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Do silvicultural practices to restore oaks affect salamanders in the short term?

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Salamanders are an important ecological component of eastern hardwood forests and may be affected by natural or silvicultural disturbances that alter habitat structure and associated microclimate. From May to August in 2008 (pre-treatment) and 2011 (post-treatment), we evaluated the response of salamanders to three silvicultural practices designed to promote oak regeneration – prescribed fire, midstory herbicide application and shelterwood harvest – and a control. We trapped salamanders using drift fences with pitfall traps in five replicates of the four treatments. Only the southern gray-cheeked salamander *Plethodon metcalfei* and the southern Appalachian salamander *P. teyahalee* were captured in sufficient numbers for robust statistical analysis. We analyzed data for these species using single-species dynamic occupancy models in statistical software program R. We allowed changes in four covariates to influence extinction probability from pre- to post-treatment implementation: 1) percent leaf litter cover; 2) percent understory cover; 3) percent CWD cover; and 4) percent canopy cover. The final combined model set describing extinction probability contained four models with $\Delta\text{AIC} < 2$ for *P. metcalfei* and nine models with $\Delta\text{AIC} < 2$, including the null model, for *P. teyahalee*. For both species, the 95% confidence intervals for model-averaged extinction probability parameter estimates overlapped zero, suggesting none were significant predictors of extinction probability. Absence of short-term salamander response in midstory herbicide and prescribed burn treatments was likely because of minor or transitory changes to forest structure. In shelterwood harvests, any potential effects of reduced canopy and leaf litter cover may have been mitigated by rapid post-treatment vegetation sprouting. Additionally, climatic conditions associated with high elevation sites and high amounts of rainfall in 2011 may have compensated for potential changes to microclimate. Continued monitoring of *Plethodon* salamanders to assess responses at longer time scales (e.g. > 3 years post-treatment) is warranted.

Ecologically, salamanders are important components of eastern hardwood forests in the United States. In some areas of the Appalachian Mountains, biomass of salamanders is twice that of birds and equal to small mammals (Burton and Likens 1975). Salamanders are an important food source for reptiles, birds and mammals and can act as regulators of forest floor invertebrates (Whitaker and Rubin 1971, Pough 1983, Davic and Hartwell Jr. 2004, Walton et al. 2006).

Members of the genus *Plethodon* are ectothermic, lungless terrestrial salamanders with direct development (no aquatic larval stage) and require moist substrates and high relative humidity for dermal respiration (Spotila 1972, Feder 1983, Petranksa 1998). Forest disturbances that substantially reduce canopy and leaf litter cover may increase risk of salamander desiccation by elevating temperatures and reducing moisture on the forest floor (Ash 1988, Petranksa et al. 1994, Harpole and Haas 1999). Additionally, reduced cover may increase the risk of predation and alter abundance and

composition of invertebrate prey (Ash 1997, Knapp et al. 2003, Homyack and Haas 2009, Matthews et al. 2010). Terrestrial salamanders may respond to habitat changes by reducing aboveground activities (e.g. foraging and mating) or by trading growth and reproduction for increased basic maintenance costs (Homyack et al. 2011). Therefore, silvicultural practices that substantially alter forest vegetation and microclimate could have negative effects on *Plethodon* populations.

Widespread oak regeneration failure – the failure of oak seedlings or saplings to attain canopy status – is a focal issue of forest land managers. Oak regeneration is especially problematic on intermediate and highly productive sites where competition from faster-growing species such as yellow-poplar *Liriodendron tulipifera* is fierce after canopy release (Aldrich et al. 2005). Several silvicultural methods for regenerating oak by altering light conditions have been proposed, but few have been experimentally tested on intermediate

to highly productive sites of southern Appalachian upland hardwood forests (Atwood et al. 2011).

Each oak regeneration method results in changes to habitat structure that could affect *Plethodon* salamanders. For example, prescribed fire may remove shrubs, increase herbaceous vegetation (Van Lear and Watt 1993), and decrease leaf litter (Kirkland Jr. et al. 1996, Greenberg et al. 2006, 2007, Waldrop et al. 2007). Midstory removal using herbicides increases indirect light to the forest floor but does not dramatically affect the forest floor structure or overstory canopy cover. Conversely, even-aged silvicultural systems such as shelterwood harvests reduce canopy cover and leaf litter, creating a high-light environment with elevated temperatures and reduced moisture on the forest floor (Geiger 1965, Brose et al. 1999, Chen et al. 1999).

Previous studies on salamander response to silvicultural disturbance often had limited experimental designs that lacked replication, focused on insufficient measures of population response, or failed to analyze detection probability (DeMaynadier and Hunter Jr. 1995, Russell et al. 2004). A review of forest management effects on southeastern herpetofauna identified only six studies with pre- and post-treatment data, treatment replication, or proper spatial and temporal referencing (Russell et al. 2004).

