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Evaluating Mechanisms of Short-term Woodland Salamander Response to Forest Management

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Abstract

Contemporary forest management often requires meeting diverse ecological objectives including maintaining ecosystem function and promoting biodiversity through timber harvesting. Wildlife are essential in this process by providing ecological services that can facilitate forest resiliency in response to timber harvesting. However, the mechanisms driving species' responses remain ambiguous. The goal of this study was to assess mechanisms influencing eastern red-backed salamander (RBS; *Plethodon cinereus*) response to overstory cover removal. We evaluated two mitigation strategies for the RBS in response to overstory removal. We used a before-after-control-impact design to study how (1) retaining residual trees or (2) eliminating soil compaction affected RBS surface counts and body condition index (BCI) up to two-years post-treatment. Additionally, we assessed how surface counts of RBS were influenced by overstory tree cover. Surface counts of RBS were not strongly influenced by overstory removal when tree residuals were retained. Body condition index increased in treatments where harvest residuals were retained. In treatments where soil compaction was eliminated, surface counts and BCI were inversely related. Finally, surface counts from both mitigation strategies were not strongly influenced by overstory cover. Overall, both mitigation techniques appeared to ameliorate impacts of overstory removal on RBS. These results highlight the importance of understanding mechanisms driving species' responses to forest management. To reduce the perceived negative effects of overstory removal on RBS, incorporating these mitigation measures may contribute to the viability and stability of RBS populations. Incorporating species' life history traits into management strategies could increase continuity of ecological function and integrity through harvesting.

Keywords Amphibian · Plethodon · Central Appalachia · Ecological forestry · Salamander · West Virginia

Introduction

Forest management in the twenty-first century seeks to balance multiple ecological goals, including promoting biodiversity and maintaining ecosystem function post-harvest. Preserving biodiversity and ensuring continuity of functionality and integrity of forests through harvesting can be facilitated by bottom-up measures at small-scales, such as the retention of biological legacies (e.g., downed coarse woody debris, standing dead trees) which can provide important refugia for vertebrate and invertebrate biota (Nappi et al., 2015; Wermelinger et al., 2017). Indeed, forest certification standards now include retention and physical arrangement of downed woody materials as one approach for promoting forest health, forest structure, and biodiversity (Sustainable Forestry Initiative, 2015). Historically, however, many organisms closely associated with biological legacies (e.g., herpetofauna, insects, mycorrhiza) were not prioritized when developing harvesting guidelines

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or when considering post-harvest conditions. Research on the effects of forestry practices on lower trophic level species is growing and thus providing empirical data for managers to implement in their harvesting prescriptions. However, there is a continual need to develop management guidelines that consider these species' life history traits because they offer myriad ecosystem services to forest systems. Guidance on how to best promote habitat for these different taxa has broad implications for retaining important ecological processes in forest systems post-harvest.

Woodland salamanders (genus *Plethodon*) are one species group that was historically overlooked when developing forest management guidelines (deMaynadier and Hunter, 1995). Forest managers and researchers now have a greater understanding of the ecological roles these salamanders play in forest systems (Homyack et al., 2010; Barrett et al., 2014; Hocking and Babbitt, 2014). Woodland salamanders are numerically dominant in forested systems of the eastern United States (Burton and Likens, 1975a), which allows them to exert a strong influence on the food web in forests (Hairston, 1987). Salamanders exhibit strong top-down pressures on detritivorous forest floor invertebrates which affects forest litter decomposition rates and carbon dynamics (Wyman, 1998; Walton, 2013; Hickerson et al., 2017). Further, woodland salamanders represent a high-quality food source for many predators such as birds, mammals, reptiles, and other amphibians (Burton and Likens, 1975b; Petranka, 1998). Because of these factors, salamanders represent important linkages in the forest food web dynamic and have been considered important for ecological function and integrity (Welsh Jr. and Droege, 2001; Davic and Welsh, 2004).

There is a need to better understand the underlying mechanisms driving responses of woodland salamanders to forest management in order to provide managers with harvesting strategies that are compatible with salamander life history traits. Previous research has focused on certain forest characteristics (e.g., overstory cover, coarse woody debris, leaf litter depth) and their influence on salamanders post-harvest in order to guide forest management (Semlitsch, 2002; McKenny et al., 2006). Even-aged forest management (e.g., clearcutting and shelterwood) is often thought to be the most detrimental to woodland salamanders in the short-term (Duguay and Wood, 2002; Hocking et al., 2013a) because these techniques greatly reduce overstory cover which increases the amount of solar radiation reaching the forest floor and subsequently dries out leaf litter and increases soil temperature (Zheng et al., 2000; Brooks and Kyker-Snowman, 2008). Due to physiological constraints (e.g., thin, vascular skin; Hillman et al. 2009), woodland salamanders are at increased risk of desiccation when exposed to drier environments at the forest floor. To cope with the environmental stress, individuals will often remain belowground where soils are cooler and moisture is not as limiting. However, heavy machinery used during operational silviculture compacts soils creating physical barriers for fossorial salamanders (Steinbrenner, 1995). Further, the removal of surface refugia such as tree limbs, treetops, and other coarse woody debris (CWD) following harvesting can reduce habitat quality for salamanders and reduce the amount of time they spend at the forest floor surface (Achat et al., 2015; Peele et al., 2017). Consequently, because woodland salamanders forage and breed at the forest floor surface, harsh surface conditions, soil compaction, and low levels of CWD can affect population dynamics (Peterman and Semlitsch, 2014).

