

Effects of structural complexity enhancement on eastern red-backed salamander (*Plethodon cinereus*) populations in northern hardwood forests

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Abstract

Managing for stand structural complexity in northern hardwood forests has been proposed as a method for promoting microhabitat characteristics important to eastern red-backed salamanders (*Plethodon cinereus*). We evaluated the effects of alternate, structure-based silvicultural systems on red-backed salamander populations at two research sites in northwestern Vermont. Treatments included two uneven-aged approaches (single-tree selection and group-selection) and one unconventional approach, termed “structural complexity enhancement” (SCE), that promotes development of late-successional structure, including elevated levels of coarse woody debris (CWD). Treatments were applied to 2 ha units and were replicated two to four times depending on treatment. We surveyed red-backed salamanders with a natural cover search method of transects nested within vegetation plots 1 year after logging. Abundance estimates corrected for detection probability were calculated from survey data with a binomial mixture model. Abundance estimates differed between study areas and were influenced by forest structural characteristics. Model selection was conducted using Akaike Information Criteria, corrected for over-dispersed data and small sample size (QAIC_c). We found no difference in abundance as a response to treatment as a whole, suggesting that all of the uneven-aged silvicultural systems evaluated can maintain salamander populations after harvest. However, abundance was tied to specific structural habitat attributes associated with study plots within treatments. The most parsimonious model of habitat covariates included site, relative density of overstory trees, and density of more-decayed and less-decayed downed CWD. Abundance responded positively to the density of downed, well-decayed CWD and negatively to the density of poorly decayed CWD and to overstory relative density. CWD volume was not a strong predictor of salamander abundance. We conclude that structural complexity enhancement and the two uneven-aged approaches maintained important microhabitat characteristics for red-backed salamander populations in the short term. Over the long-term, given decay processes as a determinant of biological availability, forestry practices such as SCE that enhance CWD availability and recruitment may result in associated population responses.

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1. Introduction

Forest management practices can directly manipulate microhabitat characteristics important to terrestrial plethodontid salamanders. These characteristics include closed canopies that maintain cool, moist, interior forest microclimates. Other

important characteristics include un-compacted soils, downed coarse woody debris (CWD), and an undisturbed leaf litter layer (Semlitsch, 2002). Plethodontid salamander populations are highly indicative of rates and efficiency in several ecological processes, such as nutrient and energy cycling through forest floor biota (Welsh and Droege, 2001). Thus, understanding their population responses to alternative forestry practices (DeMaynadier and Hunter, 1998; Peterson and Maguire, 2005) would provide important information for restoration and forest management practices designed to conserve ecosystem function and forest biodiversity (Hunter, 1999; Lindenmayer and Franklin, 2002).

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Changes in terrestrial salamander populations resulting from forest management practices could have important effects on food web dynamics and nutrient cycling. Within the detrital food web, terrestrial salamander species are top predators (Burton and Likens, 1975) that regulate populations of soil invertebrates, such as hymenoptera, collembola, and araneida (Jaeger, 1972; Fraser, 1976). Consequently, they have an indirect effect on populations within critical functional groups, such as decomposer bacteria and fungi (DeMaynadier and Hunter, 1995). As secondary consumers, salamanders are, in turn, a significant food source for reptiles, birds, and small mammals (Burton and Likens, 1975; Pough, 1980). Thus, they represent a key linkage in energy cycling through higher trophic levels.

Improved understanding of the mechanisms relating modifications of forest habitat to amphibian diversity and abundance will inform development of ecologically sustainable forest management practices. These practices will aid broader regional and sub-regional efforts to conserve amphibian biodiversity (Putz and Viana, 1996). Studies in the northern United States have focused primarily on the effects of intensive forest management practices (clear-cutting and even-aged management) on amphibian populations (Pough et al., 1987; DeMaynadier and Hunter, 1998). For instance, significantly lower amphibian abundances and species richness have been documented in forest stands recently subjected to even-aged timber harvesting practices (DeMaynadier and Hunter, 1995). These results were consistent across 18 studies throughout the United States that examined the effects of clear-cutting on amphibians. Amphibian densities were, on average, 3.5 times higher in unharvested controls compared with clear-cuts (DeMaynadier and Hunter, 1995). Thus, harvest practices resulting in dramatic removal of aboveground vegetative structure negatively affect the availability of suitable amphibian habitats.

The question remains, however, whether forestry practices that retain higher post-harvest levels of structure, such as uneven-aged approaches, would have similarly deleterious effects. In general, the effects of uneven-aged management approaches, such as single-tree selection, on amphibian populations are not as clear. For instance, in a study of 47 hardwood stands logged at varying levels of intensity, Ross et al. (2000) found that the abundance of salamander species increased significantly with increasing retention of basal area (live and dead). Hicks and Pearson (2003) reported similar results for hardwood stands with varying land-use histories. These results contrast with other studies of salamander abundance in northern hardwood forests following selection cutting, and firewood cutting (Pough et al., 1987; Messere and Ducey, 1998), which found no effect of harvesting.