We conducted a large-scale replicated study to determine short-term (i.e. < 3 years) response of salamanders to three oak regeneration practices (prescribed fire, midstory herbicide application, and a shelterwood harvest) and a control. Terrestrial salamanders are largely subterranean, with only a small proportion of the population captured on a given sampling occasion (Hairston 1987). Detection probability likely varies spatially and temporally (DeMaynadier and Hunter Jr. 1998, Hyde and Simons 2001, Petranka and Murray 2001). Therefore, using pre-treatment (baseline) and post-treatment data, we used the spatial and temporal replication inherent in a before–after control–impact experimental design and analyzed data with hierarchical dynamic occupancy models to determine the short-term response of *Plethodon* salamanders to the environmental changes associated with the oak regeneration treatments (MacKenzie et al. 2003).

Material and methods

Study area

Our study was conducted in Haywood County, North Carolina on Cold Mountain Game Land (CMGL) located in the Blue Ridge Physiographic Province. CMGL encompassed 1333 ha of second growth, upland mixed-oak forests with elevations ranging from 940–1280 m and was managed by the North Carolina Wildlife Resources Commission for diverse vegetation conditions attractive to a variety of wildlife species. Terrain was mountainous with gentle to steep slopes with an overstory of oak *Quercus* spp., hickory *Carya* spp. and yellow-poplar. Composition in the midstory consisted primarily of shade-tolerant species, including sourwood *Oxydendrum arboreum*, flowering dogwood *Cornus florida*, silver-bell *Halesia tetraptera*, blackgum *Nyssa sylvatica* and red

maple *Acer rubrum*. The precipitation averaged 1200 mm annually.

We established five, 5-ha units of the four treatments for a total of 20 units. Treatment units were separated by a > 10-m buffer and contained mature (> 70 years old), fully stocked, closed-canopied stands where oaks comprised at least 10% of the overstory tree basal area (≥ 25.0 cm dbh). We selected stands that contained > 1000 oak seedlings ha⁻¹, few ericaceous shrubs, ~2 m² ha⁻¹ of basal area beneath the main canopy, and no substantial disturbance within the last 15–20 years (Keyser et al. 2008). All treatment units were between 940–1240 m in elevation. Aspect varied within and among treatment units because of complex topography. We randomly assigned the prescribed fire, midstory removal using herbicide, and shelterwood harvest treatments to units, resulting in a completely randomized design.

Treatments

We evaluated the initial phase (1–2 years post-treatment) of three long-term oak regeneration practices: prescribed burns at ~4-year intervals, midstory removal using herbicide with re-application after three years, and a shelterwood harvest followed by a prescribed fire after three years. Specifically, our study evaluated the response of *Plethodon* salamanders to four treatments: 1) one prescribed burn, 2) one midstory herbicide treatment, 3) a shelterwood harvest with 30–40% basal area retention, and a 4) control.

Two of the five prescribed burn replicate units were burned in April 2009 with the remaining three units burned in April 2010. In midstory herbicide replicate units, competing midstory trees were treated with Garlon 3A using the hack-and-squirt method in late summer 2008 to reduce

Table 1. List of a priori candidate models used in dynamic occupancy of *Plethodon metcalfi* and *P. teyahalee* on Cold Mountain Game Land, Haywood County, NC. Covariates are changes in estimates from pre- (i.e. 2008) to post- (i.e. 2011) oak regeneration treatments. ψ = pretreatment year, ϵ = extinction probability, p = detection, γ = colonization probability, canopy = percent canopy cover, CWD = percent coarse woody debris cover, leaf litter = percent leaf litter cover, understory = percent understory cover.

Model
ψ (elevation), γ (.), ϵ (.), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (canopy), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (CWD), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (leaf litter), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (understory), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (canopy, CWD), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (canopy, leaf litter), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (canopy, understory), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (CWD, leaf litter), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (CWD, understory), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (leaf litter, understory), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (canopy, CWD, leaf litter), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (canopy, leaf litter, understory), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (canopy, CWD, understory), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (CWD, leaf litter, understory), p (date, leaf litter)
ψ (elevation), γ (.), ϵ (canopy, CWD, leaf litter, understory), p (date, leaf litter)

total basal area by 25–30% without creating new canopy gaps (Loftis 1990). Shelterwood harvest replicate units were harvested from winter 2009 to early summer 2010 with the goal of leaving approximately 30–40% of the original stand basal area and enhancing light conditions on the forest floor (Brose et al. 1999). Trees felled with standard chainsaws and grapple cutters were dragged by rubber tire skidders to log landings where loaders filled haul trucks. Some units required skid trails due to steep areas. During this study, no silvicultural manipulation occurred in the control plots (Keyser et al. 2008, Raybuck et al. 2012).