Mitigating the negative effects of loss of overstory cover from forest management through practices such as reduced soil compaction and greater CWD retention to maintain stable salamander populations through harvesting has been of interest. Previous work in hardwood forests of eastern North America and the Appalachian region has shown that increased retention of overstory cover through partial harvesting approaches, such as uneven-aged management (e.g., group selection, single-tree selection), can result in higher relative densities of salamanders compared to even-aged treatments that remove greater amounts of overstory (Hocking et al., 2013a; Harper et al., 2015; Mahoney et al., 2016). Greater retention of the overstory limits the amount of solar radiation reaching the forest floor which retains microclimates generally compatible with the physiology of salamanders (e.g., wetter, cooler; Homyack et al., 2011). However, multiple stand entries are required to complete an entire rotation which can accumulate negative effects for salamanders by compacting soils (Homyack and Haas, 2013). Greater amounts of CWD can also mitigate the negative effects of even-aged forest management by providing surface refugia that maintains suitable environmental conditions underneath logs and rocks and allows individuals to remain at the surface for longer periods of time (Grover, 1998; Moseley et al., 2009; Strojny and Hunter, 2009; Carusco, 2016). These mitigation measures likely help retain woodland salamanders post-harvest, but which measures are most important for retaining salamanders remains ambiguous. Because these mitigation measures are often jointly undertaken, isolating the ultimate reason for salamander responses is confounded.

We quantified relative abundance and body condition responses for a woodland salamander, the eastern red-backed salamander (RBS; *Plethodon cinereus*), to two different mitigation techniques, CWD retention and limiting soil compaction, to evaluate their potential for retaining suitable habitat conditions post-harvest. The goal of our study was to assess, separately, which mitigation measure was most influential for RBS relative abundance (i.e., surface count) and body condition index (BCI) post-harvest

relative to pre-harvest and an unharvested control. Understanding the mechanisms driving woodland salamander abundance and BCI in response to forest management elucidates information on which forest characteristics to manage in multi-use forestry. Forest management techniques that promote biodiversity to help maintain ecosystem function provides managers with the necessary tools to develop guidelines for managing healthy forest systems.

Materials and Methods

Study Area

This study was conducted on three West Virginia Division of Natural Resources (WVDNR) wildlife management areas (WMA) located in West Virginia, USA: Beury Mountain WMA (BMWMA), Lewis Wetzel WMA (LWWMA), and Little Canaan WMA (LCWMA; Fig. 1). West Virginia lies within the central Appalachian region and is characterized by rugged topography and extensive deciduous and coniferous forests (Küchler, 1964). Forest composition at BMWMA was mixed hardwood and oak-hickory (*Quercus* spp.-*Carya* spp.), LWWMA was oak-hickory and cove hardwood, and LCWMA was maple-beech-birch (*Acer* spp.-*Fagus* spp.-*Betula* spp.) forest types (Küchler, 1964). Elevations at study sites ranged from 224–1132 m (BMWMA: 610–1108 m, LWWMA: 224–475 m, LCWMA: 944–1132 m). West Virginia's humid continental climate is characterized by warm summers and cool to cold winters with daily mean spring and fall temperatures of 10.0 °C and summer temperature of 21.0 °C. Mean annual precipitation levels in West Virginia were 76, 127, and 102 cm in the western, central, and eastern portions of the state, respectively, with the heaviest precipitation occurring during spring and summer (NOAA, 2020).

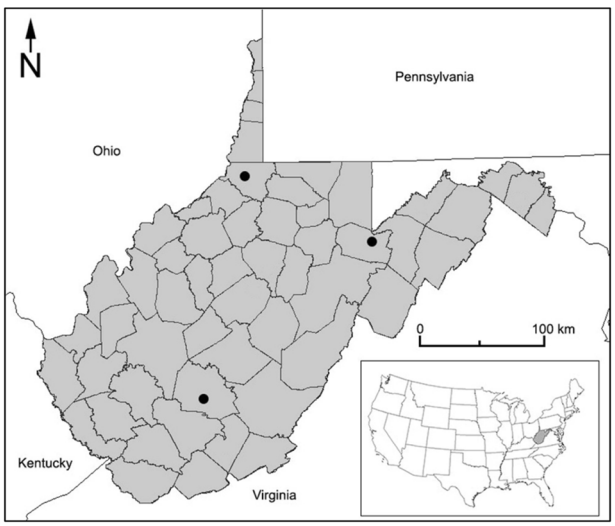

Fig. 1 County-level map of West Virginia, USA, showing three wildlife management areas (black dots; Beury Mountain WMA [south-central WV], Lewis Wetzel WMA [north-central WV], and Little Canaan WMA [northeast WV]) used to assess eastern red-backed salamanders (*Plethodon cinereus*) response to retention of whole tree harvest residuals following harvesting and elimination of soil compaction during 2016–2019

Study Design

We sampled in treatments that were subjected to two different overstory cover reduction prescriptions. The first approach consisted of tree cutting via feller buncher, where all felled trees were dropped in the stand and remained in the stand following cutting. This prescription was used to evaluate RBS response to increased CWD. With this approach, overstory cover reduction was conducted within mature forests along the edges of rights-of-way (e.g., underground gas pipelines and overhead utility lines) at all three WMAs, with two block replicates per WMA (Fig. 1). A single block replicate consisted of five independent experimental units (hereafter "cut-back borders") with each assigned one of five experimental treatments. Treatment plots within each block replicate were presumed to be subjected to similar biotic and abiotic environmental constraints because block replicates along rights-of-way were located along one or two rights-of-way of similar widths within the same WMA. We assigned treatments within each block replicate by randomly selecting one of two target residual basal area levels (4.5 m^2/ha or 14.0 m^2/ha basal area retention) and one of two cutting depths into the forest (30 m or 45 m wide, perpendicular to forest edge) for each cut-back border with one cut-back border randomly designated as a control (i.e., no tree cutting). Each cut-back border was 300 m in linear distance along the forest edge and ≥200 m apart (Fig. 2A). In each cut-back border plot, four salamander sampling points were located 15 m from the forest edge and spaced 75 m apart (Fig. 2A). Two vegetation sampling points were also located 15 m from the forest edge and spaced 150 m apart (Fig. 2A).

