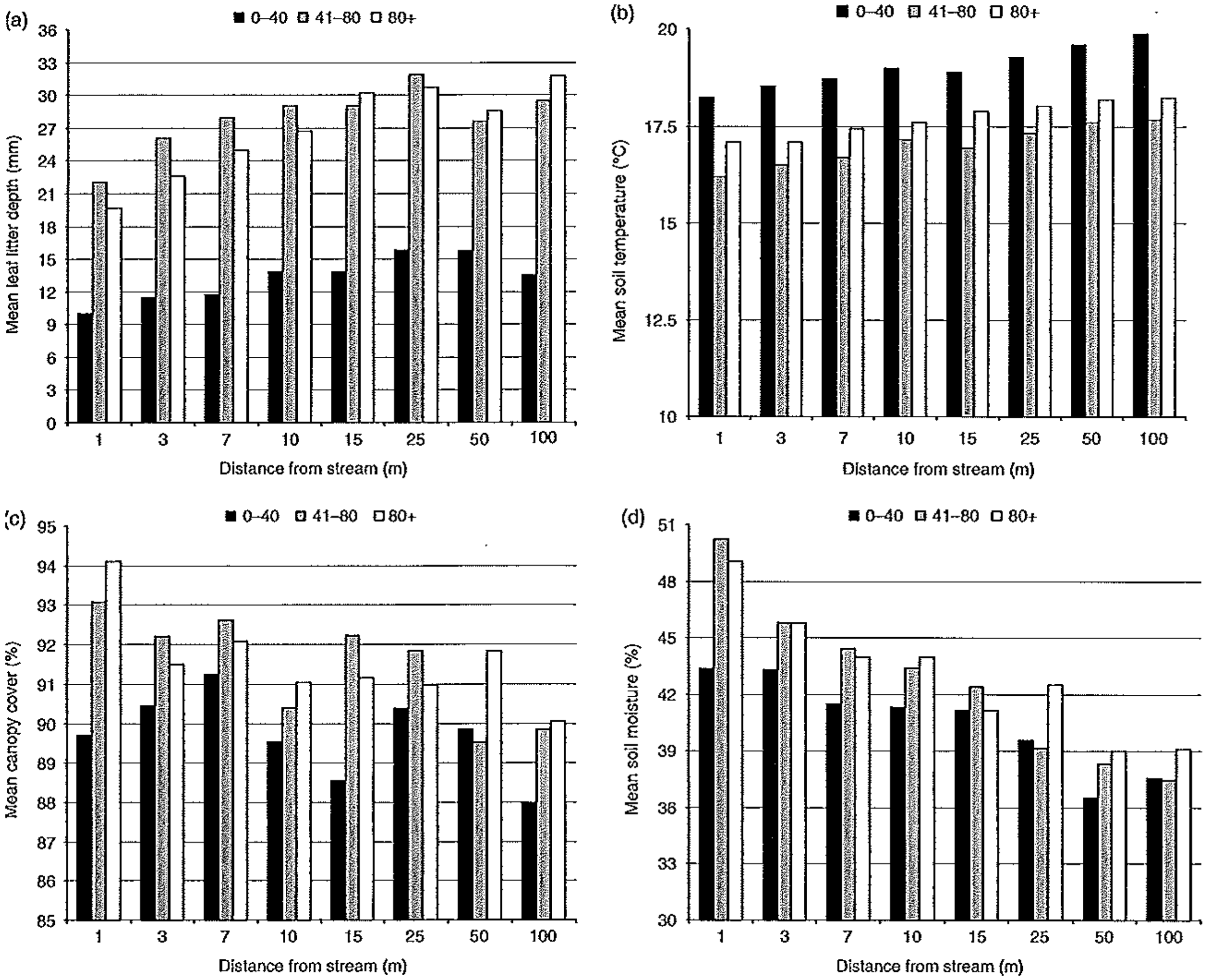

Figure 3 (a–d) Average values for leaf litter depth, soil temperature, canopy cover and soil moisture as distance from the stream increases, respectively.

Table 2 Environmental variables[a] for riparian areas in three different stand age-classes[b]

	Stand age (years)			ANOVA	
Environmental variables	0–40	41–80	80+	$F_{(2,11)}$	P
Leaf litter depth (mm)	$13.2^{\dagger}$ (0.6)	27.9^{*} (0.9)	26.9^{*} (0.8)	128.89	<0.001
Soil temperature (°C)	19.0 (0.7)	17.0 (0.7)	17.7 (1.2)	1.06	0.390
Soil moisture (%)	$40.6^{\dagger}$ (0.4)	42.7^{*} (0.4)	43.1^{*} (0.4)	8.30	0.011
Canopy cover (%)	$89.7^{\dagger}$ (0.2)	91.5^{*} (0.5)	91.6^{*} (0.2)	8.02	0.012
Elevation (m)	882.0 (48.4)	995.5 (85.6)	1003.3 (110.0)	0.64	0.552

[a] Mean and standard error values.