Salamander sampling

In 2008 (pre-treatment) and 2011 (post-treatment), we sampled salamanders from mid-May to mid-August in all 20 units. We established six randomly oriented single-arm drift fence arrays in 2008 (Todd et al. 2007) with three fences installed at a lower slope site (e.g. lower one-third of each unit) and three fences at an upper slope site (Greenberg and Waldrop 2008). In two of the treatment replicates (one herbicide and one control), we were unable to establish an upper site because of steep and rocky terrain. A fourth fence was installed at each lower and upper site that had fences by 2011. Drift fences were > 10 m apart and constructed of 7.6-m sections of aluminum flashing with a 19-l bucket buried at each end, flush with the ground. We placed a moist sponge in each bucket to provide moisture for captures. We had five observers in 2008 and four in 2011. Each drift fence was checked at least every two days; we checked fences daily after rain events. We recorded each captured individual to species and released it immediately at the capture location.

All procedures used in our study were in accordance with the Society for the Study of Amphibians and Reptiles guidelines for field research, and approved by the Institutional Animal Care and Use Committee of North Carolina State University (permit no. 08-035-O).

Habitat data

At the middle drift fence in the lower and upper slope site of each unit, we recorded aspect (1 = northern to eastern aspects [mesic]; 0 = southern to western aspects [xeric]) and elevation. We estimated elevation using a handheld GPS. Pre- and post-treatment, we measured percent canopy cover with a spherical densiometer at each drift fence (Lemmon 1956). Pre- and post-treatment, we measured percent leaf litter cover, percent understory cover, and percent cover of coarse woody debris (CWD) along a 15-m randomly oriented transect line at each drift fence at the bucket furthest

uphill. We measured percent leaf litter cover, percent understory cover (i.e. plants shorter than < 0.9 m in height), and percent CWD cover by summing the total distance for each category along each transect. Then, in each unit, we divided the total distance for each category by 90 m (six transects per unit).

Analyses

We analyzed the change in habitat variables from 2008 to 2011 using a one-way analysis of variance (ANOVA) with treatment as a class variable. When models were significant, we used Tukey's studentized range test to determine differences among treatment means. We conducted statistical tests in SAS (ver. 9.1.3, SAS Inst.).

Because abundance estimation methods using mark-recapture are often logistically difficult and ineffective for large-scale monitoring of terrestrial salamanders (Bailey et al. 2004), we used hierarchical dynamic occupancy models in package "unmarked" (Fiske and Chandler 2011) in statistical software program R to fit models for *Plethodon* species for which we had > 70 captures per year (MacKenzie et al. 2003, < www.r-project.org/ >). Dynamic occupancy models allow inference about the occurrence of species at several sites and about how changes in occurrence are driven by colonization and extinction while simultaneously allowing for imperfect detection (MacKenzie et al. 2003, Kéry and Chandler 2012). We assumed each site (i.e. drift fence array) was either occupied or not occupied by a given species before treatment implementation (i.e. 2008) and after treatment implementation (i.e. 2011). All parameters (i.e. initial occupancy, colonization, extinction and detection) can be modeled as functions of covariates (Kéry and Chandler 2012). Colonization was the probability that a site not occupied pre-treatment implementation became occupied post-treatment implementation. Extinction was the probability that a site occupied pre-treatment implementation became unoccupied post-treatment implementation.

We summarized count data for each site (i.e. drift fence array) from 2008 and 2011 and combined data into 10 sampling occasions per year per species. We ran 16 a priori candidate models with covariates on initial occupancy probability during the pre-treatment year (ψ), extinction probability (ϵ), and detection (p) while keeping colonization probability (γ) constant (Table 1). We predicted that forest changes resulting from oak regeneration treatments were most likely to result in local extinctions of salamanders and rarely colonization of locations; therefore, we identified covariates responsible for potential extinctions. We believed local-scale habitat variables allowed

Table 2. Change in habitat variables (\pm SE) from 2008 (pre-treatment) to 2011 (post-treatment) for oak regeneration treatments on Cold Mountain Game Land, Haywood County, NC: control (CONT), midstory herbicide (HERB), shelterwood harvest (SW), prescribed burns of 2009 (RX09), and prescribed burns of 2010 (RX10). CWD = coarse woody debris. Different letters indicate significantly different values ($p < 0.05$).

