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Reptile and amphibian response to oak regeneration treatments in productive southern Appalachian hardwood forest

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ABSTRACT

Forest restoration efforts commonly employ silvicultural methods that alter light and competition to influence species composition. Changes to forest structure and microclimate may adversely affect some taxa (e.g., terrestrial salamanders), but positively affect others (e.g., early successional birds). Salamanders are cited as indicators of ecosystem health because of their sensitivity to forest floor microclimate. We used drift fences with pitfall and funnel traps in a replicated Before-After-Control-Impact design to experimentally assess herpetofaunal community response to initial application of three silvicultural methods proposed to promote oak regeneration: prescribed burning; midstory herbicide; and shelterwood harvests (initial treatment of the shelterwood-burn method) and controls, before and for five years post-treatment. Species richness of all herpetofauna, amphibians, reptiles, frogs, salamanders, or snakes was unaffected by any treatment, but lizard species richness increased in the shelterwood harvest. Capture rate of total salamanders decreased post-harvest in shelterwood units after a 2–3 year delay; *Plethodon teyahalee* decreased post-harvest in shelterwoods, but also in control units. In contrast, capture rate of total lizards and *Plestiodon fasciatus* increased in shelterwood stands within the first year post-harvest. Prescribed burn and midstory herbicide treatments did not affect any reptile or amphibian species. A marginally lower proportion of juvenile to adult *P. teyahalee*, and a higher proportion of juvenile *P. fasciatus* in shelterwood than control units suggested that heavy canopy removal and associated change in microclimate may differentially affect reproductive success among species. Our study illustrates the importance of longer-term studies to detect potential changes in herpetofaunal communities that may not be immediately apparent after disturbances, and highlights the importance of including multiple taxa for a balanced perspective when weighing impacts of forest management activities.

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1. Introduction

Silvicultural methods often are used to facilitate forest restoration goals, but the resulting changes in forest structure may differentially affect vertebrate taxa. Variable responses by different taxa correspond with the type and intensity of disturbance and changes in macro- and microhabitat conditions such as canopy cover, leaf litter, shade, ground-level temperature, and moisture (DeMaynadier and Hunter, 1995; Moorman et al., 2011). Response to silvicultural disturbances are also likely to differ among taxa with different life history and microclimate requirements (Moorman et al., 2011). For example, shelterwood harvests or high-severity burns that substantially reduce canopy cover provide habitat for some early successional bird species (Askins, 2001; Greenberg et al., 2013) and butterflies and other pollinating insects (Campbell et al., 2007; Haddad and Baum, 1999; Lanham and Whitehead, 2011; Whitehead, 2003), but changes in the forest floor microclimate may negatively affect some salamander species (see DeMaynadier and Hunter, 1995; Matthews et al., 2010). Because of their abundance (Burton and Likens, 1975; Semlitsch et al., 2014), their role as predator and prey (Pough et al., 1987), and sensitivity to changing forest conditions, salamanders have been suggested to be indicators of overall ecosystem health

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(e.g., Welsh and Droege, 2001). A balanced metric of overall forest condition(s) should include a diverse suite of taxa with different habitat requirements rather than salamanders alone.

Restoration of structure and function of mixed-oak (*Quercus* spp.) forest is a focal issue of forest land managers in the eastern United States. Widespread oak regeneration failure – the failure of oak seedlings or saplings to attain canopy status- is problematic, especially on intermediate and highly productive sites after canopy release because of competition from faster-growing species such as yellow-poplar (*Liriodendron tulipifera*) (Aldrich et al., 2005). Historically, mostly anthropogenic disturbances such as frequent burning, livestock grazing, loss of American chestnut (*Castanea dentata*), and widespread logging may have promoted understory light conditions conducive to oak development (Abrams, 1992; McEwan et al., 2011), and have been largely eliminated (Greenberg et al., 2015). Silvicultural treatments to facilitate oak forest restoration involve altering forest structure to change light conditions and competition from other hardwood tree species to promote the growth of oak seedlings before canopy release, giving them a head-start against faster-growing competition.

Amphibians (class *amphibia*) and reptiles (class *reptilia*) are phylogenetically, physiologically, and ecologically distinct from one another and, therefore, should respond differently to changes in forest structure following restoration practices (Moorman et al., 2011). A growing body of literature suggests that heavy canopy removal and associated lighter, drier and warmer microclimate with reduced leaf litter cover or depth adversely affect salamander populations (see DeMaynadier and Hunter, 1995; Moorman et al., 2011) and micro-distribution (O'Donnell et al., 2015) of plethodontid salamanders. In contrast, silvicultural treatments that retain canopy cover do not appear to adversely affect salamander abundance (e.g., Harpole and Haas, 1999; Homyack and Haas, 2009). Several studies show that even one (Ford et al., 1999; Greenberg and Waldrop, 2008) or two (Matthews et al., 2010) low-severity winter prescribed burns, have little effect on salamanders. Typically, prescribed fire and other midstory treatments in upland hardwood forest do not eliminate canopy cover, coarse woody debris, or duff, which provide cover and ameliorate forest floor temperature fluctuations and moisture.

Reptile response to heavy forest canopy reduction is less studied, but some research suggests that lizards in particular may increase in sites with reduced canopy cover due to natural disturbance (Greenberg, 2001) or high-severity fire (Matthews et al., 2010). The majority of studies examining herpetofaunal response to silvicultural disturbances focus on plethodontid salamanders, likely because they are common and easy to capture compared with many other species. Yet, more comprehensive study of how silvicultural treatments affect reptiles and a wider range of amphibians is needed to direct wildlife conservation in conjunction with ecosystem restoration or other forest management objectives.

We used a replicated Before-After-Control-Impact (BACI) design to experimentally assess how herpetofaunal species and communities responded to initial application of three silvicultural methods proposed to promote oak regeneration: prescribed burning; midstory removal with herbicide (henceforth referred to as 'midstory herbicide;' initial treatment of the oak shelterwood method (Loftis, 1990); and shelterwood harvest (initial treatment of the shelterwood-burn method; Brose et al., 1999) and controls, prior to treatments (2008) and for five years (2010–2014) after initial treatments were fully implemented. Our objective was to determine if, and how, species richness or capture rate of reptiles and amphibians differed before and after treatments, or among treatments and controls. Regional Oak Study installations using the same experimental design and intended to test the same treatments (Keyser et al., 2008) are also located in the Ozark Highlands of Missouri (O'Donnell et al., 2015) and the Cumberland Plateau in Tennessee (Cantrell et al., 2013).

2. Methods

2.1. Study area

Our study was conducted in Haywood County, North Carolina on Cold Mountain Game Land (CMGL), which encompassed 1333 ha of second growth, upland mixed-oak forests with elevations ranging from 940 to 1280 m. CMGL was managed by the North Carolina Wildlife Resources Commission for diverse wildlife habitat and was located in the Blue Ridge Physiographic Province. Terrain was mountainous with gentle to steep slopes with predominant overstory trees of oak, hickory (*Carya* spp.), and yellow-poplar. Species composition in the midstory consisted primarily of shade-tolerant species, including sourwood (*Oxydendrum arboreum*) flowering dogwood (*Cornus florida*) silverbell (*Halesia tetraptera*) blackgum (*Nyssa sylvatica*), and red maple (*Acer rubrum*). The climate was characterized by warm summers and cool winters and precipitation averaged 1200 mm annually.