The differences reported by previous studies highlight the many subtler distinctions among uneven-aged practices. For instance, there are fundamental differences in the post-harvest spatial heterogeneity and degree of canopy closure associated with single-tree selection versus group-selection methods (Nyland, 1998; Seymour et al., 2002). Moreover, within either category there are subtle differences in prescriptions (e.g. choice of area-based treatment or residual basal area, q -factor,

and maximum tree diameter) that affect the amount and size distribution of post-harvest structure. These result in differences in residual stand density, basal area, aboveground biomass, leaf area index, canopy closure, and CWD recruitment (Keeton, 2005). Differences in stand structure, in turn, may affect the population densities of salamander species. The size of patches selected for group-selection cutting would be similarly important in affecting ambient environmental conditions.

Researchers with the Vermont Forest Ecosystem Management Demonstration Project (FEMDP) are investigating a range of silvicultural treatments applicable to sustainable forest management in the northern hardwood region of the north-eastern United States and southeastern Canada (Keeton, 2005). They are testing an uneven-aged harvesting approach that promotes the development of old-growth structural characteristics, termed “structural complexity enhancement” (SCE). This approach is compared against two conventional uneven-aged systems (single-tree selection and group-selection) modified to enhance post-harvest structural retention. SCE is designed to promote development of vertically differentiated canopies, variable horizontal density, re-allocation of basal area to larger diameter classes, and elevated large snag and downed log densities. These characteristics can be poorly represented in forests managed under conventional systems (Gore and Patterson, 1985; McGee et al., 1999) and because 19th century land-use practices decreased late-successional/old-growth forests by two orders of magnitude or more compared to pre-European settlement levels (Lorimer, 2001; Foster and Aber, 2004). This has important implications for regional forest age-class distributions and the resulting mix of wildlife habitats provided at landscape scales (Lorimer and White, 2003). Consequently, a goal of the FEMDP is to determine whether variants of uneven-aged silviculture, such as SCE, might have a positive effect on late-successional forest biodiversity by enhancing the availability of old-growth characteristics.

In this study, we explored mechanisms relating red-backed salamander (*Plethodon cinereus*) abundance to habitat alterations resulting from three treatments: SCE, single-tree selection, group-selection, and an un-harvested control. It is likely that stand structural characteristics associated with increased availability of suitable microclimates will have a positive influence on salamander abundance. Consequently, we hypothesized that population abundance would respond positively to SCE relative to conventional treatments and un-manipulated sites in the short term. Furthermore, we hypothesized that SCE would increase habitat availability, and therefore increase abundance in the long term. Previous research has found that salamander abundance is correlated with volume of downed CWD (Mathis, 1990; Petranka et al., 1994; DeMaynadier and Hunter, 1995; Morneau et al., 2004). Yet enhancement of CWD, such as that employed by SCE, affects both volume and density of CWD. Therefore, we also explored the effects of volume versus density of downed CWD on salamander abundance to determine if either metric was a better indicator of habitat availability and salamander abundance in northern hardwood forests.

2. Methods

2.1. Study sites

The FEMDP is being conducted at two study areas in northwestern Vermont; the Mount Mansfield State Forest (MMSF) and the University of Vermont's Jericho Research Forest (JRF). MMSF is located on the western slopes of the northern Green Mountain Range at elevations ranging from 470 to 660 m. JRF is located in the foothills at elevations ranging from 200 to 250 m. Soils are primarily loamy sands or sandy loams (JRF) and stony loams (MMSF). The sites are mature (ca. 70–100 year old), multi-aged stands dominated by *Acer saccharum* (sugar maple), *Fagus grandifolia* (American beech), and *Betula alleghaniensis* (yellow birch). *Tsuga canadensis* (eastern hemlock) is also co-dominant at JRF. Minor components include *Acer rubrum* (red maple) and *Quercus rubra* (red oak) at JRF and *Picea rubens* (red spruce) at MMSF.

2.2. Silviculture treatments

Detailed descriptions of the FEMDP's silvicultural treatments, briefly described here, are provided in Keeton (2005). There were three treatments: single-tree selection, group-selection, SCE, and an un-harvested control. Treatments were randomly applied to 2 ha units and replicated twice at the MMSF. Two additional replicates of both the SCE and the control were applied at the JRF ($n = 2$ replicates for single-tree selection and group-selection, $n = 4$ replicates for SCE and control). Treatment units were separated by 50 m (minimum) un-logged buffers to minimize cross contamination of treatment effects. Within each treatment unit there were five randomly placed 0.1 ha permanent sampling plots buffered by 15 m minimum distance from unit's edges ($n = 5$ plots per treatment unit). Experimental logging was conducted in January–February 2003, and salamander abundance was surveyed in 2004.

Prescriptions for the two conventional uneven-aged treatments (single-tree selection and group-selection) were based on a target residual basal area of $18.4 \text{ m}^2 \text{ ha}^{-1}$, maximum diameter at breast height of 60 cm, and q -factor of 1.3. Group-selection was further modified by reducing the area of individual cutting patches to approximately 0.05 ha.