[b] Means with the same symbol within rows were not significantly different (Tukey's HSD multiple comparison, $P<0.05$).

declined 55% over the first 15 years after logging. Reductions in leaf litter depth and leaf litter moisture were also reported by Ash (1995) and Buckner & Shure (1985) following clear-cutting in southern Appalachian forests.

We found overall abundances of stream salamanders sampled both during day and night were reduced in stands ≤40 years of age when compared with the older stand age-classes. While there were no significant reductions in the number of seal salamanders or Ocoee salamanders, there were significantly fewer Blue Ridge two-lined salamanders in the youngest stands (≤40 years old) in both day and night transects. A number of factors could account for this difference among species. Two-lined salamanders are relatively small and slender salamanders (<110 mm total length). Their body size leads to an increased surface area:-volume ratio and higher risk of water loss than the other larger species of salamanders (Spotila, 1972). These salamanders forage for invertebrates in the leaf litter and when this leaf litter becomes thinner, drier or both it is unlikely they will have the moisture necessary to carry on dermal respiration. Additionally, with a reduction in leaf litter, adequate populations of invertebrate prey may not be present (Ash, 1995). With a decrease in leaf litter and available space, competition with other species will likely increase for invertebrate prey. And while there were not any statistically significant decreases in seal or Ocoee salamanders (which could be due to small sample sizes), both species were nearly twice as abundant in stands ≥41 years of age during both day and night sampling (Table 1).

The amount of terrestrial habitat used by the stream salamanders in our stands between 41–80 years of age, and stands ≥81 years old was similar to values found by Crawford & Semlitsch (2007) in mature forests that were ≥80 years old. We found that terrestrial habitat use was significantly reduced in stands ≤40 years of age for the entire assemblage and each individual species. This reduction in amount of terrestrial habitat used by the stream salamanders is likely related to the reduced habitat quality (loss of leaf litter depth and decreased soil moisture) resulting from the timber harvest. The decrease in the amount of suitable terrestrial habitat results in the decreased abundance of stream salamanders in the stands <40 years of age.

Table 3 Predictive habitat variables for daytime stream salamander abundance

Predictor variable	$F_{(2,11)}$	P
Intercept	1.04	0.347
Leaf litter	18.59	0.005
Soil temperature	0.93	0.373
Soil moisture	3.91	0.095
Canopy cover	2.70	0.151
Elevation	4.47	0.079

The decrease in terrestrial habitat use by two-lined salamanders is especially important in terms of salamander abundance. Crawford & Semlitsch (2007) showed that the majority of dusky salamanders (*Desmognathus* spp.) are found within 15 m of the stream's edge, whereas two-lined salamanders occurred beyond 20 m of the stream's edge. This was likely due to competition and predation from the larger dusky salamanders (Hairston, 1987; Ransom & Jaeger, 2006). In stands ≤ 40 years of age, the two-lined salamanders are being forced closer to the stream which likely results in greater competition and predation pressures from the larger dusky salamanders and a subsequent decline in local population number.

While the seal salamanders and Ocoee salamanders seemed to be only marginally affected by stand age, the two-lined salamanders were greatly affected. The two-lined salamanders seem to be the most sensitive species to the disturbance and take the longest period of time to recover in the assemblage. We roughly estimate that it would take at least 40 years for the entire assemblage to recover to pre-disturbance levels. This estimate falls within the range of values that have been found for other plethodontid salamanders in the southern Appalachian Mountains (Petranka *et al.*, 1993; Ash, 1997; Hicks & Pearson, 2003).