2.2. Study design

In 2008, we established five, 5-ha units (approximately 225×225 m) of three oak regeneration treatments plus a control for a total of 20 units. In 2013, we reduced replication to n = 4 units per treatment for logistical reasons. We randomly assigned treatments (prescribed fire, midstory reduction using herbicide, and shelterwood harvest) and controls to each unit resulting in a completely randomized design. All units were between 940 and 1240 m in elevation and separated by a >10-m buffer. Each contained mature (>70 years old), fully stocked, closed-canopied stands where oaks comprised at least 10% of the overstory tree BA ($\geqslant$25.0-cm diameter at breast height (dbh)). We selected stands that contained abundant oak seedlings, few ericaceous shrubs, a well-developed midstory canopy layer (stems 5–25-cm dbh), and no substantial disturbance within the last 15–20 years. All treatment units were intermediate- to high-quality sites, with site index ranging 23.0–30.4 m (base-age 50).

2.3. Treatments

Treatments for the Regional Oak Study were designed to evaluate three oak regeneration practices on productive sites: (1) oak shelterwood, consisting of a midstory herbicide followed by overstory removal after about 10 years (Loftis, 1990); (2) three prescribed burns at approximately 4-year intervals, followed by overstory removal after 10–11 years, and; (3) shelterwood-burn, consisting of a heavy establishment cut with 6.8–9.0 m^2/ha of BA retention followed by a prescribed fire after 4–5 years (Brose et al., 1999), and overstory removal 2–3 years post-burn. All three treatments are designed to promote advanced oak regeneration, followed by canopy release.

Our study encompassed one year before (2008) and five years after initial treatments were fully implemented (sampled in 2010, 2011, 2013, 2014). In midstory herbicide treatment units, herbicide was applied in early fall 2008, prior to leaf fall. Trees within the midstory strata except oak or hickory (e.g., red maple, sourwood, blackgum, flowering dogwood) $\geqslant$5.0 cm and <25.0 cm dbh were treated with herbicide (~1 ml of diluted Garlon 3A solution) using the hack-and-squirt method (Loftis, 1990). Prescribed burns were conducted in all burn treatment units (two units were burned on 25 February 2009, and again on 2 April 2014; the other three units were burned only once during the study period, on 1 April 2010). All prescribed burns were cool, backing fires ignited with short, strip lighting and/or flanking strip lighting. Fire temperatures were measured at ground level and 30 cm above the ground using temperature-sensitive paint on tags placed at two locations 8 m apart in each of 6 vegetation plots spaced throughout each unit (see Section 2.5.1). On average, both the first and second burns were extensive (ground-level heat tags were burned in at least one subplot in >90% vegetation plots) but incomplete (about 25–30% of subplots within vegetation plots remained unburned) across treatment units, and many areas showed no or little evidence of burning. In the initial burns, mean maximum fire temperature in burned ($\geqslant$74 °C) plots was 153 °C (range 127–204 °C) at ground level, and 117 °C (range 85–193 °C) at 30 cm above the ground. Mean maximum fire temperature in the second burn (conducted in only two units) was 222 °C (range 79–538 °C) at ground level, and 211 °C (range 79–482 °C) at 30 cm above the ground. The shelterwood-burn treatment (Brose et al., 1999) included only the establishment cut of the shelterwood burn sequence. Trees were felled with standard chainsaws and grapple cutters, and dragged with rubber tire skidders to log landings where knuckle boom loaders filled forwarders and haul trucks; some units required skid trails due to steep slopes. Three of the establishment cuts were implemented during winter 2009–2010 and completed by March 2010; harvests in the other two shelterwood units were not completed until early June or, in one unit, well into the 2010 field season. In summary, treatments evaluated in this study included (1) midstory herbicide using Garlon 3A herbicide in 2008 (MH); (2) prescribed burn (in 2009 and 2014 in 2 units; or 2010 only in 3 units) (B), (3) establishment shelterwood cut with 6.8–9.0 m^2/ha of BA retention (SW); and (4) untreated mature forest control (C).

2.4. Herpetofaunal sampling

We trapped herpetofauna during mid-May through early August pre-treatment (2008) and after all initial treatments were implemented (2010, 2011, 2013, 2014) using randomly-oriented, 7.6-m-long aluminum drift fences spaced $\geqslant$10 m apart, with 19-l buckets buried flush with the ground at each end, and a funnel trap on both sides of each fence. During 2008 and 2010, three drift fences were established at a lower slope position (the lower one-third of each treatment unit) and three at an upper slope site (e.g., upper one-third of each unit) for a total of six fences per unit, except in one C and one SW unit where steep, rocky terrain prevented establishment of the upper-slope fences. We established a fourth drift fence at each slope position in all units in 2010 for a total of 8 fences in all treatment units (except the two with prohibitively steep terrain, with 4 fences each). Capture rate of frogs, salamanders, lizards and snakes did not differ between trap arrays in lower and upper slope positions during pre-or post-treatment trapping through 2011 (paired *t*-test; $P > 0.05$). Therefore, we consolidated all drift fences within units in 2013 to one general area to simplify trap checks, and added four fences to the two units previously having only 4 fences to total 8 fences in all treatment units. We placed a moist sponge in each bucket to provide moisture. Traps were checked approximately 5 times weekly during mid-May through mid-August each year. In 2010, one SW unit was not trapped because timber harvesting continued well into the field season, and traps in another unit were not opened until early June when all logging was completed. All reptiles and amphibians were identified to species, measured (snout-vent and tail length), weighed, marked using VIE (2008 and 2010) or toe- or scale-clipping (2011, 2013–2015), and released at the capture site. All procedures used in our study were in accordance with the Society for the Study of Amphibians and Reptiles guidelines for field research, and were approved by the Institutional Animal Care and Use Committee of North Carolina State University (Permit # 08-035-O).

2.5. Forest structure measurements

2.5.1. Overstory and midstory

We measured overstory and midstory tree density and basal area at plots or subplots throughout each treatment unit prior to (2008) and again one year after all treatments were implemented (2011). We established three 0.05-ha permanent circular plots at approximately 50 m, 112 m, and 175 m along each of two transects within each unit. Transects originated at a random distance from a corner of the downslope unit boundary line, and ran parallel to and >30 m from side boundaries. Within each 0.05-ha permanent plot, all live overstory trees $\geqslant$25 cm dbh were identified, measured (diameter at breast height) and tagged. Midstory trees $\geqslant$5 cm and <25 cm dbh were identified, measured, and tagged within a 0.01-ha subplot concentrically nested within the 0.05-ha plot.

2.5.2. Ground- and canopy cover

We measured percent bare ground within 15 m of drift fence arrays in all units pre-treatment (2008), and again each year after all treatments were implemented (2010, 2011, 2013, 2014); leaf litter and (or) rocks occupied the ground surface unless bare ground was recorded. Shrub cover was measured only in post-treatment years. Bare ground and shrub cover were measured along a 15-m randomly oriented transect line at each of 3–6 (depending on the year and unit) randomly selected drift fences, starting from the bucket furthest uphill. The same transects were used for 2008–2011 measurements, but after some fences were moved in 2013 (see above) different transects were established (2013 and 2014 measurements). Along each transect, we recorded 'start' and 'stop' distance for each category and summed the total distance along each transect. Percent cover for each category was determined by dividing the sum of its cover by the transect length. Percent canopy cover was measured at each drift fence, using a spherical densiometer held at breast height. We used the average percent cover of habitat variables across transects within treatment units for data analyses.