The harvesting prescription for SCE was based on a marking guide that used a rotated sigmoid target diameter distribution applied as a non-constant q -factor. Modifications to the marking guide also included a higher target basal area ($34 \text{ m}^2 \text{ ha}^{-1}$) and a maximum diameter at breast height of 90 cm indicative of old-growth structure. Stand potential (pre-harvest CWD volume) and literature derived targets were used to set prescriptions for enhancing snag and downed woody debris volume and density.

2.3. Field methods

2.3.1. Habitat characteristics

Habitat characteristics were assessed based on data collected in the 0.1 ha plots. We conducted a full inventory of CWD

(≥ 10 cm diameter), noting the decay status of the logs with a 1–5 classification system (Sollins, 1982) and recording whether logs were $>$ or $\leq 50\%$ suspended from the ground. Only logs considered available as salamander habitat ($\leq 50\%$ suspended from the ground) were included in our analysis. We calculated volume ($\text{m}^3 \text{ ha}^{-1}$) and density (logs ha^{-1}) of CWD by decay class for the available logs. Diameter distributions included five size classes: ≥ 10 to < 20 cm; ≥ 20 to < 30 cm; ≥ 30 to < 40 cm; ≥ 40 to < 50 cm; ≥ 50 cm.

All live and dead trees ≥ 5 cm diameter at breast height (dbh) and > 1.37 m tall were measured, and recorded by species, dbh, height, and decay stage. The Northeast Decision Model (NED-2) (Twery et al., 2005) was used to generate basal area and stem density by plot. Relative density was then calculated by dividing basal area by the square root of dbh^2 and then dividing by stem density. We tested for correlation between habitat variables with the Proc Corr function in Program SAS (SAS Institute Inc., 2001). Variables that had significant correlations ($\alpha = 0.05$) were not used as parameters in the same model, thereby avoiding issues associated with collinearity or multicollinearity (Alexandre et al., 2003). We used Proc GLM function in Program SAS (SAS Institute Inc., 2001) to test for differences in habitat characteristics between the sites and the treatments.

2.3.2. Salamander surveys

We used 8-min, time-constrained, daytime area searches to survey 4 (25.8 m long by 2 m wide) transects nested within the 0.1 ha sampling plots. Transects were placed at 90° angles beginning at plot center and terminating at the corner of the plot. To control for diurnal factors, which may influence salamander activity and distribution (Bailey et al., 2004), we rotated the order in which treatment units were surveyed, sampling an equal number of plots from each treatment type on a given day. Non-destructive methods were used to locate salamanders under natural cover objects and to search leaf litter and vegetation for salamanders foraging on the forest floor. We recorded the number of red-backed salamanders observed per transect, and resurveyed transects 6–10 days later. Research has shown that capture probabilities vary due to factors such as age, sex, size, and/or social status (Tilley, 1980; Pollock et al., 1990; Salvadio, 2001). Because of the potential heterogeneity in capture probabilities, we did not collect measurements of length/weights, or sex the salamanders for use in analyzing demographic or physiological differences between treatments. Surveys were conducted in late-May and early-June 2004.

2.3.3. Detection probability covariates

We measured air temperature (Enviro-safe[®] “Easy Read” Armor Case Thermometers -5 to 50°C) and soil temperature (Weksler Soil Thermometer -18 to 83°C) at the center of each plot. Precipitation within 24 h of the survey (0 = no rain, 1 = rain), and sky conditions (0 = clear, 1 = partly cloudy, 2 = overcast, 3 = fog, 4 = light rain, 5 = steady rain) were also noted. We determined the amount of within-survey variability by calculating the coefficients of variation ($\text{CV} = \text{mean}/\text{standard deviation}$) for the environmental variables during

surveys 1 and 2. Environmental variables with CVs exceeding 30% were modeled as covariates for p_{it} , the probability of detecting an animal given that it is present (see Section 2.4.1).

2.4. Data analysis

2.4.1. Overview of analytical approach for estimating salamander abundance

One difficulty of studying terrestrial salamander populations is they are primarily subterranean (Heatwole, 1962). Only a small fraction of their total population may be near the surface and available for counting at a given time (Welsh and Droege, 2001) and perfect detection of individuals near the surface is unlikely (Bailey et al., 2004). Due to imperfect detection probabilities raw count data should be adjusted to account for the factors influencing detection probabilities when comparing population densities across time or space (Bailey et al., 2004; Royle, 2004; Kery et al., 2005).

We used a binomial mixture model approach developed by Royle (2004) to estimate abundance adjusted for detectability from our survey data. This model allows estimates of λ_i (abundance in site i), λ (mean abundance), and p_{it} (probability that a salamander would be detected in site i during survey t , given it is present). We chose the Poisson distribution, with mean λ , as the common distribution of N_i , and used a log-linear model in which λ_i varied according to treatment, site, and habitat characteristics (Kery et al., 2005). We modeled p_{it} as logit function of precipitation, air temperature, and sky conditions. Survey histories n_{it} were constructed from $R = 240$ transects sampled on $t = 2$ occasions. Model parameters were estimated

with maximum likelihood techniques and the encounter histories with the non-linear minimization *nlm* function in the software package R (Ihaka and Gentleman, 1996; Royle, 2004). Precision of the MLEs (95% confidence intervals) were computed from profile likelihood intervals (Lebreton et al., 1992).