Although timber harvest will continue, there are techniques to mitigate the effects of the harvest on stream salamander populations. Selective harvesting techniques such as thinning and group selection have become more common. Harpole & Haas (1999) found that abundance of salamanders was lower after harvest on group selection, shelterwood and leave-tree treatments, but understory removal had no effect. Messere & Ducey (1998) found no differences in red-backed salamander (*Plethodon cinereus*) density between gaps created by selective harvesting. Other studies have suggested that even-aged timber harvesting is not the most appropriate method to maintain viable amphibian populations and alternative uneven-aged harvesting techniques (e.g. selective harvesting) would conserve these populations (Grialou, West & Wilkins, 2000; Karraker & Welsh, 2006). While these studies are on fully terrestrial plethodontids, our results indicate the same conclusion is

Table 4 Summary of night-time occurrence distances[a] (m) from stream edge of a stream salamander assemblage in the southern Appalachian Mountains in three different stand age-classes[b]

	Stand age (years)			ANOVA	
Species	0–40	41–80	80+	$F_{(2,11)}$	P
Stream	9.5†, 13.1 n=82	21.2*, 24.9 n=176	21.8*, 25.5 n=215	18.27	0.001
Desmognathus monticola	2.3†, 3.6 n=18	5.6*, 7.0 n=40	5.6*, 6.9 n=50	10.15	0.005
Desmognathus ocoee	4.0†, 5.6 n=35	7.6*, 9.2 n=60	7.5*, 9.2 n=72	8.02	0.010
Eurycea wilderae	20.3†, 23.9 n=29	39.4*, 43.0 n=76	40.4*, 44.0 n=93	50.27	<0.001

[a]Mean core habitat distance with upper 95% confidence interval, respectively.
[b]Means with the same symbol within rows were not significantly different (Tukey's HSD multiple comparison, P<0.05).

potentially true for stream-breeding plethodontids. By reducing the loss of leaf litter and overall canopy cover, declines of stream salamander assemblages can be kept to a minimum. Marsh *et al.* (2004) found that colonization of forested areas declined with increased distance from these areas for red-backed salamanders. Considering the limited dispersal capability of plethodontid salamanders, a timber harvest plan that rotated cut times and sites along streams might be most successful in mitigating local population declines.

Even though a plethora of research on the impacts of even-aged timber harvest has been done over the past 10 years on terrestrial plethodontid salamanders, there remains a serious lack of understanding on the impacts of forest management on stream-breeding salamanders, especially the mechanisms of change (but see Ashton *et al.*, 2006). We have provided estimates of the timber harvest impacts on stream salamander abundance and terrestrial habitat use as well as a conservative estimate of the return time of assemblages to pre-disturbance levels. If we accept that salamanders are critical indicators of ecosystem health and function (Welsh & Droege, 2001), we hope our research stimulates future work on forestry management practices, mechanisms of change, variation among species or life stages, impacts on the long-term persistence of amphibian populations and maintenance of Appalachian biodiversity (e.g. Olson *et al.*, 2007).

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References

Ash, A.N. (1995). Effects of clear-cutting on litter parameters in the southern Blue Ridge Mountains. *Castanea* **60**, 89–97.

Ash, A.N. (1997). Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge Mountains. *Conserv. Biol.* **11**, 983–989.

Ash, A.N. & Pollock, K.H. (1999). Clearcuts, salamanders, and field studies. *Conserv. Biol.* **13**, 206–208.

Ashton, D.T., Marks, S.B. & Welsh, H.H. Jr. (2006). Evidence of continued effects from timber harvesting of lotic amphibians in redwood forests of northwestern California. *Forest Ecol. Mgmt.* **221**, 183–193.

Buckner, C.A. & Shure, D.J. (1985). The response of *Peromyscus* to forest opening size in the southern Appalachian Mountains. *J. Mammal.* **66**, 299–307.

Burton, T.M. & Likens, G.E. (1975). Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. *Copeia* **1975**, 541–546.

Constantine, N.L., Campbell, T.A., Baughman, W.M., Harrington, T.B., Chapman, B.R. & Miller, K.V. (2004). Effects of clearcutting with corridor retention on abundance, richness, and diversity of small mammals in the Coastal Plain of South Carolina, USA. *Forest Ecol. Mgmt.* **202**, 293–300.

Covington, W.W. (1981). Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. *Ecology* **62**, 41–48.

Crawford, J.A. & Semlitsch, R.D. (2007). Estimation of core terrestrial habitat for stream-breeding salamanders and delineation of riparian buffers for protection of biodiversity. *Conserv. Biol.* **21**, 152–158.

Crawford, J.A. & Semlitsch, R.D. (2008). Abiotic factors influencing abundance and microhabitat use of stream salamanders in southern Appalachian forests. *Forest Ecol. Mgmt.* **255**, 1841–1847.

Cushman, S.A. (2006). Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biol. Conserv.* **128**, 231–240.

Davic, R.D. & Welsh, H.H. Jr. (2004). On the ecological role of salamanders. *Annu. Rev. Ecology Evol. Syst.* **35**, 405–434.