2.6. Statistical analyses

We used repeated measures ANOVAs (Proc Mixed; SAS 9.3) in a completely randomized design with compound symmetry covariance structure to examine effects of treatment, year, and treatment $\times$ year interactions for all analyses of habitat variables and herpetofauna. All herpetofaunal capture data were standardized for small differences in trapping effort, by using captures per 100 fence nights (100 FNs; 1 fence night was 2 pitfall and 2 funnel traps per fence, open for one night). Response variables analyzed were species richness of all herpetofauna, amphibians, reptiles, frogs, salamanders, lizards, and snakes, and relative capture rate (captures per 100 FNs) of all reptiles, amphibians, frogs, salamanders, lizards, snakes, and individual species that were sufficiently common. Data were arcsine square root transformed (percentages) or square root transformed as needed to meet assumptions of normality for ANOVAs.

We were unable to accurately calculate detection probability due to low recapture rates (<1% probability of recapture). In addition, because *Plethodon* salamanders are known to spend most of their time underground or under cover objects (O'Donnell et al., 2014; O'Donnell et al., 2016), and detectability likely varies among herpetofaunal taxa, we considered our capture data to be a measure of relative surface activity, rather than relative abundance per se.

In all repeated measures ANOVAs, we considered treatment, year, and their interaction to be fixed effects, and unit within treatment to be a random effect and the repeated subject factor. Our primary interest was in treatment × year interaction effects as indicators that at least one treatment was responding differently from the others between pre-treatment (2008) and post-treatment years (2010, 2011, 2013, 2014). A non-significant treatment × year interaction indicated that treatment differences were consistent between pre-treatment and post-treatment years, and that there was a consistent difference among years across treatments (including C). Where significant treatment × year interactions were present, we used the least square means for partitioned F-tests (SLICE option) in PROC MIXED (SAS 9.3) to examine the significance of treatments within years, and years within treatments.

We used Fisher's Exact tests to determine if the ratio of juveniles to adults for commonly captured species, including the southern Appalachian salamander (*Plethodon teyahalee*) (Northern slimy salamander (*Plethodon glutinosis*) complex; Highton and Peabody, 2000) (J ⩽ 58 mm SV; Homyack and Haas, 2009), southern gray-cheeked salamander (*Plethodon metcalfi*) (*Plethodon jordani* complex; Highton and Peabody, 2000) (J ⩽ 40 mm SV; Hairston, 1983), and five-lined skink, (*Plestiodon fasciatus*) (J ⩽ 52 mm SV; Vitt and Cooper, 1986), was equally dispersed between C and SW treatments only, 3–4 years post-treatment. To increase capture numbers, we pooled data from 2013 and 2014, and pooled across units within treatments.

3. Results

3.1. Forest structure

Live tree density differed among treatments ($F_{3,15} = 11.65$; $P = 0.0003$) and years ($F_{1,15} = 106.73$; $P < 0.0001$), and a treatment × year interaction effect was detected ($F_{3,15} = 15.02$; $P < 0.0001$). Following treatment implementation, tree density decreased in MH and SW treatments (by 47% and 70%, respectively) but no change was detected in B or C (Fig. 1a). Decreased live tree density was primarily due to herbicide-caused mortality of smaller (⩾5 cm and <25 cm dbh) midstory trees in the MH treatment, and by harvesting both midstory and overstory trees (⩾25 cm dbh) in SW. Accordingly, post-treatment basal area reduction (11% reduction) in MH was relatively small and not significantly different from pre-treatment or other treatments. In contrast, basal area was reduced by 65% in SW due to removal of large trees, and differed significantly from pre-harvest and from other treatments (treatment $F_{3,15} = 3.13$; $P = 0.0572$; year $F_{1,15} = 135.63$; $P < 0.0001$; treatment × year interaction $F_{3,15} = 69.59$; $P < 0.0001$) (Fig. 1b).

Treatment effects were significant for percent canopy cover and shrub cover; year and treatment × year interaction effects were detected for canopy, shrub, and bare ground (Table 1). Prior to treatment, percent canopy and bare ground did not differ among treatments (pre-treatment shrub cover was not measured). Canopy cover was reduced by 50% after harvesting in SW (2010), and remained lower than other treatments through 2014, but increased to about 70% by 2013 and 2014 (Table 1; Fig. 2a) as sprouts and saplings increased in height and overstory crowns expanded. Canopy cover did not significantly change after MH or B treatments, or in C (Table 1; Fig. 2a). The percentage of bare ground increased in both SW and B units after treatments (2010), but decreased to pre-treatment levels in B by 2011, and in SW by 2013 as deciduous trees and shrubs dropped their leaves in autumn; increased bare ground in B in 2014 was due to the second prescribed burn in two of the B units (Table 1; Fig. 2b). Percent

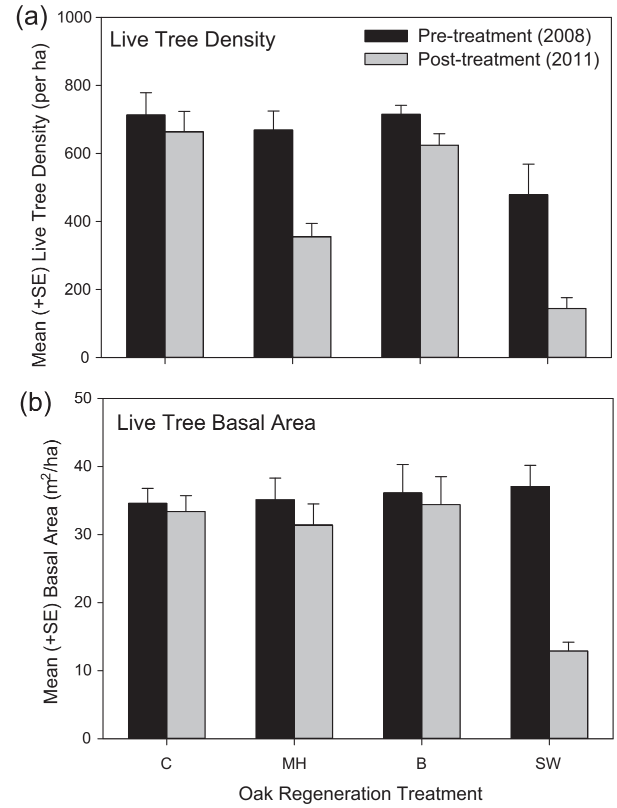

Fig. 1. Mean (±SE) live (a) tree density (number per ha) and; (b) basal area (m^2/ha) of trees (⩾5 cm dbh) before (2008) and after (2011) three oak regeneration treatments and control on Cold Mountain Game Land, Haywood County, NC. Treatments were control (C), midstory herbicide (MH), prescribed burn (B), and shelterwood harvest (SW).

cover of shrubs was similar among treatments immediately after treatment implementation (2010), but increased in subsequent years in SW beginning in 2011; by 2014, shrub cover in SW averaged 95% due to stump sprouting, seedling growth, and post-disturbance proliferation of blackberry (*Rubus* spp.) (Table 1; Fig. 2c).