The second overstory cover reduction approach consisted of an herbicide hack-and-spray technique to mimic canopy basal area retained in crop tree or shelterwood harvests (i.e., 9.0–14.0 m^2/ha target basal area retention) with trees receiving herbicide remaining standing following treatment. This approach was conducted within interior mature forests at one WMA (Fig. 1) to evaluate minimizing soil compaction. There were five block replicates consisting of two independent experimental units (hereafter "regeneration stands") with each unit assigned one of two experimental treatments. Treatment plots within each block replicate were presumed to be subjected to similar biotic and abiotic environmental constraints. We randomly assigned the hack-and-spray (HS) and a control (i.e., no tree-cutting) treatment

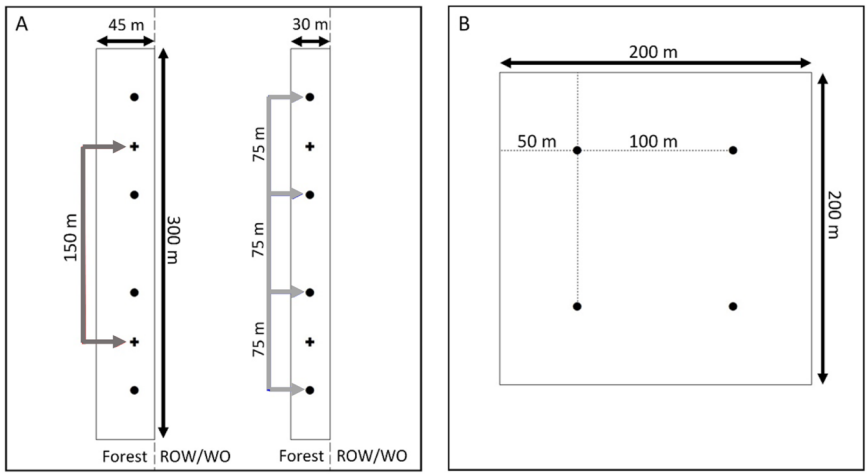

Fig. 2 Cut-back border plot layout (**A**) with salamander (black dots) and vegetation sampling points ("+") for each harvest width factor level (30 and 45 m) along pipelines, powerlines, and wildlife openings ("ROW/WO"). Regeneration stands plot layout (**B**) with salamander and vegetation sampling points (black dots)

to the two experimental units in each block replicate. Herbicide in the HS treatment was applied via stem-injection or cut-stump to a subset of all trees using 6% solution of Arsenal® (active ingredient Imazapyr, 28.7% a.i.) or 3% solution of Arsenal® AC (active ingredient Imazapyr 53.1% a.i.) in a water carrier for the stem-injection treatment and using 50% solution of Razor®-Pro, Glyphosate® 41, or Roundup®-Pro (all containing 41% Glyphosate a.i.) in a water carrier for the cut-stump treatment. Each regeneration stand was 4 ha (200 m × 200 m) in size and roughly square in shape, and all were ≥200 m apart to ensure sampling independence (Fig. 2B). In each regeneration stand, four salamander and vegetation sampling points were spaced at the corners of a 100 m × 100 m square grid with the grid centered on the middle of the stand and located 50-m from the stand edge (Fig. 2B).

In cut-back borders and regeneration stands, we used a before-after-control-impact (BACI) framework. This approach allows for causal inference of relationships between treatments and salamander responses through time (Eberhardt, 1976). We collected one-year of pre-treatment data and two-years of post-treatment data on the vegetation and salamander community.

Salamander Sampling

We quantified RBS response to cut-back borders and regeneration stands using a combination of artificial and natural cover objects. At each sampling point, we conducted three survey visits annually during 2017–2019. Visit 1 was 15 April–6 May, visit 2 was 1–16 May, and visit 3 was 17 June–9 August. Artificial coverboards at each sampling point consisted of nine (3 × 3 arrangement spaced ~1 cm apart), 20.0 × 10.0 × 2.5 cm wooden boards cut from hardwood species from the region (American basswood [*Tilia americana*], American sycamore [*Platanus occidentalis*], and yellow poplar [*Liriodendron tulipifera*]). Coverboards were placed at sampling points at least one month prior to sampling to allow them to weather (Hesed, 2012). Natural cover objects were logs or rocks ≥40 mm at the narrowest dimension and located within a 5-m radius of each artificial coverboard location. All eligible natural cover object dimensions (length and width, in mm) were measured prior to salamander sampling during the pre-harvest period. We marked natural cover objects with stake flags to maintain consistent sampling effort across visits and years. Use of a combination of artificial and natural cover objects for sampling can produce valid indices of terrestrial salamander populations (Smith and Petranka 2000).

During each visit we turned over all coverboards and natural objects, which we then returned to their original position for future sampling. After capturing a salamander, we measured snout-vent length (SVL; anterior edge of the snout to the distal end of the cloaca) to the nearest 0.1 mm using a dial caliper and recorded body mass to the nearest 0.1 g using a Pesola spring scale. We clipped the tail of each captured individual to identify subsequent recaptures. We sprayed clipped tails with an antiseptic to minimize potential for infection, and sterilized clippers with 95% ethanol and an open flame to minimize potential for disease transmission. Salamanders were released at their original point of capture.

Vegetation and Topographic Characteristics

We measured vegetation and topographic characteristics at two sampling points within each cut-back border (Fig. 2A) and four sampling points within each regeneration stand (Fig. 2B). Sampling techniques and variables collected were consistent across cut-back borders and regeneration stands. Within an 11.3 m radius (0.4 ha) circular plot centered on each sampling point, we measured diameter-at-breast height

(DBH) of all live trees ≥11.4 cm DBH to the nearest 0.1 cm using DBH tapes. At each sampling point, we also measured percentage of live overstory cover (delineated at ≥5 m above ground) using a 25 cm × 25 cm transparent plexiglass panel, divided into a 5 × 5 grid, held overhead (Hachè et al. 2013).

We derived topographic variables surrounding each sampling point using 3-m scale digital elevation model data (WVGIS, 2019) within ArcGIS (ESRI, 2018). Five variables (slope percent, slope aspect, slope position, slope configuration, and elevation) were calculated using zonal statistics to generate a mean value within a 50-m radius surrounding each sampling point. Slope percent, slope aspect, slope position, and slope configuration were combined to derive a topographic relative moisture index (TRMI), which ranged from 0 (xeric soil) to 60 (mesic soil; Parker, 1982).