2.4.2. Experimental treatment and site effects on salamander abundance

Our first analysis focused on experimental treatment and site effects. We evaluated four models to determine which factors most strongly influenced λ_i . Model A: λ_i was held constant across treatments and sites, notated $\lambda (\cdot)$. Model B: λ_i was a function of treatment effects alone. Model C: λ_i was a function of site effects alone. Model D: λ_i was a function of treatment and site. Treatments were coded as a categorical variable with the control as the reference, and site was coded as a categorical variable with MMSF as the reference.

2.4.3. Exploratory analysis of habitat characteristics effects on salamander abundance

For our second analysis we explored whether variability in forest structure among vegetation sample plots would influence λ_i . We evaluated 20 models including habitat characteristics to determine which factors most strongly influenced λ_i at this microscale. Table 1 provides a reference for the 20 models. Site was treated as a categorical variable with MMSF as the reference. All other covariates were standardized and treated as continuous variables. In Model 1, λ_i was held constant across sites. Models 2–20 represented four subsets of models. Each subset included models with just the primary parameters of

Table 1
Reference chart for parameter variations of 20 competing habitat models estimating mean site abundance, λ_i , and detection probabilities, p_{it}

Model	Detection probabilities, p_{it} , environmental covariates	Mean abundance λ parameters								
		Constant abundance $\lambda (\cdot)$	Density ^a CWD 1–2	Density ^a CWD 3–5	Vol. ^a CWD 1–2	Vol. ^a CWD 3–5	Total ^a vol. CWD	Total ^a density CWD	Site ^a	Relative ^a density
1	×	×								
2	×		×	×						
3	×		×	×						×
4	×		×	×					×	
5	×		×	×					×	×
6	×									×
7	×								×	
8	×								×	×
9	×							×		
10	×							×		×
11	×							×	×	
12	×							×	×	×
13	×						×			
14	×						×			×
15	×						×		×	
16	×						×		×	×
17	×				×	×				
18	×				×	×				×
19	×				×	×			×	
20	×				×	×			×	×

Environmental covariates for detection probabilities p_{it} were precipitation in the past 24 h, sky conditions, and air temperature recorded at the time of the surveys.
^a Relative density of overstory trees, density of CWD (logs ha⁻¹), volume of CWD (m³ ha⁻¹).

interest, and added the effects of site and relative density. The primary parameters of interest were: Models 2–5 (density of less-decayed and more-decayed CWD); Models 6–8 (relative density of overstory trees and site); Models 9–12 (total density of CWD); Models 13–16 (volume of less-decayed and more-decayed CWD); and Models 17–20 (total CWD volume).

We selected relative density as the overstory structure covariate for λ_i because this metric integrates multiple aspects of stand structure. CWD volume and CWD density were evaluated in six unique categories: (1) total density of logs; (2) density of less-decayed logs (decay classes 1–2); (3) density of more-decayed logs (decay classes 3–5); (4) total volume of logs; (5) volume of less-decayed logs; and (6) volume of more-decayed logs. These six categories were used as CWD covariates for λ_i . Thus, we evaluated structural characteristics manipulated by treatments that could influence habitat conditions and salamander abundance over the short-term. We also evaluated structural characteristics for which distributions are predicted to change over time. These changes in distribution are expected to have a corresponding long-term influence on habitat conditions and salamander abundance.

2.4.4. Model selection and goodness-of-fit

For both experimental and exploratory analyses, we used model selection approaches to rank models and to determine the weight of evidence for each model in the candidate set (Burnham and Anderson, 2002). Model selection was based on Akaike Information Criterion (AIC), which accounts for both model fit and model complexity (Burnham and Anderson, 2002). In this method, top ranked models most strongly support the data and models with AIC scores within two units of the top ranked model have substantial support.

We used a parametric bootstrap procedure within R (*nlm* function) to assess the adequacy of fit of our AIC_c best model (MacKenzie and Bailey, 2004; Kery et al., 2005). Parameters (i.e. λ_i , p_{i1} , and p_{i2}) were fixed at the MLE obtained for the model of interest, and 500 replicate data sets were generated. The simulated values formed the reference distribution used for comparison of the observed fit statistic (Pearson's Chi-squared, χ^2) (MacKenzie and Bailey, 2004; Kery et al., 2005). The overdispersion parameter \hat{c} was calculated by dividing the observed χ^2 by the averaged of the simulated χ^2 . To correct for overdispersed data and small sample size we used the quasi-likelihood version QAIC_c (Burnham and Anderson, 2002).