3.2. Herpetofauna

We captured 1530 individuals (14 recaptures) of 13 amphibian species, and 269 individuals (4 recaptures) of 7 reptile species in 45,974 FNs during the 5 years sampled (2008, 2010, 2011, 2013, 2014) (Table 2). Species richness did not differ among treatment or years, and treatment × year interaction effects were not detected for amphibians, reptiles, or all herpetofauna (Table 3). Frog species richness was generally lowest in 2008 (but no different from 2010) and highest in 2014 (but no different from 2011 or 2013), but no treatment and no treatment × year interaction was detected (Table 3). Salamander and snake species richness did not differ among treatments or years, nor was a treatment × year interaction effect detected (Table 3). Lizard species richness differed among years, and a treatment × year interaction effect was detected (Table 3). Partitioned F-tests (SLICE option) of years within treatments indicated that in SW, pre-treatment lizard species richness was lower than richness in 2011, 2013, and 2014, and species richness was highest in 2013. Partitioned F-tests of treatment differences within years indicated that in 2013, lizard species richness was significantly higher in SW than other treatments or C (Fig. 3).

Table 1
Results of mixed model ANOVA with repeated measures testing for treatment, year, and treatment × year differences in percent cover of canopy, bare ground, and shrubs near drift fences among pre-treatment (2008)[1] and post-treatment years (2010, 2011, 2013, 2014) in oak regeneration treatments on Cold Mountain Game Land, Haywood County, NC. Treatments were control (C), midstory herbicide (MH), prescribed burn (B), and shelterwood harvest (SW). Different superscript letters within rows denote significant differences among years or treatments, respectively.

Habitat feature	ANOVA			Year diffs	Treatment diffs
	P_{trt}	P_{yr}	P_{trtxyr}		
Canopy cover (%)	$F_{3,15} = 34.11$ $P < 0.0001$	$F_{4,56.4} = 40.67$ $P < 0.0001$	$F_{12,56.3} = 5.13$ $P < 0.0001$	2008^a 2010^b 2011^b 2013^c 2014^c	C^a MH^a B^a SW^b
Bare ground (%)	$F_{3,12.1} = 2.88$ $P = 0.0799$	$F_{4,53.8} = 12.74$ $P < 0.0001$	$F_{12,53.8} = 4.11$ $P = 0.0002$	2008^a 2010^b 2011^c 2013^d 2014^d	
Shrub cover (%)	$F_{3,16.1} = 11.62$ $P = 0.0003$	$F_{3,42} = 6.35$ $P = 0.0012$	$F_{9,42.0} = 5.00$ $P = 0.0001$	2010^a 2011^a 2013^a 2014^b	C^a MH^a B^a SW^b

[1] shrub cover was not measured pre-treatment (2008).

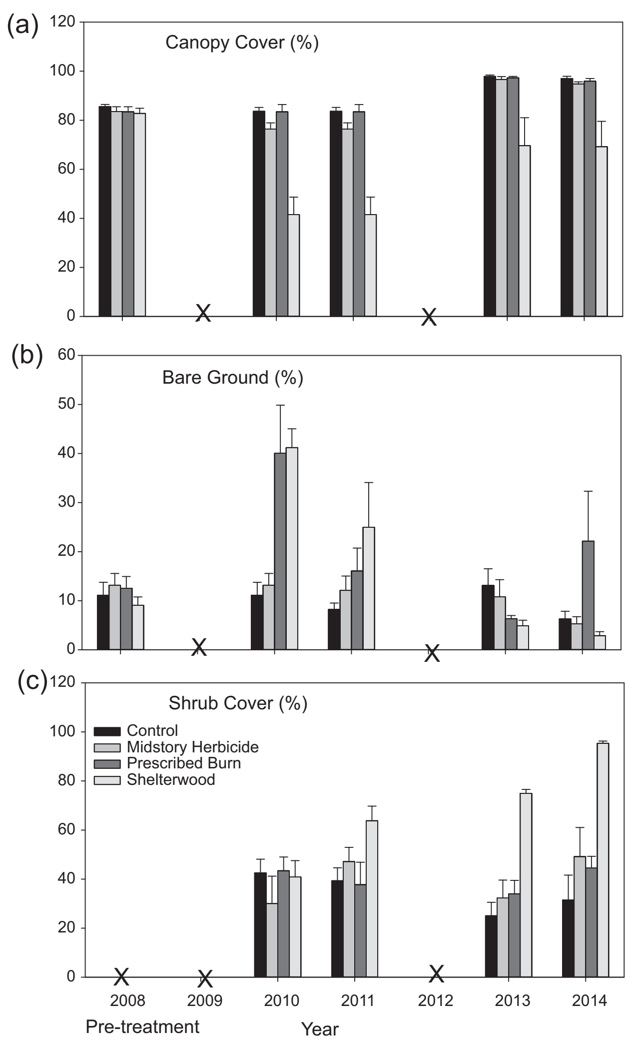

Fig. 2. Mean (+SE) percent cover of habitat variables including percent cover of (a) canopy; (b) bare ground, and; (c) shrubs, before (2008) and after three oak regeneration treatments and control on Cold Mountain Game Land, Haywood County, NC. Treatments were control (C), midstory herbicide (MH), prescribed burn (B), and shelterwood harvest (SW).

Capture rate of all amphibians did not differ among treatments, but a year effect was detected, with higher capture rate in 2011 than in 2013 or 2014, and fewer captures in 2013 than any other year; a treatment × year interaction was detected (Table 2; Fig. 4a). Partitioned F-tests of years within treatments indicated that amphibian capture rate was dynamic over time in SW, with higher capture rate in 2008, 2010, and 2011 than in 2013 or 2014 (Fig. 4a). Partitioned F-tests of treatment differences within years indicated that differences existed only in 2014, with capture rate lower in SW and C than in B (MH did not differ from other treatments).

Capture rate of all frogs did not differ among treatments, nor was a treatment × year interaction effect detected. Frog capture rate was greater in 2011 and 2014 than in 2008 or 2010 (2013 differed from no other years). Among anuran species, only *Anaxyrus americanus* was captured at sufficient rates for statistical analysis, and no treatment, year, or treatment × year interaction effect was detected (Table 2).

Capture rate of total salamanders did not differ among treatments, but overall capture rate was lower in 2013 and 2014 than other years. A significant treatment × year interaction effect was detected. Partitioned F-tests of years within treatments indicated that capture rate of total salamanders was dynamic only within SW. Capture rate in SW was higher in 2008 (pre-treatment), 2010, and 2011 but decreased in 2013 and 2014 (Table 2; Fig. 4b). However, partitioned F-tests indicated that within years, capture rate did not differ among treatments.

Only five salamander species were captured with sufficient frequency for statistical analysis. We did not detect a treatment effect for *P. teyahalee*, but overall capture rate was lower in 2013 and 2014 than in 2008 or 2011 (capture rate in 2010 differed only from 2008), and a significant treatment × year interaction effect was detected (Table 2). Partitioned F-tests of years within treatments indicated that capture rate of *P. teyahalee* was significantly dynamic within both SW and C. Within SW, capture rate of *P. teyahalee* did not differ among 2008, 2010, and 2011 but decreased significantly in 2013 and 2014 compared to prior years (Table 2; Fig. 4c). Capture rate in C were significantly higher in 2008 than all subsequent years, which did not differ from one another (Table 2; Fig. 4c). Partitioned F-tests of treatment differences within years indicated no difference in *P. teyahalee* capture rate among treatments within any single year. No treatment or treatment × interaction effects were detected for *P. metcalfi*, but overall capture rate was lower in 2013 and 2014 than in prior years (Table 2; Fig. 4d). Similarly, neither Blue Ridge two-lined salamanders (*Eurycea wilderae*) nor eastern newts (*Notophthalmus viridescens*) showed treatment or treatment × year interaction effects but capture rate differed among years. Overall capture rate of *E. wilderae* were greater in 2011 than other years, and lowest in 2013 than all other years except 2008 (which differed only from 2011). Overall capture rate of *N. viridescens* were greater in 2013 and 2014 than in 2008 or 2011 (2010 did not differ from any other year) (Table 2). No treatment, year, or treatment × year effects were detected for pygmy salamander (*Desmognathus wrighti*) (Table 2). The post-treatment (2013 and 2014) ratio of juvenile to adult *P. metcalfi* did not differ between C and SW, but

Table 2
Total individuals (and recaptures) captured during the study period (5 years; total 45,974 fence nights) and results of mixed model ANOVA with repeated measures comparing capture rates among treatments, years, and testing for treatment × year interaction effects for taxa that were sufficiently common in oak regeneration treatments on Cold Mountain Game Land, Haywood County, NC (2008, 2010, 2011, 2013, 2014). Treatments were control (C), midstory herbicide (MH), prescribed burn (B), and shelterwood harvest (SW). Different letters within rows denote significant differences among years or treatments, respectively.

