Research Article



Long-Term Herpetofaunal Response to Repeated Fuel Reduction Treatments

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ABSTRACT Fuel reduction treatments are used to reduce wildfire risk and to restore plant communities. Yet, repeated mechanical or prescribed fire treatments may gradually change forest structure and microhabitat conditions, favoring some taxa and decreasing suitability for others. We experimentally assessed long-term (intermittent years, 2003–2016) effects of repeated dormant-season mechanical and prescribed fire treatments on capture rates of reptiles and amphibians in southern Appalachian upland hardwood forests. Treatments were mechanical understory removal (twice), prescribed burning (4 times; burn-only), mechanical understory removal followed 1 year later by high-severity prescribed burns and 3 subsequent burns (mechanical + burn), and untreated controls. Initial burns were hotter in mechanical + burn than burnonly units, resulting in heavy tree mortality and increased canopy openness within 2 growing-seasons postburn. We captured 4,606 individuals of 15 amphibian and 20 reptile species. Capture rates of American toads (Anaxyrus americanus), green frogs (Lithobates clamitans), plethodontid salamanders (Plethodon spp.), and northern red salamanders (Pseudotriton ruber) were not affected by any fuel reduction treatment. The capture rate of five-lined skinks (Plestiodon fasciatus) was greater in mechanical + burn than burn-only or control units, and the capture rate of eastern fence lizards (Sceloporus undulatus) was greater in mechanical + burn than control units. Juvenile eastern fence lizard captures were greater in mechanical + burn units and increased over time, indicating that high-severity burning followed by repeated burns may improve conditions for successful recruitment. Different responses among species highlight the importance of including multiple taxa when assessing effects of forest disturbances on wildlife, and give perspective on how forest health may vary depending on target taxa. © 2017 The Wildlife Society.

KEY WORDS amphibian, anuran, fire severity, lizard, prescribed fire, repeated burn, reptile, salamander.

Prescribed burning, often in conjunction with other silvicultural methods, is commonly recommended for fuel reduction, forest restoration, and wildlife habitat improvement. Yet, major phylogenetic, physiological, and lifehistory differences among wildlife taxa indicate they should respond differently to changes in forest structure created by fire or other silvicultural or natural disturbances (Harper et al. 2016). For example, shelterwood harvests that substantially reduce canopy cover and alter the forest floor microenvironment provide habitat for shrub-scrub bird

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¹E-mail: kgreenberg@fs.fed.us ²Retired. species (Askins 2001, Rush et al. 2012), some lizard species (Matthews et al. 2010), and pollinating insects (Haddad and Baum 1999, Whitehead 2003) but reduce habitat suitability for some ground-nesting bird species (Greenberg et al. 2014) and terrestrial salamanders (Harpole and Haas 1999, Greenberg et al. 2016), at least in the short-term. In contrast, silvicultural disturbances with heavy canopy retention generally have little effect on most wildlife species (Ford et al. 1999, Harpole and Haas 1999, Homyack and Haas 2009).

Reptiles and amphibians play important ecological roles as predator and prey, and both groups are important components of biological diversity. Although frequently lumped together as herpetofauna, reptiles, and amphibians are in different taxonomic classes, as phylogenetically distinct as mammals and birds (Moorman et al. 2011). Reptiles have dry scaly skin, whereas amphibians have moist, permeable skin used for respiration, increasing susceptibility to desiccation. Most amphibians require moist microenvironments and many require water bodies for breeding; most reptiles require warmer temperatures associated with higher light levels for increased foraging activity, thermoregulation, and egg incubation (Duellman and Trueb 1986, Deeming and Ferguson 1991, Moorman et al. 2011). These physiological and life-history differences between reptiles and amphibians are likely to influence their response to altered forest structure and microclimate after fire or other disturbances.