3. Results

3.1. Treatment effects on habitat characteristics

3.1.1. Course woody debris

CWD volume and CWD density were significantly ($p < 0.05$) correlated with each other at all levels evaluated. Mean densities of available less-decayed CWD (logs ha⁻¹) were significantly different between treatments ($F = 6.81$, $p < 0.008$), size classes ($F = 6.81$, $p < 0.001$), and treatment \times size class interaction ($F = 3.27$, $p = 0.002$) (Fig. 1). Site \times treatment \times size class interaction was also significant

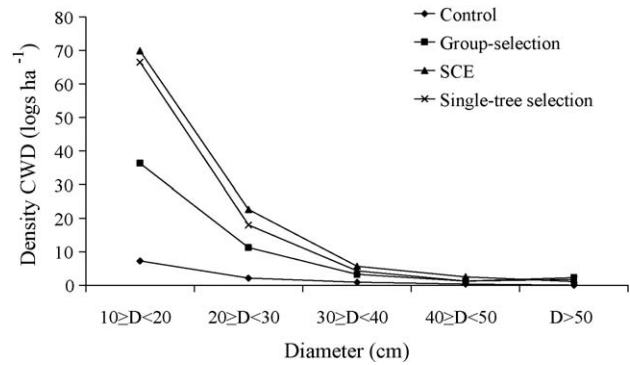


Fig. 1. Post-harvest mean densities of less-decayed CWD calculated from inventories conducted 18 months after logging. Densities for the un-harvested control and structural complexity enhancement (SCE) treatment were aggregated from inventories at the Jericho Research Forest and the Mount Mansfield State Forest sites. SCE had the greatest density of CWD (logs ha⁻¹) in the two smallest diameter size classes, while all three treatments had significantly greater densities in the smaller size classes compared to the un-harvested control.

($F = 8.30$, $p < 0.001$) with JRF SCE having twice as many logs in the smallest size class compared to MMSF. The control units were not significantly different ($p = 0.5495$).

Available mean densities of more-decayed CWD (logs ha⁻¹) had significantly different diameter distributions ($F = 38.10$, $p < 0.001$); the majority of logs were in smaller size classes. There were no significant differences between treatment types ($F = 1.43$, $p = 0.248$) treatment \times size class interaction ($F = 0.30$, $p = 0.985$), or site \times treatment \times size class interaction ($F = 0.85$, $p = 0.6442$) (Fig. 2).

3.1.2. Overstory structure

Relative density was not significantly different between SCE and the controls ($F = 0.78$, $p = 3.83$). Relative density was significantly different when comparing the controls against either single-tree selection ($F = 11.95$, $p = 0.001$) or group-selection ($F = 8.15$, $p = 0.006$) (Fig. 3). Parameter means (standard deviations) from the raw forest structure data, and mean z -scores for each treatment are presented in Table 2.

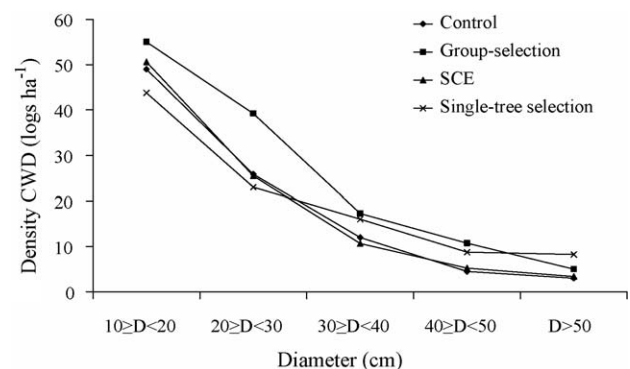


Fig. 2. Densities of more-decayed CWD (decay classes 3–5) were not significantly different between treatments or the control. Densities for the un-harvested control and structural complexity enhancement (SCE) treatment were aggregated from inventories at the Jericho Research Forest and the Mount Mansfield State Forest sites.

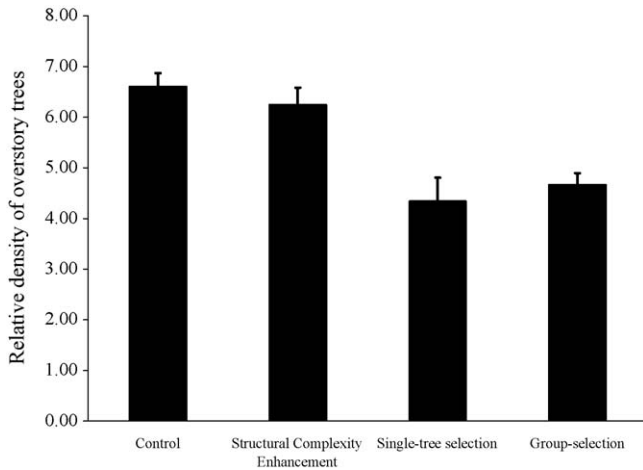


Fig. 3. Post-harvest relative density of overstory trees at the Jericho Research Forest and the Mount Mansfield State Forest were significantly different between the treatments and the un-harvested control ($F = 8.68, p < 0.001$).