Taxa	Total	P_{Trt}	P_{Yr}	P_{TrtxYr}	Year diffs	Treatment diffs
Anaxyrus americanus (American toad)	87(2)	$F_{3,13} = 0.65$ $P = 0.5988$	$F_{4,53.6} = 2.07$ $P = 0.0975$	$F_{12,53.5} = 1.70$ $P = 0.0930$		
Lithobates sylvatica (wood frog)	50(0)	–	–	–		
Anaxyrus fowleri (Fowler's toad)	12(0)	–	–	–		
Total frogs	149(2)	$F_{3,15.8} = 0.30$ $P = 0.8220$	$F_{4,53.2} = 2.55$ $P = 0.0499$	$F_{12,53.1} = 1.50$ $P = 0.1553$	2008^{a} 2010^{a} 2011^{b} 2013^{ab} 2014^{b}	
Plethodon metcalfi (southern gray-cheeked salamander)	454(8)	$F_{3,15.8} = 0.30$ $P = 0.8220$	$F_{4,53.2} = 5.49$ $P = 0.0009$	$F_{12,55.2} = 0.88$ $P = 0.5692$	2008^{a} 2010^{a} 2011^{a} 2013^{b} 2014^{b}	
Plethodon teyahalee (southern Appalachian salamander)	432(3)	$F_{3,13.4} = 0.43$ $P = 0.7326$	$F_{4,54.1} = 3.86$ $P = 0.0079$	$F_{12,54.1} = 2.29$ $P = 0.0196$	2008^{a} 2010^{bc} 2011^{ab} 2013^{c} 2014^{c}	
Notophthalmus viridescens (eastern newt)	223(0)	$F_{3,16.2} = 1.52$ $P = 0.2468$	$F_{4,55.9} = 4.82$ $P = 0.0021$	$F_{12,55.9} = 1.33$ $P = 0.2265$	2008^{ab} 2010^{ac} 2011^{b} 2013^{c} 2014^{c}	
Eurycea wilderae (Blue Ridge two-lined salamander)	125(0)	$F_{3,15.1} = 0.32$ $P = 0.8091$	$F_{4,55.5} = 9.08$ $P < 0.0001$	$F_{12,55.5} = 1.03$ $P = 0.4322$	2008^{ab} 2010^{a} 2011^{c} 2013^{b} 2014^{a}	
Desmognathus wrighti (pygmy salamander)	92(0)	$F_{3,15.1} = 1.34$ $P = 0.2991$	$F_{4,54.5} = 2.26$ $P = 0.0742$	$F_{12,54.5} = 0.70$ $P = 0.7472$		
D. ocoee (Ocoee salamander)	22(0)	–	–	–		
Pseudotriton ruber (northern red salamander)	16(0)	–	–	–		
P. serratus (southern redback salamander)	13(0)	–	–	–		
D. fuscus (northern dusky salamander)	3(1)	–	–	–		
D. aeneus (seepage salamander)	1(0)	–	–	–		
Total salamanders	1,381(12)	$F_{3,15.0} = 0.90$ $P = 0.4633$	$F_{4,54.7} = 4.02$ $P = 0.0063$	$F_{12,54.7} = 4.64$ $P = 0.0225$	2008^{a} 2010^{a} 2011^{a} 2013^{b} 2014^{b}	
Thamnophis sirtalis (eastern garter snake)	96(0)	$F_{3,15.7} = 0.76$ $P = 0.5355$	$F_{4,57.8} = 2.37$ $P = 0.0633$	$F_{12,49.7} = 0.68$ $P = 0.8629$		
Diadophis punctatus (northern ringneck snake)	80(0)	$F_{3,10.1} = 1.26$ $P = 0.3409$	$F_{4,49.7} = 2.55$ $P = 0.0503$	$F_{12,49.7} = 0.68$ $P = 0.8629$		
Carphophis amoenus (eastern worm snake)	10(0)	–	–	–		
Elaphe obsoleta (black rat snake)	1(0)	–	–	–		
Total snakes	187(0)	$F_{3,11.1} = 1.71$ $P = 0.2208$	$F_{4,52} = 4.56$ $P = 0.0031$	$F_{12,51.9} = 0.46$ $P = 0.9271$	2008^{a} 2010^{b} 2011^{b} 2013^{b} 2014^{b}	
Plestiodon fasciatus (five-lined skink)	62(3)	$F_{3,16.5} = 9.88$ $P = 0.0006$	$F_{4,57.6} = 5.77$ $P = 0.0006$	$F_{12,57.6} = 5.01$ $P < 0.0001$	2008^{a} 2010^{a} 2011^{bc} 2013^{b} 2014^{ac}	C^{a} MH^{a} B^{a} SW^{b}
Plestiodon anthracinus (coal skink)	9(0)	–	–	–		
Sceloporus undulatus (eastern fence lizard)	11(1)	–	–	–		
Total lizards	82(4)	$F_{3,16.7} = 4.64$ $P = 0.0155$	$F_{4,57.1} = 5.78$ $P = 0.0006$	$F_{12,57.1} = 4.70$ $P < 0.0001$	2008^{a} 2010^{a} 2011^{bc} 2013^{b} 2014^{ac}	C^{a} MH^{a} B^{a} SW^{b}
Total amphibians	1530(14)	$F_{3,14.9} = 0.87$ $P = 0.4769$	$F_{4,54.6} = 4.03$ $P = 0.0062$	$F_{12,54.5} = 2.17$ $P = 0.0267$	2008^{ab} 2010^{ab} 2011^{a} 2013^{c} 2014^{b}	
Total reptiles	269(4)	$F_{3,13.5} = 3.35$ $P = 0.0516$	$F_{4,54.1} = 2.94$ $P = 0.0284$	$F_{12,54.1} = 0.83$ $P = 0.6228$	2008^{a} 2010^{b} 2011^{b} 2013^{ab} 2014^{b}	

Table 3
Results of mixed model ANOVA with repeated measures comparing species richness of all herpetofauna, reptiles, amphibians, frogs, salamanders, lizards, and snakes among treatments, years, and testing for treatment × year interaction effects in oak regeneration treatments on Cold Mountain Game Land, Haywood County, NC, (2008, 2010, 2011, 2013, 2014). Treatments were control (C), midstory herbicide (MH), prescribed burn (B), and shelterwood harvest (SW). Different letters among years within rows denote significant differences.