Statistical Analyses

Treatment effects on RBS surface counts and body condition index

We modeled surface counts and BCI of RBS in cut-back borders and regeneration stands using stacked Bayesian generalized linear mixed-effects models (GLMMs). We modeled surface counts in GLMMs using a Poisson process model and modeled BCI using a Gaussian process model. For the BCI metric, we regressed the natural logarithm of body mass on the natural logarithm of SVL to generate a least-squares trendline for each individual salamander and then used the residuals to calculate BCI for each individual, following Gabor (1995). Because differences in BCI of salamanders at different study sites could be due to broad environmental characteristics (e.g., temperature, latitude) and not treatments across study sites, we calculated a separate trendline for each of the three study sites using only individuals captured at that study site.

For surface count and BCI models, we used diffuse prior distributions for all covariates and environmental variables (Gaussian [mean = 0, variance = 100]) because we were uncertain of the relationships between cut-back border or regeneration stand treatments and salamanders. We used a Gaussian distribution (mean = 0, variance = τ) prior with a hyperparameter τ from an inverse Gamma distribution ($\alpha = 1$, $\beta = 1$) for our random sampling point and study site effects. Continuous variables in all models were standardized to have a mean of 0 and standard deviation of one prior to analysis. We obtained posterior distributions of model parameters by running three parallel Markov chain Monte Carlo simulations of 101,000 iterations with a burn-in of 1000 iterations at a thinning rate of 100, yielding 3000 samples for posterior distributions.

We assessed model fit with a posterior predictive check, where we compared Chi-square goodness-of-fit tests between an observed posterior predictive distribution and a simulated posterior predictive distribution. We calculated a Bayesian *p*-value, p_B, as the probability to obtain a Chi-square test statistic that is at least as extreme as the observed Chi-square test statistic and assumed reasonable fit if $0.1 < p_B < 0.9$ (Gelman et al., 2014). Model convergence was assessed using the Brooks-Gelman-Rubin statistic and assumed adequate when all parameter Rhat values <1.1 (Brooks and Gelman, 1998). Data analyses were performed in R version 4.0.3 (R Core Team, 2020) using a Bayesian framework in JAGS (Plummer, 2017) called from the package jagsUI (Kellner, 2015). Posterior means are presented as slope coefficients with 95% lower and upper credible intervals (CI). We drew conclusions about treatment effects by inspecting regression coefficients from Eq. 1 or Eq. 2 below and by using contrasts (Casella, 2008) to compare log expected surface counts or expected BCI between treatment levels and no-harvest controls. Strength of regression coefficients and contrasts were based on 95% CIs of posterior distributions not overlapping 0. Further statistical details related to specific treatments are provided below.

Cut-back borders Our GLMM for surface counts and BCI in cut-back borders incorporated a full-factorial design with cut-back border treatment factor levels harvest width (30 m and 45 m) and harvest intensity (14 m^2/ha and 4.5 m^2/ha basal area retention). The full-factorial design allows for the comparison between cut-back borders that received tree cutting and did not receive tree cutting (i.e., control), the comparison between cut-back border width factor levels (30 m and 45 m), and the comparison between cut-back border intensity factor levels (14 m^2/ha and 4.5 m^2/ha basal area retention).

We modeled expected surface count or BCI y_{ijk} at sampling point i within treatment plot j during year k as a function of an intercept β, a sampling point random effect (SP_i) to account for the heterogeneity among points and repeated observations at the same point and a study site random effect (SS_i), three environmental variables (CO_i, $ELEV_i$, $TRMI_i$), the effect of time ($TIME_k$; 1 = one-year post-treatment and 2 = two-years post-treatment) and cut-back border factor levels (Eq. 1).

$$y_{ijk} = \beta + SP_i + SS_i + CO_i + ELEV_i + TRMI_i + TRT_{ijk} + W45_{ijk} + BA4.5_{ijk} + TRT_{ijk} \times TIME_k \quad (1)$$

The term *TRT* corresponded to cut-back borders that received tree cutting, with the baseline factor levels 30 m for cut-back border width and 14 m^2/ha for cut-back border harvest intensity. Term *W45* corresponded to the 45-m cut-back border width factors level and *BA4.5* corresponded to

Table 1 Total number of individuals captured (excluding recaptures) for each salamander species (excluding eastern red-backed salamanders) by cut-back border treatment and regeneration stand treatment at three wildlife management areas (WMAs) Beury Mountain WMA, Lewis Wetzel WMA, and Little Canaan WMA in West Virginia 2016–2019

	Cut-back borders					Regeneration stands	
	Control	30 m 14 m^2/ha	30 m 4.5 m^2/ha	45 m 14 m^2/ha	45 m 4.5 m^2/ha	Control	Hack-and-spray
Allegheny mountain dusky salamander (*Desmognathus ochrophaeus*)							
Pre-treatment	0	0	1	0	0	1	5
One-year Post-treatment	0	0	0	0	0	0	2
Two-year Post-treatment	0	0	2	0	0	0	5
Northern red salamander (*Pseudotriton ruber*)							
Pre-treatment	0	0	0	0	0	1	0
One-year Post-treatment	0	0	0	0	0	0	0
Two-year Post-treatment	1	0	0	0	0	0	0
Northern slimy salamander (*Plethodon glutinosus*)							
Pre-treatment	0	0	3	2	5	4	7
One-year Post-treatment	5	1	3	0	0	4	8
Two-year Post-treatment	1	1	1	3	2	5	7
Wehrle's salamander (*Plethodon wehrlei*)							
Pre-treatment	0	0	0	1	2	2	1
One-year Post-treatment	1	3	1	0	0	0	2
Two-year Post-treatment	1	1	0	0	1	3	1

the 4.5 m^2/ha cut-back border harvest intensity factor level. We included elevation (*ELEV*) and *TRMI* as environmental variables to account for topographic variability and the number of natural cover objects (logs and rocks) present at each sampling point (*CO*). When modeling BCI, we excluded the cover object variable (*CO*) because our sampling unit was the individual for the BCI analysis while our sampling unit for the surface count analysis was each set of coverboards and natural cover objects. We did not include overstory cover as a covariate because of the collinearity between harvest intensity treatments and overstory cover levels.