Habitat variable	CONT	HERB	SW	RX09	RX10	F	p_{int}
Canopy cover (%)	-2.0 \pm 0.9A	-7.2 \pm 2.7A	-41.2 \pm 6.3B	-5.3 \pm 0.2A	3.5 \pm 1.9A	22.0	< 0.001
Leaf litter cover (%)	11.4 \pm 7.1A	14.1 \pm 7.8A	-47.1 \pm 9.2B	1.3 \pm 2.4A	-3.0 \pm 2.6A	11.4	< 0.001
CWD cover (%)	0.2 \pm 0.2A	0.7 \pm 0.2A	5.8 \pm 1.6B	-3.1 \pm 0.4A	-0.9 \pm 2.0A	8.1	0.001
Understory cover (%)	-3.2 \pm 4.8A	17.1 \pm 12.3AB	52.6 \pm 6.0C	43.6 \pm 8.1BC	19.8 \pm 4.9ABC	7.4	0.002

Table 3. Mean number of salamander species captured per treatment site (lower and/or upper) in 2008 (\pm SE)/2011 (\pm SE) on Cold Mountain Game Land, Haywood County, NC: control (CONT), midstory herbicide (HERB), shelterwood harvest (SW), prescribed burns of 2009 (RX09), and prescribed burns of 2010 (RX10). Drift fence arrays were open for 15 552 trap nights in 2008 and 17 800 trap nights in 2011.

Species	CONT	HERB	SW	RX09	RX10	Total
<i>Plethodon metcalfi</i>	2.2 \pm 1.2/2.0 \pm 0.9	2.4 \pm 0.6/2.0 \pm 0.7	4.5 \pm 1.9/2.6 \pm 2.2	-/-	7.7 \pm 2.5/5.0 \pm 1.7	224
<i>Plethodon teyahalee</i>	3.6 \pm 0.9/1.9 \pm 0.7	2.9 \pm 0.9/2.7 \pm 0.8	4.3 \pm 1.1/4.6 \pm 0.9	1.0 \pm 0.4/1.0 \pm 0.6	1.5 \pm 0.8/2.5 \pm 0.8	220
<i>Eurycea wilderae</i>	0.3 \pm 0.2/1.0 \pm 0.4	-/2.2 \pm 0.8	0.4 \pm 0.2/3.1 \pm 1.6	-/-	0.8 \pm 0.7/0.8 \pm 0.3	70
<i>Desmognathus wrighti</i>	-/0.2 \pm 0.2	-/0.2 \pm 0.2	0.1 \pm 0.1/0.1 \pm 0.1	-/-	0.7 \pm 0.2/6.5 \pm 4.1	49
<i>Notophthalmus viridescens</i>	0.9 \pm 0.5/0.2 \pm 0.1	0.4 \pm 0.2/0.3 \pm 0.2	0.4 \pm 0.3/0.6 \pm 0.4	1.5 \pm 0.6/1.3 \pm 0.5	0.5 \pm 0.2/0.8 \pm 0.3	44
<i>Desmognathus ocoee</i>	-/-	-/-	-/-	-/-	0.5 \pm 0.1/2.3 \pm 1.2	17
<i>Pseudotriton ruber schencki</i>	0.4 \pm 0.3/0.3 \pm 0.2	-/-	-/-	-/-	-/-	7
<i>Plethodon serratus</i>	-/0.1 \pm 0.1	-/0.2 \pm 0.1	0.3 \pm 0.2 / -	-/0.3 \pm 0.3	-/-	6
<i>Desmognathus aeneus</i>	-/-	0.1 \pm 0.1/-	-/-	-/-	-/-	1

us to understand the mechanisms that might be causing salamander response to silvicultural manipulations better than the large-scale treatment classifications. Thus, we did not use treatment as a covariate of salamander occupancy dynamics, but instead investigated the habitat metrics at the drift fence level. More specifically, we subtracted the 2008 estimates from the 2011 estimates to quantify the change in each covariate.

Because of the large number of potential models, we followed a procedure to identify covariates that affected extinction probability. We allowed elevation to influence initial occupancy because this variable is known to affect occurrence of salamander species (Ford et al. 2002, Takahashi and Pauley 2010). We allowed change in percent leaf litter cover and date to influence detection because these variables were most likely to affect salamander activity patterns (Ash 1995, Petranka 1998). We allowed changes in four covariates to influence extinction probability from pre- to post-treatment implementation: 1) percent leaf litter cover; 2) percent understory cover; 3) percent CWD cover; and 4) percent canopy cover. Hence, we modeled elevation on the initial occupancy process, date and percent leaf litter cover on the detection process, and every combination of the four covariates on the extinction process for 15 of the 16 candidate models (Table 1). The remaining candidate model was the null extinction probability model. We standardized all covariates before analysis. We tested covariates for collinearity using the correlation function in Excel. We removed a covariate if it was >0.6 correlated with another covariate. We ranked convergent models using Akaike's information criterion (AIC) (Burnham and Anderson 2002). We used R package "MuMIn" to obtain model-averaged point estimates of the parameters (Barton 2013). We used a parametric bootstrap procedure with a chi-square fit statistic to assess goodness of fit of the AIC best model (Hosmer et al. 1997, Kéry and Chandler 2012).