Taxa	P_{Trt}	P_{Yr}	P_{TrtxYr}	Year diffs
Total herpetofauna	$F_{3,15.4} = 0.13$ $P = 0.9398$	$F_{4,55.3} = 0.63$ $P = 0.6466$	$F_{12,55.3} = 1.12$ $P = 0.3654$	
Total amphibians	$F_{3,15.4} = 0.31$ $P = 0.8162$	$F_{4,55.1} = 2.21$ $P = 0.0800$	$F_{12,55.1} = 0.76$ $P = 0.6845$	
Total frogs	$F_{3,12.6} = 0.59$ $P = 0.6310$	$F_{4,52.9} = 4.05$ $P = 0.0061$	$F_{12,52.8} = 1.53$ $P = 0.1428$	2008^{a} 2010^{ab} 2011^{bc} 2013^{bc} 2014^{c}
Total salamanders	$F_{3,16} = 0.64$ $P = 0.5978$	$F_{4,55.7} = 1.69$ $P = 0.1642$	$F_{12,55.7} = 1.30$ $P = 0.2425$	
Total reptiles	$F_{3,15.2} = 0.92$ $P = 0.4549$	$F_{4,56.6} = 0.81$ $P = 0.5235$	$F_{12,56.6} = 0.93$ $P = 0.5243$	
Total lizards	$F_{3,16.6} = 0.94$ $P = 0.4453$	$F_{4,56.9} = 3.67$ $P = 0.0100$	$F_{12,56.8} = 2.66$ $P = 0.0067$	2008^{ab} 2010^{ac} 2011^{cde} 2013^{df} 2014^{ae}
Total snakes	$F_{3,13.7} = 0.64$ $P = 0.5992$	$F_{4,55.9} = 2.02$ $P = 0.1047$	$F_{12,55.8} = 0.58$ $P = 0.8465$	

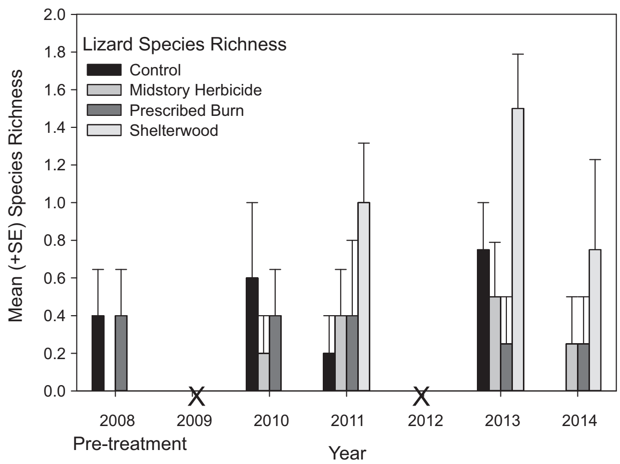

Fig. 3. Mean (±SE) species richness of lizards before (2008) and after three oak regeneration treatments and control on Cold Mountain Game Land, Haywood County, NC. Treatments were control (C), midstory herbicide (MH), prescribed burn (B), and shelterwood harvest (SW).

P. teyahalee showed a marginally higher proportion of juveniles than adults in C than in SW (P = 0.0680; Table 4).

Capture rate of all reptiles did not differ among treatments, but overall capture rate was lower in 2010, 2011, and 2014 compared to 2008 (2013 did not differ from any other year); no treatment × year interaction effect was detected (Table 2; Fig. 5a). Among reptile taxa, the capture rate of snakes did not differ among treatments, nor was there a treatment × year interaction effect, but capture rate was greater in 2008 than in other years (Table 2). No treatment, year, or treatment × year interaction effects were detected for either ringneck snakes (*Diadophis punctatus*) or common garter snakes (*Thamnophis sirtalis*) (Table 2). In contrast, the capture rate of all lizards (Table 2; Fig. 5b) and *P. fasciatus* (Table 2; Fig. 5c) (comprising 76% of all lizards) was greater in SW than other treatments or C (treatment effect), and was overall (year effect) lower in 2008 and 2010 than 2011 or 2013 (2014 differed only from 2013) (Table 2; Fig. 5c). We also detected a treatment × year effect. Partitioned F-tests of years within treatments indicated that capture rate of lizards and *P. fasciatus* was dynamic over time only within SW. Initially, capture rate in SW was low, and did not differ between 2008 (pre-treatment) and 2010 (immediately post-treatment), but subsequently increased (2011, 2013, 2014). Partitioned F-tests of treatment differences within years indicated that capture rate was greater in SW than other treatments or C in 2011, 2013, and 2014 (Fig. 5c). Post-treatment (2013 and 2014), the ratio of juvenile to adult *P. fasciatus* was greater SW than C (Table 4).

Table 4
Fisher's exact tests comparing *Plethodon teyahalee*, *Plethodon metcalfi*, and *Plestiodon fasciatus* age-class structure (2013–2014 only) between control (C) and shelterwood (SW) treatments on Cold Mountain Game Land, Haywood County, NC. Numbers of captures within each treatment type are separated by commas. Significance was set at P < 0.05 and df = 1 for all comparisons.

Treatment comparison	Juveniles		Adults		Fisher's exact
	C	SW	C	SW	Test (P)
Plethodon teyahalee	12	2	9	8	0.0680
P. metcalfi	2	1	9	3	1.0000
Plestiodon fasciatus	2	5	0	35	0.0244