Regeneration stands We modeled expected surface count or BCI y_{ijk} at sampling point i within treatment plot j during year k as a function of an intercept β, a sampling point random effect (SP_i) to account for the heterogeneity among points and repeated observations at the same point, three environmental variables (CO_i, $ELEV_i$, $TRMI_i$), the effect of time ($TIME_k$; 1 = one-year post-treatment and 2 = two-years post-treatment), and regeneration treatment HS (Eq. 2).

$$y_{ijk} = \beta + SP_i + CO_i + ELEV_i + TRMI_i + HS_{ijk} + HS_{ijk} \times TIME_k \quad (2)$$

The term *HS* corresponded to hack-and-spray treatment that received herbicide. We included *ELEV* and *TRMI* as environmental variables to account for topographic variability and the number of natural cover objects (logs and rocks) present at each sampling point (*CO*). Similar to the analysis of BCI in cut-back borders, we excluded the cover object variable (*CO*) when modeling BCI.

Overstory cover effect on RBS surface counts

Cut-back borders and regeneration stands were both subjected to overstory reduction during treatment. We used a stacked Bayesian GLMM to assess the influence of overstory cover on RBS surface counts in cut-back borders and regeneration stands, separately, to compare slope coefficients and assess whether salamander counts were strongly influenced by presence of overstory cover in either prescription. For each GLMM, we included a binary variable indicating whether overstory removal occurred in each plot (0 = no overstory removal [pre-treatment and control plots] or 1 = had some level of overstory removal [30-m wide, 45-m wide, 14 m^2/ha retention, and 4.5 m^2/ha retention for cut-back borders at one-year and two-year post-treatment; HS for regeneration stands at one-year and two-year post-

Table 2 Annual mean and standard error of live basal area and overstory cover variables in cut-back border harvest width (30 m and 45 m) and harvest intensity (14 m^2/ha and 4.5 m^2/ha basal area retention) combinations and the unharvested control at six block replicates at three wildlife management areas (WMAs) Beury Mountain WMA, Lewis Wetzel WMA, and Little Canaan WMA in West Virginia 2016–2019

	Control	30 m 14 m^2/ha	30 m 4.5 m^2/ha	45 m 14 m^2/ha	45 m 4.5 m^2/ha
Live basal area (m^2/ha)					
Pre-treatment	72.5 ± 12.6	84.8 ± 9.5	83.4 ± 12.5	84.1 ± 4.3	85.7 ± 8.6
One-year Post-treatment	72.5 ± 12.6	47.6 ± 9.8	38.4 ± 13.2	49.6 ± 7.8	30.8 ± 8.0
Two-year Post-treatment	72.5 ± 12.6	37.2 ± 8.0	16.2 ± 5.3	41.2 ± 6.5	23.0 ± 5.7
Overstory cover (%)					
Pre-treatment	85.8 ± 3.8	82.1 ± 5.1	83.6 ± 6.0	92.1 ± 3.1	97.9 ± 0.4
One-year Post-treatment	85.8 ± 3.8	67.9 ± 6.0	19.1 ± 4.9	56.6 ± 6.0	20.3 ± 4.7
Two-year Post-treatment	85.8 ± 3.8	67.3 ± 6.5	30.6 ± 5.9	57.7 ± 6.1	24.6 ± 6.1

treatment] following the parameterization of *TRT* in Eq. 1 and *HS* in Eq. 2). We modeled surface counts following parameterization of Eq. 1 for cut-back borders and Eq. 2 for regeneration stands, but only included the terms *TRT*, *TRT* × *TIME*, and *TRT* × *overstory cover* as predictor variables for cut-back borders and the terms *HS*, *HS* × *TIME*, and *HS* × *overstory cover* as predictor variables for regeneration stands. Prior distributions and model checking followed Eqs. 1 and 2 parameterizations.

Results

We captured a total of 183 RBS over 320 sampling events in cut-back borders of which 174 individuals had morphological measurements taken (44 during pre-treatment, 53 during one-year post-treatment, and 77 during two-year post-treatment). In regeneration stands, we captured 213 RBS over 120 sampling events of which 202 had morphological measurements taken (59 during pre-treatment, 83 during one-year post-treatment, and 60 during two-year post-treatment). Our posterior predictive checks indicated that our surface count models were a reasonable fit (p_b = 0.39 and 0.66 for cut-back borders and regeneration stands, respectively) as were our BCI models ($p_b = 0.54$ and 0.51 for cut-back borders and regeneration stands, respectively). We captured four other salamander species during the study (Table 1), with counts too low for analyses: Allegheny Mountain dusky salamander ($n = 17$, *Desmognathus ochrophaeus*), northern red salamander ($n = 2$, *Pseudotriton ruber*), northern slimy salamander ($n = 65$, *Plethodon glutinosus*), and Wehrle's salamander ($n = 16$, *Plethodon wehrlei*).

Vegetation

Post-harvest, basal area was reduced in all cut-back border treatments but was lowest in the 4.5 m^2/ha retention treatments at one-year and two-year post-treatment (Table 2). Greater reductions of basal area in the 4.5 m^2/ha retention treatments directly resulted in lower levels of overstory cover being retained following treatment, with overstory cover levels also lowest in the 4.5 m^2/ha retention treatments at one-year and two-year post-treatment. Following hack-and-spray treatment in regeneration stands, basal area and overstory cover were slightly reduced one-year post-treatment with additional decreases by two-year post-treatment (Table 3), a similar trend to what was observed in cut-back borders.