Table 2
Habitat characteristics were transformed into standard normal deviates (z -scores)

Habitat characteristic	Raw data Mean (S.D.)	Mean z -scores			
		C ^a	SCE ^a	S ^a	G ^a
Density of CWD (logs ha⁻¹)					
Total available ^b	39.62 (20.42)	-0.26	0.15	0.03	0.08
Available less-decay ^b	19.37 (15.72)	-0.35	0.26	0.07	0.02
Available more-decay ^b	45.55 (12.84)	0.04	-0.10	-0.03	0.09
Total	50.10 (14.33)	-0.31	0.20	0.07	0.05
Decay classes 1–2	44.45 (21.01)	-0.37	0.27	0.10	0.00
Decay classes 3–5	30.70 (23.85)	0.06	-0.11	-0.04	0.09
Overstory					
Relative density	5.78 (1.59)	0.17	0.10	-0.15	-0.12

Negative mean z -scores (–) indicate the treatments mean value for the parameter was <the overall mean. Positive z -scores indicate the treatments mean value for the parameter was greater than the overall mean.

^a C: un-manipulated control; SCE: structural complexity enhancement; S: single-tree selection; G: group-selection.

^b Course woody debris (CWD) $\leq 50\%$ suspended from the ground was considered available habitat for salamanders.

3.2. Red-backed salamander survey results

We counted a total of 714 red-backed salamanders during the two survey occasions: 477 at the MMSF and 237 at the JRF (Table 3). The number of salamanders counted per transect ranged from 0 to 7. Four other species were observed during the

Table 3
Total number of red-backed salamanders (mean per transect) during $t = 2$ salamander surveys

Species	Jericho Research Forest		Mount Mansfield State Forest			
	Control	SCE	Control	SCE	Single-tree selection	Group-selection
Eastern red-backed salamander	89 (1.11)	148 (1.85)	133 (1.66)	91 (1.14)	104 (1.30)	149 (1.86)

course of this study. Eastern newts (*Notophthalmus viridescens*) were the next most common species observed on all treatments and the control. This was the only other species observed at JRF. At MMSF, northern dusky salamanders (*Desmognathus fuscus*) were observed in the control and SCE stands. A spotted salamander (*Ambystoma maculatum*) was observed in SCE and a spring salamander (*Gyrinophilus porphyriticus*) was observed in the control stand.

3.3. Model selection and goodness-of-fit

3.3.1. Detection probability covariates

There was a high amount (CV > 30%) of within survey variability for precipitation, sky conditions, and air temperature. Seventy-five percent of surveys were conducted following precipitation in the past 24 h with 17% of surveys occurring during fog, drizzle, or rain. Air temperature ranged from 7.5 to 29 °C averaging 17 °C. Soil temperature ranged from 8 to 16 °C averaging 11 °C and was not significantly different between treatments. The effect of the environmental covariates on p_{it} was similar in the experimental and exploratory analyses (see below). Precipitation within the past 24 h had the greatest effect on p_{it} reducing detection probability. Air temperature and sky conditions had a slight positive effect p_{it} . The detection probability was estimated to be 42%.

3.3.2. Experimental treatment and site effects on salamander abundance

The model of λ_i as a function of site was ranked as the best QAIC_c model of the set testing treatment effects (Table 4). The model including site and treatment was also ranked highly, however the additional treatment parameters did not improve model deviance. Site was estimated to have a large effect on abundance. At MMSF red-backed salamander abundance was estimated to be 12.7 per transect in the control treatment, compared to 6.8 per transect in the control treatment at JRF.

3.3.3. Exploratory analysis of habitat characteristics effects on salamander abundance

Model 5 was the top ranked model of the 20 models evaluated (Table 5). This model included density of less-decayed and more-decayed CWD, site, and overstory relative density. Salamander mean abundance was positively related to the density of more-decayed logs. Less-decayed logs and overstory relative density did not appear to have much of an effect on salamander abundance. Three additional models had Δ QAIC_c values <2.0 (Table 5). These models made up the 95% confidence set. All four of the top ranked models included a site effect similar to that estimated for the treatment effect models.

Table 4
QAIC_c ranking of experimental analyses models

Model name	−2log(II)	ΔQAIC _c	k	ω _i	λ _i					p _{it}				
					β _{intercept}	β _{site}	β _{SCE} ^a	β _S ^a	β _G ^a	βp _{i1}	βp _{i2}	β _{precipitation}	β _{sky}	β _{air}
Site	1521.12	0.00	8	0.54	2.541	−0.616				−2.589	−0.332	−0.209	0.023	0.052
Site + treatment	1521.07	0.49	11	0.43	2.544	−0.626	0.009	−0.002	0.000	−2.588	−0.336	−0.213	0.022	0.052

^a C: un-manipulated control; SCE: structural complexity enhancement; S: single-tree selection; G: group-selection. Treatments and site were coded as categorical variables, with control as the reference for treatment and Mount Mansfield as the reference for site. {logit(p_{it}) = ((βp_{i1} + βp_{i2}) + β₁ × precipitation + β₂ × sky conditions + β₃ × air temperature)} {log(λ_i) = (β₀ + β₁ × site)}.