Results

Elevation ($F_{4,14} = 2.12$, $p = 0.12$) and aspect ($F_{4,31} = 1.96$, $p = 0.13$) were similar among treatments. From pre- to post-treatment, shelterwood harvest units showed the most marked habitat changes; percent understory cover increased by 53%, percent leaf litter cover declined by 47%, percent canopy cover declined by 41%, and percent CWD cover increased by 6% (Table 2). Prescribed burns of 2009 showed a 44% increase in percent understory cover (Table 2). Habitat variables in the midstory herbicide treatment and prescribed burns of 2010 were similar to control units from pre- to post-treatment (Table 2).

Salamander sampling

We captured a total of 607 salamanders during the course of the study. Drift fences were open for 15 552 trap nights in 2008 and 17 800 trap nights in 2011. Captures included 224 *Plethodon metcalfi*, 220 *P. teyahalee*, 70 blue ridge two-lined salamanders *Eurycea wilderae*, 49 pygmy salamanders *Desmognathus wrighti*, 44 eastern newts *Notophthalmus*

Table 4. Beta (β) estimates, standard errors (SE), z-values and p-values of covariates on detection (logit-scale) and extinction probability (logit-scale) from the AIC best model for estimating dynamic occupancy of *Plethodon metcalfi* and *Plethodon teyahalee* following oak regeneration treatments from 2008 (pre-treatment) to 2011 (post-treatment) on Cold Mountain Game Land, Haywood County, NC. Covariates represent changes in habitat estimates from pre- (i.e. 2008) to post- (i.e. 2011) oak regeneration treatments. canopy = percent canopy cover, CWD = percent coarse woody debris cover, leaf litter = percent leaf litter cover.

Species	Detection (logit-scale)					Extinction (logit-scale)				
	Covariate	β	SE	Z	p(> z)	Covariate	β	SE	z	p(> z)
<i>P. metcalfi</i>	(intercept)	-1.84	0.21	-8.60	<0.01	(intercept)	-0.24	0.57	-0.42	0.67
	date	-0.02	0.00	-3.52	<0.01	CWD	0.88	0.53	1.67	0.09
	leaf litter	0.11	0.10	1.09	0.28					
<i>P. teyahalee</i>	(intercept)	-1.82	0.16	-11.41	<0.01	(intercept)	-1.51	0.70	-2.15	0.03
	date	<0.01	<0.01	-1.17	<0.24	canopy	0.80	0.65	1.23	0.22
	leaf litter	0.11	0.08	1.35	0.18					

viridescens, 17 Ocoee salamanders *D. ocoee*, seven blackchin red salamanders *Pseudotriton ruber schencki*, six southern red-backed salamanders *P. serratus*, and one seepage salamander *D. aeneus* (Table 3). Only *P. metcalfi* and *P. teyahalee* were captured in sufficient numbers for robust statistical analysis. In 2008 and 2011, we captured 132 and 92 *P. metcalfi* and 114 and 106 *P. teyahalee*, respectively.

Plethodon metcalfi and *P. teyahalee* had sufficient detections to model. No covariates were correlated. The AIC best model for dynamic occupancy of *P. metcalfi* ($\chi^2 = -8.63$, SE = 74.1, p = 0.60) allowed change in percent CWD cover to influence extinction probability ($\beta = 0.88$, SE = 0.53, z = 1.67, p = 0.09, Table 4), but the final combined model set describing extinction probability of *P. metcalfi* contained four models with $\Delta AIC < 2$ (Table 5). We obtained extinction probability parameter estimates for *P. metcalfi* by using the model-averaged values from these top four models, which included changes in percent canopy cover ($\beta = -0.34$, SE = 0.54, z = 0.63, p = 0.53), percent CWD cover ($\beta = 0.87$, SE = 0.58, z = 1.50, p = 0.13), and percent understory cover ($\beta = -0.14$, SE = 0.45, z = 0.32, p = 0.75) on the extinction probability process

Table 5. Model set including all models with an Akaike's Information Criterion (AIC) <2 from the AIC best model with difference in AIC (ΔAIC), model weight (w_i), and number of parameters (K) for estimating dynamic occupancy of *Plethodon metcalfi* following oak regeneration treatments from 2008 (pre-treatment) to 2011 (post-treatment) on Cold Mountain Game Land, Haywood County, NC. Covariates represent changes in habitat estimates from pre- (i.e. 2008) to post- (i.e. 2011) oak regeneration treatments. *indicates the null model, which was not included in the top models or the model-averaged estimates. ψ = pretreatment year, ϵ = extinction probability, p = detection, γ = colonization probability, ele = elevation, canopy = percent canopy cover, CWD = percent coarse woody debris cover, leaf litter = percent leaf litter cover.