Table 3 Annual mean and standard error of live basal area and overstory cover variables in the regeneration stand hack-and-spray treatment (HS) and unharvested control at five block replicates at two wildlife management areas (WMAs) Beury Mountain WMA and Little Canaan WMA in West Virginia 2017–2019

	Control	Hack-and-Spray
Live basal area (m^2/ha)		
Pre-treatment	58.9 ± 5.4	69.4 ± 4.5
One-year Post-treatment	58.9 ± 5.4	60.5 ± 4.8
Two-year Post-treatment	58.9 ± 5.4	45.7 ± 3.1
Overstory cover (%)		
Pre-treatment	91.7 ± 4.0	90.0 ± 1.9
One-year Post-treatment	91.7 ± 4.0	80.3 ± 5.3
Two-year Post-treatment	91.7 ± 4.0	74.6 ± 6.6

Cut-Back Borders

Cut-back border treatment (*TRT*) had no detectable influence on RBS counts relative to the control. Further, contrasts between factor levels of harvest width and harvest intensity and the control over time did not have a strong influence on counts (Fig. 3a). The number of cover objects (*CV*) positively influenced RBS counts (slope coefficient = 0.39, 95% upper and lower CIs = [0.05, 0.76]). Percent overstory cover in treated plots (*TRT*) did not strongly influence counts (0.06 [-0.19, 0.31]) (Fig. 4).

For BCI, the cut-back border treatment by time interaction (*TRT* × *TIME*) had a positive influence on RBS (0.26 [0.07, 0.45]), with higher BCI in cut-back border treatments

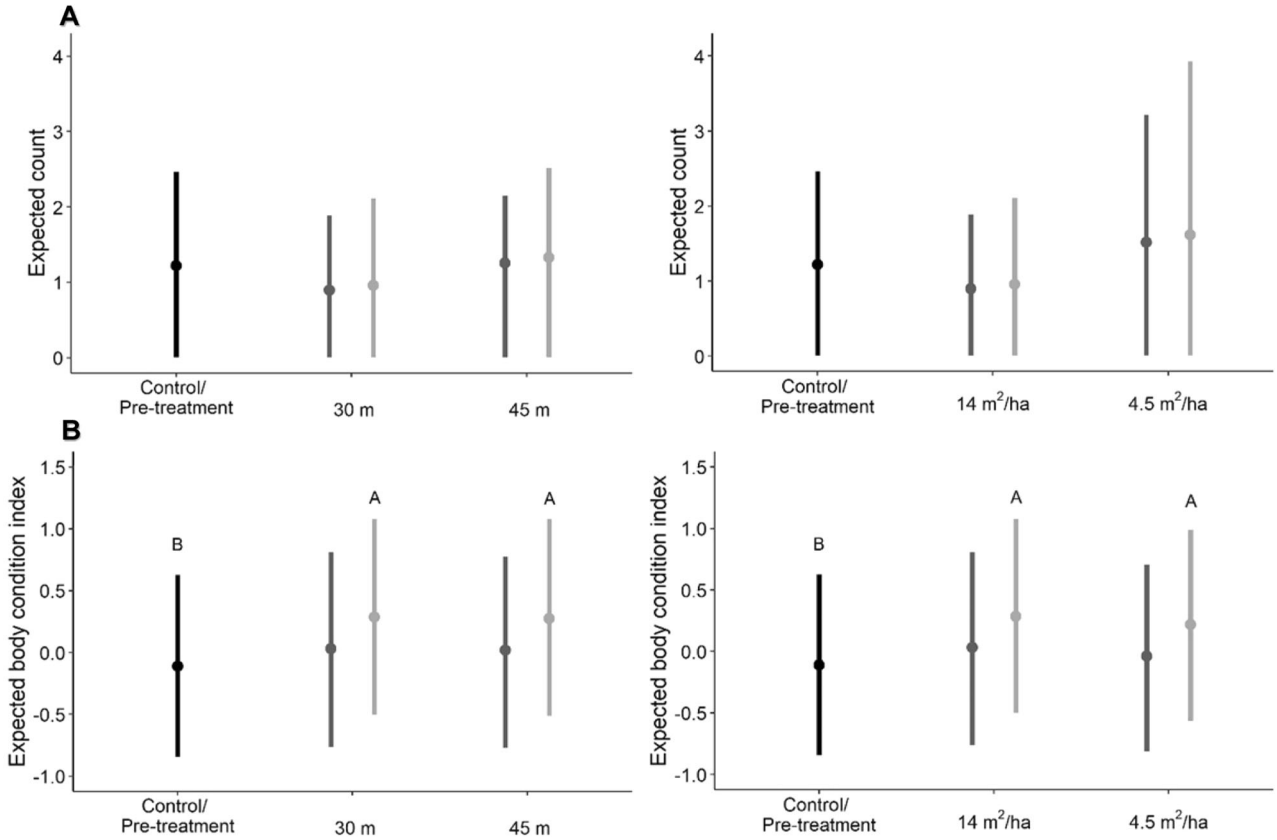

Fig. 3 Mean plot-level (three sampling visits at four sampling points in each of six cut-back border plots) expected surface count (**A**) and body condition index (**B**) with 95% credible intervals of eastern red-backed salamanders (*Plethodon cinereus*) in cut-back border harvest width levels (30 and 45 m; left) and harvest intensity levels (14 m^2/ha and 4.5 m^2/ha basal area retention; right) at one-year and two-year post-treatment compared to the unharvested control/pre-treatment at six block replicates at three wildlife management areas (WMAs) Beury Mountain WMA, Lewis Wetzel WMA, and Little Canaan WMA in West Virginia. Alphabetic notation above point estimates indicates differences within post-treatment years based on non-overlapping 95% credible intervals of posterior distributions. Point estimates without alphabetic notation indicate no differences

at two-year post-treatment relative to the control. Based on contrasts, BCI was higher in the 30-m (0.40 [0.08, 0.72]) and 45-m (0.38 [0.09, 0.66]) widths and at 14 m^2/ha (0.40 [0.08, 0.72]) and 4.5 m^2/ha (0.33 [0.05, 0.61]) residual basal area at two-year post-treatment relative to the control (Fig. 3b).

Regeneration Stands

The hack-and-spray treatment (*HS*) had a positive influence on RBS counts (1.09 [0.35, 1.85]) relative to the control. Based on contrasts, counts were higher in the HS at one-year post-treatment (0.44 [0.04, 0.85) but not at two-year post-treatment (Fig. 5a). Elevation (*ELEV*) had a positive influence on salamander counts (0.58 [0.37, 0.82]). Percent overstory cover in the HS treatment did not have a detectable influence on counts (0.14 [−0.59, 0.97]) (Fig. 4).