Table 5
QAIC_c ranking of exploratory analyses models

Model no.	−2log(II)	ΔQAIC _c	k	ω _i	λ _i						p _{it}				
					β _{intercept}	β _{site} ^a	β _{relden} ^b	β _{totd} ^c	β _{density} ^c CWD 1–2	β _{density} ^c CWD 3–5	βp _{i1}	βp _{i2}	β _{precipitation}	β _{sky}	β _{air}
5	1511.07	0.00	11	0.40	2.651	−0.630	−0.020		−0.079	0.304	−2.875	−0.307	−0.205	0.040	0.059
12	1512.77	1.26	10	0.21	2.631	−0.708	0.043	0.121			−2.643	−0.388	−0.255	0.022	0.048
4	1513.22	1.64	10	0.18	2.629	−0.674			0.074	0.094	−2.699	−0.336	−0.217	0.030	0.053
11	1513.61	1.80	9	0.16	2.629	−0.654		0.112			−2.699	−0.336	−0.230	0.027	0.050

Four of the 20 competing habitat characteristic models had QAIC_c < 2. The model with the lowest QAIC_c is in bold type. Model 5 = {logit(p_{it}) = ((βp_{i1} + βp_{i2}) + β₁ × precipitation + β₂ × sky conditions + β₃ × air temperature)} {log(λ_i) = (β₀ + β₁ × site + β₂ × relden + β₃ × density CWD 1–2 + β₄ × density CWD 3–5)}.

^a Site was coded as a categorical variable with Mount Mansfield as the reference site.

^b Relative density of overstory trees.

^c Available density of course woody debris (CWD logs ha^{−1}) (<50% suspended from the ground); totd = total density; density less-decayed logs (CWD 1–2); density more-decayed logs (3–5).

The JRF was estimated to have approximately one-half as many red-backed salamanders as the MMSF study area. The top four ranked models also included density of downed CWD. Volume of CWD was not included in any of the top models.

3.3.4. Goodness-of-fit

The goodness-of-fit testing approach was needed to ensure that the models in the model set adequately described the observed data. The top ranked model (Model 5, $\chi^2 = 29.30$) was slightly over-dispersed compared to the average of the bootstrap simulated data ($\chi^2 = 25.14$), with a $\hat{c} = 1.17$. We therefore adjusted the QAIC_c scores by forcing $\hat{c} = 1.17$ for all analyses.

4. Discussion

4.1. Effects of coarse woody debris on salamander population abundance

Contrary to our expectations, red-backed salamander abundance did not differ significantly between SCE and the other treatments or controls. Our study found these variants of uneven-aged silviculture, all of which had been modified to enhance post-harvest structural retention, had little or no negative impact on salamander abundance. Low-impact silvicultural techniques were effective in maintaining suitable habitat for and populations of red-backed salamanders following timber harvest.

The lack of an immediate, post-harvest treatment effect may be attributed, in part, to consistent densities of well-decayed CWD (decay classes 3–5) across all treatment and control units. These were residual logs recruited prior to treatment. That the density of well-decayed CWD had the greatest influence on red-backed salamander abundance is strongly supported by our modeling results. Bartman et al. (2001) reported similar results which may be attributed in part to high densities of well-decayed CWD as well as the high elevation and north-facing aspect of their study site. They described their study site as being “littered with American chestnut (*Castanea dentata*) trees killed by chestnut blight in the early 1900s.” Their results contrast with other studies conducted in the southern Appalachians (Harpole and Haas, 1999; Knapp et al., 2003) which found negative responses to increasing canopy disruption. Commercially harvested forests in southern Appalachian tend to be oak-dominated on slopes with southern and western aspects (Smith, 1994), while higher salamander densities are found on northeastern exposures and lower portions of slopes at higher elevations (Harper and Guynn, 1999). Consequently, harvesting sites with cooler, moister local or regional climates may reduce the impact on terrestrial salamander populations.

Over the long-term salamander abundances are likely to respond to differences between the treatments. Structural complexity enhancement, as an alternative approach, enhanced long-term CWD recruitment potential (Keeton, 2005), thereby increasing future habitat availability for woody debris-dependent salamanders. Our models suggest that the cumula-

tive effect of both maintaining short-term habitat availability and enhancing future CWD recruitment are likely to result in an increase in terrestrial salamander populations over time. Thus, we predict a lagged population response to CWD enhancement. Because red-backed salamanders are an important component of northern hardwood ecosystems (Burton and Likens, 1975; Welsh and Droege, 2001), maintaining and enhancing the microhabitat characteristics they require is likely to have a positive effect on ecosystem functioning as a whole.

Our study found that density of CWD was a strong indicator of red-backed salamander habitat availability and population abundance. Downed CWD provides salamanders with moist retreats to use for rehydration, nesting, and protective cover (DeMaynadier and Hunter, 1995), and also provides important habitat for salamander prey (Jabin et al., 2004). All of our top ranked models showed that CWD density had a positive effect on salamander abundance, while none of our top models included CWD volume. These results contrast with other studies which found abundance correlated with volume (Mathis, 1990; DeMaynadier and Hunter, 1995; Morneault et al., 2004). However, the variation in forest types and added complexity of salamander communities in some regions may influence the importance of one metric over the other. We conclude, consequently, that salamander abundance in northern hardwood forests is more closely associated with CWD density rather than volume. Terrestrial salamanders are territorial and will defend their cover objects, such as rocks and logs, from intrusion by other salamanders (Smith and Pough, 1994; Townsend et al., 1998; Jaeger et al., 2000). The association we found between log density and red-backed salamander abundance may be related to adult territoriality. In northern hardwood forests, greater log densities across a range of sizes may provide more retreats. This would support greater densities of salamanders compared to the presence of only a few large logs – though collectively representing a large volume – guarded by resident pairs.