Model	AIC	ΔAIC	w_i	K
ψ (ele), γ (.), ϵ (CWD), p (date, leaf litter)	957.07	0.00	0.24	8
ψ (ele), γ (.), ϵ (CWD, understory), p (date, leaf litter)	958.97	1.90	0.09	9
ψ (ele), γ (.), ϵ (canopy), p (date, leaf litter)	959.04	1.97	0.09	8
ψ (ele), γ (.), ϵ (canopy, CWD), p (date, leaf litter)	959.05	1.98	0.09	9
ψ (ele), γ (.), ϵ (.), p (date, leaf litter)*	959.22	2.15	0.08	7

(Supplementary material Appendix 1). The AIC best model for dynamic occupancy of *P. teyahalee* ($\chi^2 = 17.8$, SE = 22.4, p = 0.16) allowed change in percent canopy cover to influence extinction probability ($\beta = 0.80$, SE = 0.65, z = 1.23, p = 0.22, Table 4), but the final combined model set describing extinction probability of *P. teyahalee* contained nine models with $\Delta AIC < 2$, including the null model (Table 6). We obtained extinction probability estimates of *P. teyahalee* by using the model-averaged values from these top nine models, which included percent canopy cover ($\beta = 0.79$, SE = 0.65, z = 1.21, p = 0.23), percent CWD cover ($\beta = 0.85$, SE = 0.78, z = 1.09, p = 0.28), percent leaf litter cover ($\beta = -0.66$, SE = 0.52, z = 1.27,

Table 6. Model set including all models with an Akaike's information criterion (AIC) <2 from the AIC best model with difference in AIC (ΔAIC), model weight (w_i), and number of parameters (K) for estimating dynamic occupancy of *Plethodon teyahalee* following oak regeneration treatments from 2008 (pre-treatment) to 2011 (post-treatment) on Cold Mountain Game Land, Haywood County, NC. Covariates represent changes in habitat estimates from pre- (i.e. 2008) to post- (i.e. 2011) oak regeneration treatments. *The null model had the second lowest AIC compared to the AIC best model. ψ = pretreatment year, ϵ = extinction probability, p = detection, γ = colonization probability, ele = elevation, canopy = percent canopy cover, CWD = percent coarse woody debris cover, leaf litter = percent leaf litter cover, understory = percent understory cover.

Model	AIC	ΔAIC	w_i	K
ψ (ele), γ (.), ϵ (canopy), p (date, leaf litter)	1413.19	0.00	0.12	8
ψ (ele), γ (.), ϵ (.), p (date, leaf litter)*	1413.52	0.33	0.10	7
ψ (ele), γ (.), ϵ (canopy, leaf litter), p (date, leaf litter)	1413.97	0.77	0.08	9
ψ (ele), γ (.), ϵ (leaf litter), p (date, leaf litter)	1414.00	0.81	0.08	8
ψ (ele), γ (.), ϵ (canopy, CWD), p (date, leaf litter)	1414.04	0.85	0.08	9
ψ (ele), γ (.), ϵ (leaf litter, understory), p (date, leaf litter)	1414.09	0.89	0.08	9
ψ (ele), γ (.), ϵ (understory), p (date, leaf litter)	1414.17	0.98	0.08	8
ψ (ele), γ (.), ϵ (canopy, leaf litter, understory), p (date, leaf litter)	1414.28	1.08	0.07	10
ψ (ele), γ (.), ϵ (canopy, understory), p (date, leaf litter)	1414.45	1.26	0.07	9

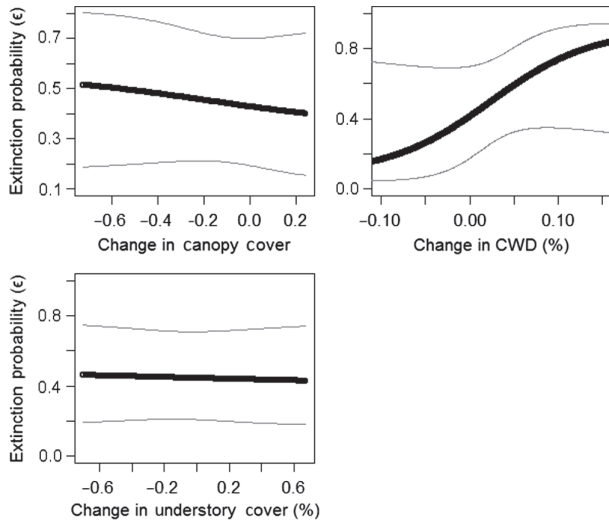


Figure 1. Expected extinction probability (ϵ) and 95% confidence intervals for the southern gray-cheeked salamander (*P. metcalfi*) derived from the model average of four models with $\Delta\text{AIC} < 2$, which included estimated changes in percent canopy cover, percent CWD (coarse woody debris) cover, and percent understory cover from 2008 (pre-treatment) to 2011 (post-treatment) for oak regeneration treatments on Cold Mountain Game Land, Haywood County, NC: control, midstory herbicide, shelterwood harvest, prescribed burns of 2009, and prescribed burns of 2010.