Body-condition index was overall negatively influenced by cut-back border treatments (*TRT*) (−1.12 [−1.49, −0.76]). However, the interaction term indicated that BCI

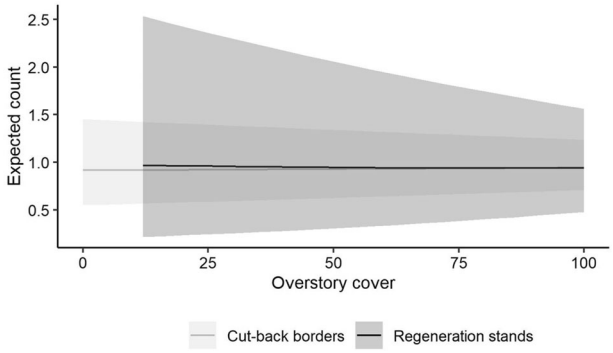

Fig. 4 Expected count and 95% credible intervals of eastern red-backed salamanders (*Plethodon cinereus*) as a function of overstory cover in cut-back borders and regeneration stands at three wildlife management areas (WMAs) Beury Mountain WMA, Lewis Wetzel WMA, and Little Canaan WMA in West Virginia during 2016–2019

was positively influenced by the treatment-time interaction (0.81 [0.58, 1.06]) which indicates a different direction of response in one-year vs two-year post treatment (Fig. 5b).

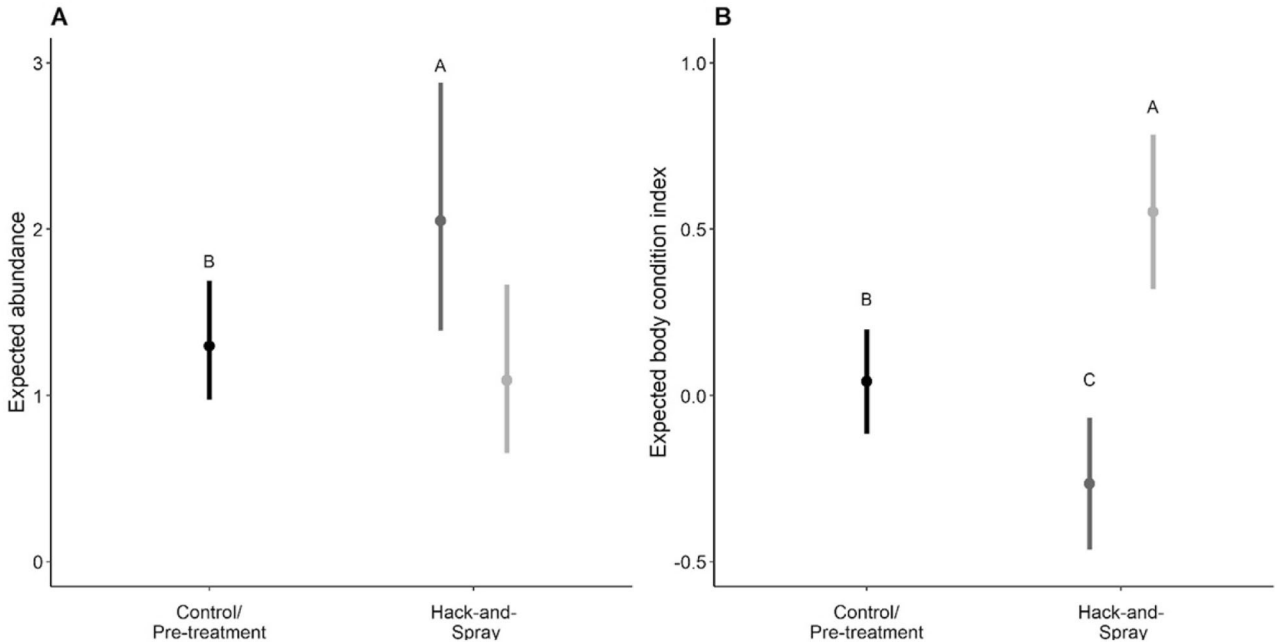

Fig. 5 Mean plot-level (three sampling visits at four sampling plots in each of five regeneration stands) expected count (**A**) and body condition index (**B**) and 95% credible intervals of eastern red-backed salamanders (*Plethodon cinereus*) in regeneration stands at one-year and two-year post-treatment periods, and the unharvested control/pre-treatment period at two wildlife management areas (WMA) Beury Mountain WMA and Little Canaan WMA. Alphabetic notation above point estimates indicates differences within post-treatment years based on non-overlapping 95% credible intervals of posterior distributions. Point estimates without alphabetic notation indicate no differences

Contrasts determined that BCI was lower in the HS (−0.30 [−0.51, −0.10]) at one-year post-treatment but higher in the HS (0.51 [0.26, 0.76]) at two-year post-treatment relative to the control (Fig. 5b).

Discussion

Ecosystem-based management strategies aim to incorporate many ecological goals into forest planning. Using this strategy, forestry prescriptions mimic natural disturbances to retain physical characteristics thought to be important for a variety of taxa. Often, these habitat characteristics are prioritized for mammals or songbirds, but these prescriptions could also benefit salamanders with planning and consideration of what physical features are important for salamander populations. Woodland salamanders are a group of species that provide a myriad of ecosystem services, but there is much information still needed regarding how forestry approaches can create optimal post-harvest habitat characteristics for many of these species. Here we have provided an assessment of two potential factors (retaining residual trees and eliminating soil compaction) that are outcomes of forest management activities and their effects on woodland salamanders. A greater understanding of the mechanistic drivers from forestry prescriptions will allow managers to directly incorporate these measures into their forest planning to help mitigate negative effects from forest management.