4.2. Effects of overstory structure on salamander population abundance

Microclimate on the forest floor is highly sensitive to changes in canopy closure (Chen et al., 1999). Loss of canopy cover typically results in more extreme environmental conditions across the open patches, such as temperature and solar radiation increases and soil moisture decreases (Chen et al., 1999). Salamanders are poikilotherms; their body temperatures closely resemble those of the microhabitats they occupy, both in terms of mean levels and variability (Feder, 1983). Variability caused by unstable microclimates could have serious energetic consequences, causing a decline in productivity and population densities (Feder, 1983). Therefore, salamanders may avoid patches with highly variable microclimate by limiting their time on the surface (vertical migration) or abandoning the habitat (horizontal migration) (Heatwole, 1962). Lower population densities and detection probabilities could be indicative of microclimate variability. However, low-impact forestry methods (McEvoy, 2004), such as those used by

the FEMDP, were designed to limit environmental extremes across the area of application. For example, group-selection cutting patches were each approximately 0.05 ha in size (Keeton, 2005), which is smaller than the 0.1–0.5 ha groups typical for the region, and all three methods were designed to increase retention of post-harvest basal area. Relative density had only a small effect on the abundance of red-backed salamanders. These results are indicative of the high levels of structure retained by all the treatments and are consistent with other studies. For example, salamander abundance in northern hardwood forests was not significantly affected by selective logging, or firewood harvesting (Pough et al., 1987; Messere and Ducey, 1998; Ross et al., 2000). However, salamander abundance was shown to be affected by the amount of residual basal area (Ross et al., 2000). These results support the argument that subtle differences in prescription that affect the amount and size distribution of post-harvest structure will have an effect on terrestrial salamander populations.

4.3. Site effects on salamander abundance

Abundance estimates of red-backed salamanders at JRF were nearly one-half those estimated at MMSF. These differences in estimated abundance may be due to higher precipitation and cooler climate at MMSF (Thompson and Sorenson, 2000). The site at MMSF is 270–410 m higher in elevation. Harper and Gynn (1999) reported similar results wherein salamander abundances were correlated with elevation. JRF also had well-drained soils composed primarily of loamy-sands or sandy-loams while MMSF soils were primarily stony-loams. These differences in soil type may have influenced soil moisture levels, and therefore habitat quality. The estimated abundance and the unadjusted mean number of salamanders per transect for our controls were nearly twice as high at MMSF compared to JRF. In contrast, the unadjusted count data at JRF's SCE was 1.6 times greater than at MMSF. This difference could be attributed to JRF's SCE treatments having a much greater density of less-decayed CWD compared to MMSF's SCE. Less-decayed CWD provides lower quality habitat and lacks well-developed burrows for escaping detection. However, clustering of less-decayed CWD, in conjunction with the warmer, drier conditions at JRF, could have resulted in salamanders congregating under these cover objects, thereby making them easier to count (Bailey et al., 2004).

4.4. Other factors influencing salamander abundance

Climate conditions during early summer 2004 may have contributed to the lack of observable treatment effects. Vermont received higher than average precipitation (129%) and experienced lower than average temperatures (-1.2°F) (Northeast Regional Climate Center, 2004) during the summer of 2004. Weather conditions and moisture influence salamander activity levels (Heyer et al., 1994; Grover, 1998), and, hence, affect detection probabilities (Williams and Berkson, 2004). In our study, salamanders may have responded to the cool, moist climate by increasing their activity on the surface in open areas.

Above average precipitation levels and cooler temperatures also may have increased soil and fine debris moisture retention. This may explain why we found salamanders utilizing fine debris located under open canopies, even in the middle of group-cuts, as daytime refugia. Had climatic conditions been reversed, overstory relative density may have been more important in moderating microclimate conditions across the plot, and we might have detected a treatment effect on salamander densities.

5. Management implications

Red-backed salamanders are important components of northern hardwood forest ecosystems, influencing ecosystem processes such as decomposition rates and nutrient cycling (Wyman, 1998). We found that structure-based, variants of uneven-aged forestry practices, such as structural complexity enhancement, are effective in maintaining red-backed salamander populations, and potentially, by inference, related ecosystem functions. It is possible that biodiversity associated with similar habitat requirements would also benefit from SCE. These positive effects are in part due to the maintenance of canopy cover, which decreases microclimate variability across the patch. Canopy cover was spatially variable but highest, in aggregate, in SCE units compared to the other treatments (Keeton, 2005).

Incorporating management for CWD density into forestry practices is essential to provide habitat for debris-dependent salamander species. Our results show that structure-based methods, such as SCE, can enhance CWD densities, at least over the short-term. While long-term CWD recruitment and persistence dynamics following treatment are uncertain (see Keeton, 2005), the biological availability of downed logs will certainly increase with decay processes over time, providing more habitat for salamanders and other debris-dependent organisms.

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