Because of their apparent sensitivity to microclimate (Welsh and Droege 2001), terrestrial salamanders have been suggested as an indicator of forest health. However, a mature, intact forest condition is not synonymous with forest health; a forest condition may be healthy for some species but not others. For example, abundance of fence lizards (Sceloporus undulatus or S. woodi) is greater in open, recently burned longleaf pine (Pinus palustris) sandhills (Steen et al. 2013), open-canopy burned mixed pine-hardwood forest (Fouts et al. 2017), large, wind-created canopy gaps in upland hardwood forest (Greenberg 2001), and cut and burned sand pine (P. clausa) scrub (Greenberg et al. 1994) than in closed canopy forests, indicating that open, heavily disturbed forests are healthy for those species. A balanced metric of forest health at the landscape level should include a diverse suite of wildlife taxa with potential as indicators of various forest conditions, because no single condition benefits all species.

Heavy research focus on terrestrial salamanders as indicators of forest health (Ash 1988, Harpole and Haas 1999, Homyack and Haas 2009, Ford et al. 2010, O'Donnell et al. 2015) is partly because they are abundant, and easily captured using visual searches or coverboards (O'Donnell and Semlitsch 2015) compared to many other amphibian or reptile species (Moorman et al. 2011). In contrast, drift fences with pitfall traps sample multiple, surface-active reptile, and amphibian species, providing a broader overview of community-level response to disturbances, and allowing for assessment of various species with different life-history requirements, as potential indicators of forest conditions.

Wildlife response to fuel reduction treatments, especially when repeated, may vary over time. Several short-term studies indicated that low-intensity dormant-season prescribed burns in upland hardwood forest had a minimal and transient effect on forest structure or wildlife (O'Donnell et al. 2015, Raybuck et al. 2015, Seiboldt 2015, Greenberg et al. 2016). However, repeated burning could have additive effects on habitat attributes, such as canopy cover, shrub density, or leaf litter depth, and associated changes in forest floor microclimate, food, and cover resources that might alter habitat suitability for various taxa over the long-term. Additionally, there could be a time lag in fire-induced changes, most notably delayed mortality of overstory trees (Waldrop et al. 2016). Prescribed fire is not a precise forest management tool; weather, fuel types and volumes, vegetation structure, topography, and ground moisture affect fire intensity and consequent post-fire tree mortality (Knapp et al. 2009). Although changes in forest structure associated with high-severity fires may affect some herpetofaunal species in the short-term (Matthews et al. 2010, Fouts et al. 2017), we are unaware of long-term, communitylevel studies of herpetofaunal response to fire severity in upland hardwood forest. Hence, long-term studies (>10 yrs) are needed to document delayed changes to vegetation structure and associated herpetofaunal or other wildlife communities, in relation to repeated burning and fire severity.

We used a randomized complete block experimental design to experimentally assess long-term reptile and amphibian response to repeated fuel reduction treatments by mechanical understory removal (twice), dormant season, low-intensity prescribed burning (4 times), or mechanical understory removal followed a year later by a high-severity prescribed burn, and 3 subsequent burns, in upland hardwood forest. Initial prescribed burns in the mechanical + burn treatment resulted in heavy tree mortality due to hotter fires fueled by cut shrubs and small trees remaining on the forest floor for a year prior. In contrast, prescribed burns in the burn-only treatment were relatively lower-intensity and, generally, did not kill trees. We reported early results after initial treatment implementation (Greenberg and Waldrop 2008), and again after a second prescribed burn in both burn treatments (Matthews et al. 2010). Since then, we conducted a third and fourth prescribed burn in both burn treatments, and a second mechanical understory removal in the mechanical treatment. The long-term study, with repeated fuel reduction treatment applications, provided an opportunity to examine experimentally long-term (14-year) changes in reptile and amphibian communities. We hypothesized a third and fourth burn in the mechanical + burn treatment would maintain open, young forest conditions created by initial high-severity burns, and thereby yield greater capture rates of common lizard species but decreased captures of terrestrial salamanders; repeated low-intensity dormant-season prescribed fires in the burn-only treatment would cause additional delayed overstory mortality, leading to increased lizard capture rates and decreased salamander capture rates; and 2 repeated mechanical understory removal treatments would not affect capture rates of lizards or salamanders in the mechanical-only treatment.