A common outcome of all forms of forest management is the reduction of the overstory layer due to the removal of standing timber, and percent overstory cover and woodland salamander density are often strongly positively correlated (Tilghman et al., 2012). In our study, the overstory layer in cut-back border treatments was reduced using heavy machinery, which is typical in operational silviculture, while the overstory layer in regeneration stands was reduced using a hack-and-spray method by hand crews. The effect of overstory cover reduction on woodland salamanders is often immediate (Knapp et al., 2003; Hocking et al., 2013b; Mossman et al., 2019). Certainly, the initial years following tree cutting impose the greatest physiological challenges to woodland salamanders, as shade from the midstory and overstory layers are at their lowest relative levels. This results in drier and hotter conditions at the soil surface that are often not compatible with salamander physiology (Hillman et al., 2009; Homyack et al., 2011). However, overstory cover did not have a strong influence on RBS counts in cut-back borders or regeneration stands in our study. This could indicate that both overstory reduction mitigation techniques that we assessed may have counteracted the negative effects of overstory removal, either by providing downed CWD or eliminating soil compaction. However, it is unlikely that overstory cover alone drives

woodland salamander populations following tree cutting (Otto et al., 2014).

Eastern red-backed salamander surface counts were not significantly reduced in cut-back border treatments following cutting relative to the control. The lack of responses we observed to treatments may be due to the retention of downed CWD following cutting as we detected a positive response to number of natural cover objects. Downed CWD can increase habitat quality for woodland salamanders by creating surface refugia that moderates microclimates at the forest floor (Otto et al., 2013; Peele et al., 2017). These conditions may allow individuals to remain at the surface for extended periods of time. Because many woodland salamanders forage at the surface (Jaeger, 1980; Homyack et al., 2011), surface conditions that allow for greater time at the surface would increase foraging opportunities for individuals and thus could improve body condition. Body condition index was higher in cut-back border treatments at two-year post-treatment relative to the control. The increase in BCI could be due to increased prey densities stemming from greater amounts of downed CWD as was reported by Dennis et al. (2018) and Garrick et al. (2019), although we did not explicitly test for this relationship. Beyond the presence of downed CWD, the stage of decay of CWD can also affect habitat quality for salamanders (McKenny et al., 2006; Mossman et al., 2019). Mazerolle et al. (2021) reported the presence of well-decayed CWD in irregular shelterwood harvests as a reason for higher salamander abundances relative to unharvested controls. However, Mazerolle et al. (2021) also found that BCI was higher in strip-cutting treatments, where there were greater amounts of early-stage decay, indicating that woodland salamander density and BCI responses can vary in relation to the amount of downed CWD present.

Ecological forestry practices include retaining some pre-harvest downed CWD levels post-harvest because it provides important structure and habitat for an array of taxa, including woodland salamanders (Franklin et al., 2007). The stage of decay can also influence the suitability of downed CWD for woodland salamanders, as well-decayed CWD offers more-suitable refugia (Grover, 2000). However, retaining large pieces of well-decayed downed CWD in stands following operational silviculture can be logistically difficult (Bunnell and Houde, 2010). Whole trees were kept on-site following cutting in our study, and while the decay stage of felled trees immediately following cutting was potentially suboptimal for woodland salamanders it likely provided some level of protection from the environmental conditions at the surface (Harmon et al., 1986; McCarthy and Bailey, 1994). Indeed, artificial coverboards that were deployed pre-treatment showed signs of decay by one-year post-treatment, indicating that recently felled trees could immediately provide habitat at the surface for salamanders to help mitigate the loss of overstory cover.

Reducing soil compaction is another approach to mitigate the loss of overstory cover but separating the effects of overstory removal (typically using heavy machinery) from soil compaction can be challenging. Soil compaction inhibits movement potential for salamanders near the surface, which can have significant effects on the dynamics of salamander populations (Homyack et al., 2011). Contemporary forest management prescriptions, however, have been able to reduce the level of soil compaction using updated management practices (e.g., reducing the forest road footprint in harvested areas). Additionally, soil compaction is often not ubiquitous throughout the stand so the effects of soil compaction on salamanders are likely restricted to micro-sites within the stand. In our study, the decrease in overstory cover in the HS treatment at one-year and two-year post-treatment did not strongly influence RBS counts from pre- to two-year post-treatment, indicating that soil compaction may be an important mechanism affecting the woodland salamander population at the surface.

Eastern red-backed salamander surface counts increased in HS stands immediately following treatment, but this appears to come with the tradeoff of those individuals being in poorer health. If food resources were consistent across time (Westby-Gibson et al., 2017), then greater densities of salamanders at the surface increased intraspecific competition for food. Homyack et al. (2010) reported that RBS in low density areas had higher prey counts in their stomachs compared to high-density areas, which supports the notion of increased intraspecific competition in our study. However, invertebrate populations, the primary food source for woodland salamanders, generally decrease immediately following overstory removal (Perry and Herms, 2016) due to changes in forest floor temperature and moisture (Gray et al., 2002). We observed a 10% mean decrease in overstory cover at one-year and two-year post-treatment periods which may not have been substantial enough to elicit a change in the invertebrate community or was not drastic enough from year-to-year to physiologically stress salamanders or change forest floor community dynamics.

Conclusion

Contemporary forest management seeks to find ways to improve the compatibility of silviculture prescriptions with ecosystem processes to enhance continuity between pre-treatment and post-treatment conditions. Incorporating wildlife species that provide functional services to forests, like woodland salamanders, into management not only can help maintain wildlife diversity, but it also can be compatible with timber management and harvesting objectives. While some operational silviculture prescriptions are not completely compatible with biodiversity, this research

provides evidence that steps can be taken to mitigate the negative effects of forest management on woodland salamander populations. Retaining greater amounts of downed CWD following harvesting and reducing soil compaction during harvesting both appear to mitigate impacts of reduced overstory cover on RBS in the short-term. Our results highlight the importance of developing forest management activities that are compatible with woodland salamanders' life history traits. Our findings indicated that these mitigation strategies helped ameliorate overstory removal on RBS, however, population-level responses by salamanders can be delayed which can result in misleading guidance. Therefore, longer-term assessments of these strategies and other potential mitigation techniques will help elucidate relationships between physical structures associated with forest management prescriptions and woodland salamanders.

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Compliance with ethical standards

Conflict of interest The authors declare no competing interests.

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