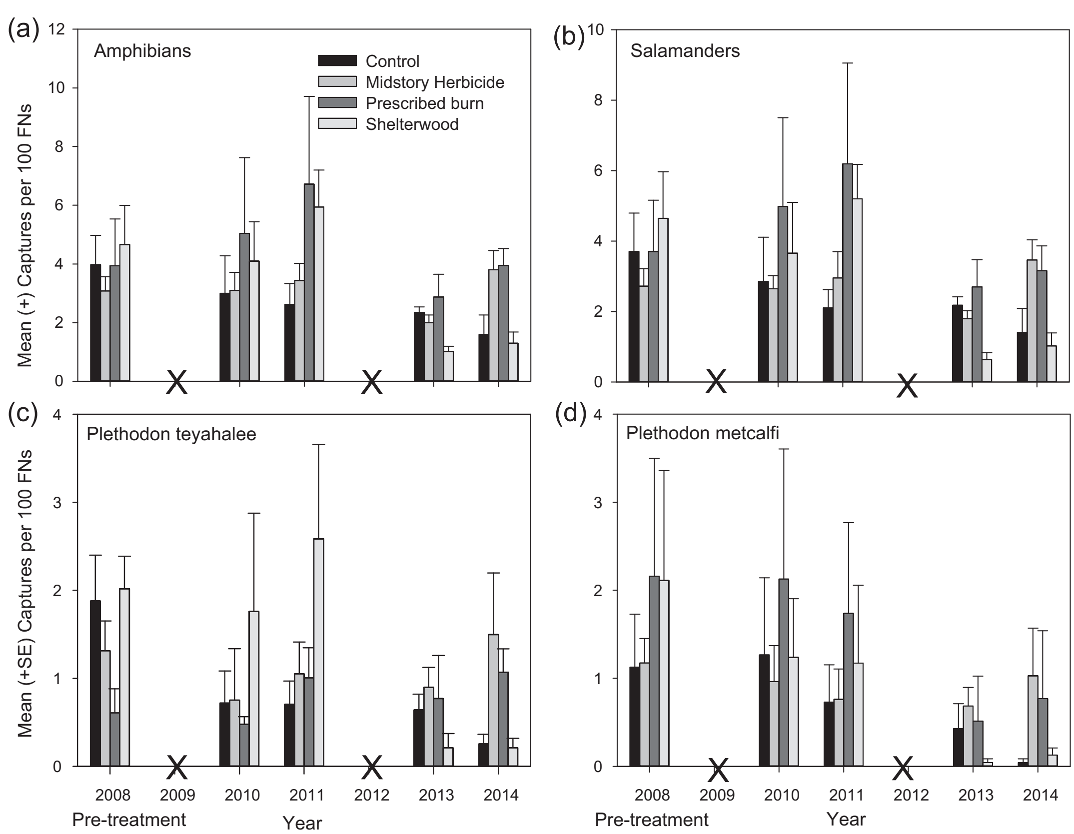

Fig. 4. Mean (±SE) captures of (a) all amphibians, (b) all salamanders, (c) *P. teyahalee*, and; (d) *P. metcalfi* per 100 FNs before (2008) and after three oak regeneration treatments and control on Cold Mountain Game Land, Haywood County, NC. Treatments were control (C), midstory herbicide (MH), prescribed burn (B), and shelterwood harvest (SW).

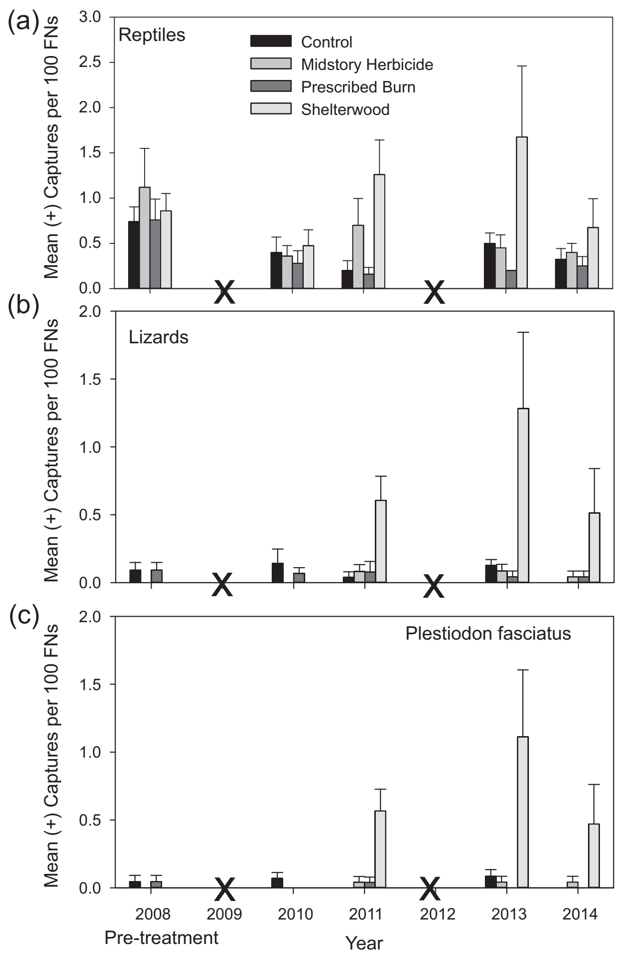

Fig. 5. Mean (±SE) captures of (a) all reptiles, (b) all lizards, and; (c) *P. fasciatus* per 100 FNs before (2008) and after three oak regeneration treatments and control on Cold Mountain Game Land, Haywood County, NC. Treatments were control (C), midstory herbicide (MH), prescribed burn (B), and shelterwood harvest (SW).

4. Discussion

Our results corroborated several other studies in upland hardwood forest showing that terrestrial salamander abundance (or capture rate) was reduced within a few years after substantial canopy removal (i.e., shelterwood harvest or clearcut), but not after treatments involving understory manipulation by herbicide or low-intensity winter prescribed burns, with the forest canopy left intact (e.g., Homyack and Haas, 2009). In contrast, post-harvest capture rate of lizards was much higher in SW compared to other treatments or C, likely in response to the same changes in microclimate that were detrimental to salamanders (Matthews et al., 2010). Capture rate of other tested herpetofaunal species, including most salamander species, did not show a response to any treatment. Our study highlights the importance of including multiple taxa for a balanced perspective, when examining the impacts of restoration-related silvicultural disturbance on wildlife.

Several other studies indicate that post-harvest declines in salamander abundance (or capture rate) may not be evident for one or two years, possibly due to high site fidelity or reduced reproductive success that becomes evident by reduced capture rate over time (Ash, 1988; Bartman et al., 2001; Ford et al., 2000; Knapp et al., 2003). Shorter-term (1–2 years post-treatment) results of this study (Raybuck et al., 2015), and a companion Regional Oak Study installation in a Tennessee upland hardwood forest (Cantrell et al., 2013) showed no effect of tested oak regeneration treatments on capture rate of *Plethodon* salamanders, using drift fences with pitfall and funnel traps. However, O'Donnell et al. (2015), using area-constrained searches, reported decreased post-treatment abundance and surface activity of southern red-back salamanders (*Plethodon serratus*) in shelterwood, midstory herbicide, and prescribed burn units immediately after treatments in the companion Regional Oak Study installation in Ozark Highlands of Missouri.

Other research indicates that terrestrial salamander abundance (or capture rate) is closely associated with leaf litter depth and cover and moisture at ground level (e.g., O'Donnell et al., 2014). In our study, reduced canopy cover likely reduced moisture and increased temperature at ground level, and heavy machinery used for shelterwood harvests initially increased the percentage of bare ground and reduced leaf litter cover, potentially accounting for decreased capture rate of *P. teyahalee* in SW. However, the understory and the associated litter layer recovered rapidly as stump sprouts, seedling, and shrubs proliferated and dropped leaves each autumn. Interestingly, decreasing *P. teyahalee* capture rate coincided with recovery of shade and ground cover in SW, suggesting that reasons for post-disturbance decline may be complex. In our study, *P. teyahalee* capture rate also declined in control plots between pre- and post-treatment periods. Hence, declining captures of *P. teyahalee* in SW units should be interpreted with caution; in fact, concurrent changes in capture rate in both SW and C possibly could have been due to large-scale changes in surface environmental conditions or precipitation during that time period.

Other short-term studies indicated that effects of heavy canopy removal on salamanders can occur rapidly. For example, Sattler and Reichenbach (1998) reported fewer Peaks of Otter salamanders (*Plethodon hubrichti*) in central Appalachian clearcuts within 1–2 years post-harvest compared to recent shelterwood harvests and controls. Harpole and Haas (1999) reported that salamander abundance deceased 1–3 years after group selection, shelterwood, leave-tree, and clearcut harvests in Virginia upland hardwood forests. Hence, longer-term studies are needed to capture temporal trends in relative abundance or surface activity that may change rapidly or gradually following harvests and other silvicultural activities.

Although our study period included only 4–5 years after all treatments were implemented, other studies indicate that a relatively lower capture rate of salamanders persists for a prolonged period after heavy or complete canopy removal (Herbeck and Larsen, 1999; Petranka et al., 1994; Pough et al., 1987). Estimates of recovery time range from 13 years (Harper and Guynn, 1999) to a century (Petranka et al., 1994; also see Ash, 1997; Ash et al., 2003; Ford et al., 2002a; Pough et al., 1987; Hocking et al., 2013; Homyack and Haas, 2009). Recovery times may in part depend on species and site characteristics associated with moisture and productivity, such as slope and aspect (Ford et al., 2002b).