Goldstein, M.I., Wilkins, R.N. & Lacher, T.E. Jr. (2005). Spatiotemporal responses of reptiles and amphibians to timber harvest treatments. *J. Wildl. Mgmt.* **69**, 525–539.

Gram, W.K., Porneluzi, P.A., Clawson, R.L., Faaborg, J. & Richter, S.C. (2003). Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark forests. *Conserv. Biol.* **17**, 1324–1337.

Grialou, J.A., West, S.D. & Wilkins, R.N. (2000). The effects of forest clearcut harvesting and thinning on terrestrial salamanders. *J. Wildl. Mgmt.* **64**, 105–113.

Hairston, N.G. (1987). *Community ecology and salamander guilds*. UK: Cambridge University Press.

Harper, C.A. & Guynn, D.C. Jr. (1999). Factors affecting salamander density and distribution within four forest types in the Southern Appalachian Mountains. *Forest Ecol. Mgmt.* **114**, 245–252.

Harpole, D.N. & Haas, C.A. (1999). Effects of seven silvicultural treatments on terrestrial salamanders. *Forest Ecol. Mgmt.* **114**, 349–356.

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

Hicks, N.G. & Pearson, S.M. (2003). Salamander diversity and abundance in forests with alternative land use histories in the Southern Blue Ridge Mountains. *Forest Ecol. Mgmt.* **177**, 117–130.

Hyde, E.J. & Simons, T.R. (2001). Sampling plethodontid salamanders: sources of variability. *J. Wildl. Mgmt.* **65**, 624–632.

Karraker, N.E. & Welsh, H.H. Jr. (2006). Long-term impacts of even-aged timber management on abundance and body condition of terrestrial amphibians in Northwestern California. *Biol. Conserv.* **131**, 132–140.

Marsh, D.M., Thakur, K.A., Bulka, K.C. & Clarke, L.B. (2004). Dispersal and colonization through open fields by a terrestrial woodland salamander. *Ecology* **85**, 3396–3405.

Messere, M. & Ducey, P.K. (1998). Forest floor distribution of northern redback salamanders, *Plethodon cinereus*, in relation to canopy gaps: first year following selective logging. *Forest Ecol. Mgmt.* **107**, 319–324.

Olson, D.H., Anderson, P.D., Frissell, C.A., Welsh, H.H. Jr. & Bradford, D.F. (2007). Biodiversity management approaches for stream-riparian areas: perspectives for Pacific Northwest headwater forests, microclimates, and amphibians. *Forest Ecol. Mgmt.* **246**, 81–107.

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

Petranka, J.W. (1998). *Salamanders of the United States and Canada*. Washington, DC: Smithsonian Institution Press.

Petranka, J.W., Brannon, M.P., Hopey, M.E. & Smith, C.K. (1994). Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. *Forest Ecol. Mgmt.* **67**, 135–147.

Petranka, J.W., Eldridge, M.E. & Haley, K.E. (1993). Effects of timber harvesting on southern Appalachian salamanders. *Conserv. Biol.* **7**, 363–370.

Petranka, J.W. & Murray, S.S. (2001). Effectiveness of removal sampling for determining salamander density and biomass: a case study in an Appalachian streamside community. *J. Herpetol.* **35**, 36–44.

Petranka, J.W. & Smith, C.K. (2005). A functional analysis of streamside habitat use by southern Appalachian salamanders: implications for riparian forest management. *Forest Ecol. Mgmt.* **210**, 443–454.

Ransom, T.S. & Jaeger, R.G. (2006). An assemblage of salamanders in the southern Appalachian Mountains revisited: competitive and predatory behavior? *Behaviour* **143**, 1357–1382.

Semlitsch, R.D. (2000). Principles for management of aquatic breeding amphibians. *J. Wildl. Mgmt.* **64**, 615–631.

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

Swank, W.T., Vose, J.M. & Elliott, K.J. (2001). Long-term hydrologic and water quality responses following commercial clearcutting of mixed hardwoods on a southern Appalachian catchment. *Forest Ecol. Mgmt.* **143**, 163–178.

Welsh, H.H. Jr. & Droege, S. (2001). A case for using plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. *Conserv. Biol.* **15**, 558–569.

Wilkerson, E., Hagan, J.M., Siegel, D. & Whitman, A.A. (2006). The effectiveness of different buffer widths for protecting headwater stream temperature in Maine. *Forest Sci.* **52**, 221–231.