STUDY AREA

We conducted our study on the 5,841-ha Green River Game Land (35° 17'0900N, 82° 19'42"W, blocks 1 and 2; $35^{\circ}15'42"N$, 82° 17'27"W, block 3) in Polk County, North Carolina, USA. The Game Land is in the mountainous Blue Ridge Physiographic Province of western North Carolina, characterized by a temperate climate with warm, humid summers, and mild winters. Average annual precipitation is 1,638 mm and is distributed evenly throughout the year, and average annual temperature is 17.6°C. Soils are primarily of the Evard series (fine-loamy, oxidic, mesic, Typic Hapludults), which are very deep (>1 m) and well-drained in mountain uplands (Keenan 1998). Elevation ranged from approximately 366-793 m. The Game Land was 97% forested, and had been managed for wildlife conservation since its purchase in the 1950s (North Carolina Wildlife Resources Commission 2014). Common wildlife species included white-tailed deer (Odocoileus virginanus), wild turkey (Meleagris gallopavo), and gray squirrel (Sciurus carolinensis). The upland hardwood forest was composed mainly of oaks (Quercus spp.) and hickories (Carya spp.). Shortleaf pine (P. echinata) and Virginia pine (P. virginiana) were on ridgetops, and white pine (P. strobus) occurred in moist coves. Forest age within experimental units ranged from about 85 to 125 years. Predominant shrubs were mountain laurel (Kalmia latifolia) along ridge tops and on upper southwest-facing slopes, and rhododendron (Rhododendron maximum) in mesic areas. Prior to the first prescribed burns in 2003, none of the sites had been thinned or burned.

METHODS

Study Design

We selected 3 study areas (blocks) within the Game Land based on size (capacity to accommodate 4 experimental units each), forest age, cover type, and management history, to ensure consistency in baseline conditions among the treatments. Perennial streams bordered and (or) traversed all 3 replicate blocks. Minimum size of experimental units within blocks was 14 ha, to accommodate 10-ha core areas with 20m wide buffers around each. Dirt roads or fire lines separated some of the experimental units but did not traverse any, and wooded trails traversed some experimental units.

We assigned 3 fuel reduction treatments and an untreated control randomly within each of the 3 study blocks, for 12 experimental units. Treatments were 1) repeated prescribed burns (burn-only; 4 times in Feb or Mar 2003, 2006, 2012, and 2015); 2) repeated mechanical felling of all shrubs and small trees >1.4 m tall and <10.2 cm in diameter at breast height (dbh) with a chainsaw (mechanical-only; twice in winters 2001–2002 and 2011–2012); and 3) initial mechanical cutting of the understory (winter 2001–2002) followed by 4 prescribed burns (mechanical + burn; burns timed with burn-only units; Table 1). Cut fuels were left scattered onsite

resulting in little or no vertical structure initially, with subsequent recovery in mechanical-only.

During the first prescribed burns (Mar 2003), flame lengths of 1-2 m occurred throughout all burn units, but flame lengths reached up to 5 m in localized spots within blocks, where topography or intersecting flame fronts contributed to erratic fire behavior (Waldrop et al. 2016). Loading of fine woody fuels on mechanical + burn units, where the shrub layer was felled, was approximately double that on control and burn-only sites. Average fire temperature at 30 cm aboveground was much hotter in mechanical + burn than burn-only (370°C and 180°C, respectively). The second burn (Mar 2006) was less intense, with flame lengths generally <1.5 m. Average temperature 30 cm aboveground was 155°C in burn-only units and 222°C in mechanical + burn units (Waldrop et al. 2016). We did not measure fire temperatures in the third and fourth burns, but we observed that they were low-intensity with flame lengths < 2 m.