$p = 0.20$), and percent understory cover ($\beta = -0.55$, $\text{SE} = 0.48$, $z = 1.16$, $p = 0.25$) (Supplementary material Appendix 1). The 95% confidence intervals for all covariates overlapped zero, suggesting none were significant predictors of extinction probability for *P. metcalfi* (Fig. 1) or

P. teyahalee (Fig. 2). The relationships between covariates and extinction probability had large confidence intervals, and expected extinction probability changed relatively little across gradients for most covariates (Fig. 1, 2). However, expected extinction probability did increase from 0.2 to 0.8 with increasing percent CWD cover for *P. metcalfi* (Fig. 1), but variance was high and the relationship was not significant.

Discussion

In the short-term (< 3 years), *Plethodon metcalfi* and *P. teyahalee* populations did not appear to be affected negatively by the experimental oak regeneration treatments. The weak relationship that suggests extinction probability for *P. metcalfi* increases with increasing CWD cover is counter to studies that showed salamanders use and benefit from CWD (Herbeck and Larsen 1999, McKenny et al. 2006, Semlitsch et al. 2009). CWD increased following shelterwood harvests, so the relationship between CWD and extinction probability may have been linked to greater risk of extinction in shelterwood harvests. In fact, *P. metcalfi* captures following shelterwood harvests were ~50% less than pre-treatment. In this case, other unmeasured environmental changes following shelterwood harvests (e.g. soil moisture) may have influenced salamander occupancy dynamics.

Our results concur with several other studies indicating that salamanders generally show no response or slightly increase in abundance following herbicide applications (Cole et al. 1997, Hood et al. 2002, Brunjes et al. 2003, Homyack and Haas 2009, Cantrell et al. 2013) or single prescribed burns (Ford et al. 1999, 2010, Keyser et al. 2004, Greenberg

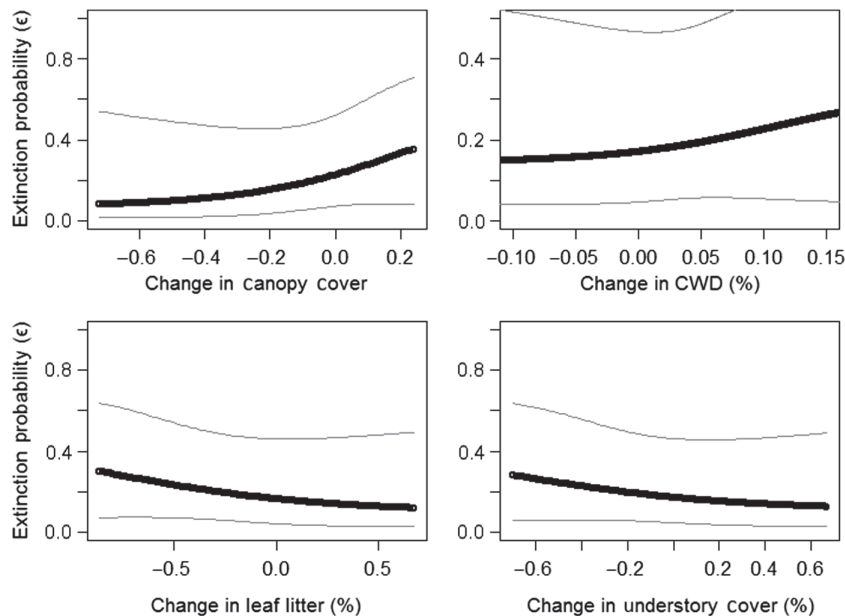


Figure 2. Expected extinction probability (ϵ) and 95% confidence intervals for the southern Appalachian salamander (*P. teyahalee*) derived from the model average of nine models with $\Delta\text{AIC} < 2$, which included estimate changes in percent canopy cover, percent CWD (coarse woody debris) cover, percent leaf litter cover, and percent understory cover from 2008 (pre-treatment) to 2011 (post-treatment) for oak regeneration treatments on Cold Mountain Game Land, Haywood County, NC: control, midstory herbicide, shelterwood harvest, prescribed burns of 2009, and prescribed burns of 2010.

and Waldrop 2008). In fact, Keyser et al. (2004) reported no detectable differences in abundance of *P. cinereus* after high-intensity prescribed burns that substantially reduced leaf litter. In our study, prescribed fires were cool and relatively low-intensity with maximum ground level temperatures of 131°C. Post-burn occupancy did not decline, indicating short-term environmental changes following single prescribed fires were not enough to impact *P. metcalfi* or *P. teyahalee*. Rapid recovery of leaf litter and understory cover may have mitigated potential stresses on moisture-sensitive *Plethodon*.