Causes of salamander decline following heavy canopy removal are unknown, but hypotheses include emigration, mortality due to desiccation or starvation, retreat underground (Semlitsch et al., 2009), or reduced fecundity (e.g., Homyack and Haas, 2009). Semlitsch et al. (2008) reported a large proportion of pond-breeding Ambystomid salamanders, and a smaller proportion of frogs and toads moving out of recent clearcut harvests. Other studies indicate that salamanders retreat under cover objects (O'Donnell et al., 2015) or belowground, and reduce surface activity after prescribed fire (O'Donnell et al., 2016) or drought (Grover, 1998; Jaeger, 1980). These behavioral changes in response to disturbances highlight the uncertainty involved in drawing conclusions about changes in abundance based on capture rate alone.

The drift fence arrays we used to sample herpetofauna may yield different results than other methods used to study herpetofaunal response to silvicultural treatments in uplands, including coverboards (e.g., Hocking et al., 2013; Pough et al., 1987; Reidel et al., 2008) or active searches (e.g., Homyack and Haas, 2009; O'Donnell et al., 2015; Petranka et al., 1994). Whereas these other methods likely yield important metrics of relative abundance for Plethodontid salamanders, they also introduce bias. For example, coverboards likely attract salamanders, which use them as refugia, and thus may affect their microdistribution and associated estimates of abundance (Marsh and Goicochea, 2003). Further, weather can affect surface activity and use of cover objects, further confounding results (Heatwole, 1962; O'Donnell et al., 2014). Similarly, surface searches are a 'snapshot' sampling method that may be heavily influenced by weather and time of day or night (O'Donnell et al., 2015). Coverboards and surface searches are best used for sampling terrestrial salamanders, contributing to a heavy research focus on salamanders and a de-emphasis on the importance of other herpetofaunal species or communities. In contrast, although not without bias (e.g., trespass or escape by some species), drift fences that are continuously, concurrently open in all treatment units, sample surface activity ("availability") across changing weather conditions and activity periods, and also sample a greater diversity of amphibian and reptile species than other methods. Nonetheless, our capture methods did not address behavioral changes of herpetofaunal species in relation to changing environmental conditions in the different treatments and control, and thus the basis of our conclusions are limited to relative changes in surface activity and capture rate after silvicultural treatments.

Several studies have found a lower proportion of juveniles to adults of some *Plethodon* species (and *Desmognathus ochrophaeus*; Homyack and Haas, 2009) on recently harvested sites, indicating that reproductive success may decline after heavy canopy removal (Ash et al., 2003; Hocking et al., 2013; Homyack and Haas, 2009; Reichenbach and Sattler, 2007; Reidel et al., 2008; Sattler and Reichenbach, 1998). Our results also suggested a lower proportion of juvenile to adult *P. teyahalee* in 3–4 year old SW than in C. However, low sample sizes render this conclusion uncertain; further research is warranted to determine the causes, lower fecundity or otherwise, for reduced salamander capture rate after heavy canopy removal.

In our study, lizards, primarily *P. fasciatus*, showed a much different response to restoration treatments than *P. teyahalee*, with a higher capture rate in SW within a year after harvesting. Other studies have also reported increased lizard abundance, especially eastern fence lizard (*Sceloporus undulatus*), following substantial canopy reduction (Greenberg, 2001; Greenberg and Waldrop, 2008; Matthews et al., 2010; McLeod and Gates, 1998). Following timber harvests, Renken (2006) determined that juvenile *S. undulatus* captures were double that of adults, suggesting that the lizards experienced an immediate boost in reproductive rates in disturbed sites, or these sites were colonized primarily by juveniles. *S. undulatus* was relatively uncommon at our higher elevation study area. We documented a higher proportion of *P. fasciatus* juveniles to adults, but also captured more adults, in SW than C, suggesting that areas with heavy canopy reduction may both attract *P. fasciatus* and enhance reproductive success.

Restoration treatments retaining an intact forest canopy, including the B and MH treatments, had no measurable effect on any herpetofauna. In contrast, other research (Matthews et al., 2010) shows that high-severity fires that kill trees, substantially reduce canopy cover, and create forest floor microclimate somewhat analogous to conditions after shelterwood harvests may potentially lead to declines in *Plethodon* salamanders and increased lizard densities. Several other studies also indicate that changes to herpetofaunal communities are associated with heavy canopy removal, but alterations to the midstory alone have a negligible effect, whether by mechanical means (Matthews et al., 2010; Pough et al., 1987), herbicide (Cantrell et al., 2013; Homyack and Haas, 2009; Harpole and Haas, 1999) or low-intensity winter prescribed fire (Floyd et al., 2001; Ford et al., 1999, 2010; Greenberg and Waldrop, 2008; Keyser et al., 2004; Matthews et al., 2010; Moseley et al., 2003). Messere and Ducey (1998) also found that salamander densities were similar among gaps created by selective logging, gap edges, and forest during the first year after logging, suggesting that small reductions in overstory may have a negligible effect in the short term. O'Donnell et al. (2015) reported decreased, short-term abundance and surface activity of *P. serratus* after winter prescribed burns in the Ozark Highlands Regional Oak Study, which they attributed to increased post-burn use of cover objects. Similarly, Ford et al. (2010) found increased use of coverboards by *D. ochrophaeus* and *Plethodon cinereus* in twice-burned sites for at least 2 years compared to pre-burn or unburned controls.

5. Conclusions

In our study, heavy canopy removal in SW resulted in reduced capture rate of total salamanders after 2 years, but increased captures of a lizard species, *P. fasciatus*. Other restoration practices to increase oak regeneration, including MH and B, did not affect any herpetofaunal species. The different responses between salamanders and *P. fasciatus* were likely because of their differing life history traits, which affected their response to a lighter, drier and warmer microclimate with more bare ground and reduced leaf litter cover or depth in SW. Our results illustrate how taxa with different life history requirements respond differently to restoration-related disturbances. Disturbances causing substantial reductions in canopy cover are associated with changes in the forest floor microclimate that may negatively affect some salamander species (see DeMaynadier and Hunter, 1995; Moorman et al., 2011), but concurrently provide habitat for early successional birds (Askins, 2001; Greenberg et al., 2013), butterflies and other pollinating insects (Campbell et al., 2007; Haddad and Baum, 1999; Lanham and Whitehead, 2011), and lizards. In addition, because most forest restoration disturbances occur at a relatively small scale, adverse effects are usually localized, transient, and unlikely to affect sensitive wildlife species at a landscape or regional level (Moorman et al., 2011). We suggest that species other than terrestrial salamanders are also important indicators of habitat condition and illustrate trade-offs in responses among species after silvicultural disturbances. Forest managers must understand and consider how management actions will affect multiple wildlife species in relation to their conservation status, habitat requirements, and habitat availability. Forested landscapes can promote biological diversity by creating a temporal and spatial mosaic of different aged forests, including abundant mature forest, through a sustainable rotation of timber harvests and other silvicultural activities (e.g., Shifley and Thompson, 2011; Greenberg et al., 2013). Our study illustrates the importance of longer-term studies to detect potential changes in herpetofaunal communities that may not be immediately apparent after forest restoration practices, and highlights the importance of including multiple taxa for a balanced perspective, when examining the impacts of forest restoration activities on wildlife.

Conflict of interest

The authors declare that they have no conflict of interest.

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