Although shelterwood harvests resulted in substantial reductions in canopy and leaf litter cover, environmental conditions unique to our study sites may have precluded short-term changes in *Plethodon* occupancy. A concurrent study within the mid-Cumberland Plateau of southern Tennessee examined the short-term response (1–2 years) of herpetofauna to a shelterwood harvest with 30–40% basal area retention. Similar to our findings, no negative responses for herpetofauna species, including for the northern slimy salamander *P. glutinosus*, were detected (Cantrell et al. 2013). Conversely, other studies have documented short-term *Plethodon* declines following shelterwood harvests, suggesting that as little as 41% overstory reduction may result in declines similar to clearcuts (Harpole and Haas 1999, Knapp et al. 2003, Homyack and Haas 2013). In our study, rapid stump sprouting and understory recovery, as well as increased CWD following shelterwood harvests may have provided salamanders with sufficient cover, shade and moisture, travel corridors, and foraging opportunities despite declines in tree canopy cover (Grover 1998, Morneault et al. 2004, Patrick et al. 2006, Rundio and Olson 2007, Semlitsch et al. 2009). Emigration or mortality, which normally begins late in the first year following disturbance and in subsequent years because of starvation and dehydration (Knapp et al. 2003), may have been offset by high levels of precipitation in 2011. Average precipitation from May to August for Haywood County is 488 mm compared to 1090 mm recorded in 2011. High rainfall may have compensated for potential moisture reductions due to canopy removal by maintaining moisture levels within the tolerance limits of *Plethodon* salamanders. Additionally, the relatively cool climate of our high elevation sites may have mitigated some of the microclimatic conditions that likely were associated with post-harvest salamander declines in other studies (Harper and Guynn Jr. 1999).

Our short-term sampling window (< 2 years post-harvest) may have been insufficient to detect impacts on terrestrial salamanders in shelterwood units (DeMaynadier and Hunter Jr. 1995). Studies indicate that *Plethodon* salamanders can show high site fidelity for up to two years following silvicultural disturbance (Ash 1988, Messere and Ducey 1998, Ford et al. 2000, Bartman et al. 2001). However, lower salamander abundance has been documented in forest stands 2–10 years following > 50% canopy removal as compared to mature forest (Pough et al. 1987, Ash 1988, Petranksa et al. 1993, Reichenbach and Sattler 2007). Similarly, declines in reproductive success may not be evident for more than three years following forest disturbance (Ash et al. 2003, Patrick et al. 2006, Cummer

and Painter 2007, Matthews et al. 2010). Ash et al. (2003) noted that *P. jordani* captures in 10-year old clearcuts had proportionately fewer juveniles and adult males in reproductive condition.

Planned activities associated with the oak regeneration prescriptions at these sites, including repeated prescribed burns in the prescribed fire treatment units and prescribed burns in the shelterwood harvest treatment units, may have additive effects on salamanders by repeatedly or further reducing canopy, understory and leaf litter cover. Repeated prescribed fires that potentially facilitate growth of oak seedlings to a competitive size (Van Lear and Watt 1993) could compound treatment effects (e.g. reduced leaf litter and moisture at the forest floor) and affect *Plethodon* salamanders by decreasing relative humidity in burrows (Floyd et al. 2001). Additionally, the combination of shelterwood harvests and prescribed fires may substantially change habitat conditions compared to each of these disturbances alone. For example, Matthews et al. (2010) captured 68–72% fewer salamanders in mechanical fuel reduction treatments followed by two prescribed fires than in twice-burned treatments alone. The high severity prescribed fires in the mechanical and twice burned treatment units led to substantial overstory mortality compared to the lower-severity prescribed burns in the burn only treatment units (Matthews et al. 2010).

Conclusions

Minor changes to habitat structure following midstory herbicide treatments, rapid re-establishment of understory cover in shelterwood harvests and prescribed burns, and microclimatic conditions of high elevation sites may have contributed to maintaining *Plethodon* populations following oak regeneration treatments in the short-term. However, planned activities associated with the oak regeneration prescriptions, such as prescribed burns following shelterwood harvests, may have additive effects on salamanders. Additionally, lags in demographic response may cause delayed declines in *Plethodon* populations. Therefore, longer-term studies are necessary to assess salamander response to varying frequencies and combinations of oak regeneration treatments that could affect microclimatic conditions.

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Supplementary material (available online as Appendix wlb.00076 at <www.wildlifebiology.org/readers/appendix>). Appendix 1.