Habitat Sampling

We measured select stand-level habitat features during or close to years when we sampled herpetofauna (Table 2). We measured tree (>10 cm dbh) density and basal area within 10, 0.05-ha $(10 \times 50 \text{ m})$ vegetation plots, located at grid points $(50 \times 50 \text{ m})$ spaced at 50-m intervals throughout each experimental unit, starting from a randomly selected origin (Waldrop et al. 2016). We measured shrub (woody stems $<10 \text{ cm dbh and } \ge 1.4 \text{ m in height}$ stem density (including all stems within sprout clumps) within 5, $10- \times 10-m$ subplots within each vegetation plot. We measured leaf litter depth through 2015 at 3 m, 7.6 m, and 12.2 m along each of 3 randomly oriented, 15-m transects originating approximately 2 m from grid points in a randomly selected direction (Waldrop et al. 2016). We measured percent canopy openness at drift fence-level, using a spherical densiometer, at the center bucket of each randomly located drift fence array (see Herpetofaunal Sampling below) within each experimental unit during summer (leaf on) as a crude metric of understory light and microclimate. We used the average of all habitat measurements (plots, quadrats, or transects) for each experimental unit $(n=3 \text{ replicates per treatment or } n=3 \text{ replicates per$ control) for statistical analyses.

Table 1. Timing of repeated, dormant-season fuel reduction treatments applied to experimental units (n = 3 per treatment), and years when we trapped reptiles and amphibians (May–Aug) within the Green River Game Land, Polk County, North Carolina, USA, 2001–2016. Treatments were a mechanical understory removal followed by a high-severity burn, and low-severity burn, each followed by 3 subsequent burns; a mechanical understory removal (2 applications); and controls (n = 3 per treatment).

Treatment	2001-2002	2002-2003	2005-2006	2011-2012	2014-2015
Control Mechanical-only Burn-only Mechanical + burn Herpetofaunal trapping ^c	mechanical mechanical ^a	burn burn ^b 2003 2004	burn burn ^b 2006 2007	mechanical burn burn ^b 2014	burn burn ^b 2015 2016

^a Mechanical understory removal only.

^b Prescribed burn only.

^c Traps opened continuously and concurrently as follows: 5 May-2 July and 28 July-18 August 2003, 7 May-16 August 2004, 17 May-16 August 2006, 15 May-13 August 2007, 21 May-11 August 2014, 14 May-9 August 2015, and 16 May-5 August 2016.

Herpetofaunal Sampling

We trapped reptiles and amphibians using drift fence arrays that were open continuously and concurrently during May-August in all units, after all initial treatments were fully implemented (2003 and 2004), again after a second prescribed burn in burn-only and mechanical + burn (2006 and 2007), again after a second mechanical thinning in mechanical-only and a third prescribed burn in burn-only and mechanical + burn (2014), and again after a fourth prescribed burn in burn-only and mechanical + burn (2015-2016; Table 1). We also trapped briefly prior to treatments (2001) but excluded those data here because the season (late summer-fall) and length of trapping period (56 nights) were not comparable to subsequent data. However, pre-treatment data indicated that species richness and capture rates of all taxa did not differ among treatments (Greenberg and Waldrop 2008). The number of operational drift fence arrays was consistent across all treatment units each year but differed among years. We installed 2 arrays for trapping in 2003–2004. We started the 2006 trapping season with 2 arrays but added a third to each unit; the original 2

were opened concurrently during mid-season 2006, and all 3 arrays were operational for the 2007 trapping season. We pulled out all arrays after the 2007 season but re-installed them in 2014 at the same or nearby location of original trap arrays. We started the 2014 trapping season with 3 arrays but added a fourth to each unit; the fourth array was opened in all units a week after trapping began in 2014, and all were operational for the entire 2015 and 2016 trapping seasons. The number of array nights (number of arrays × the number of nights operational) totaled 20,772 across all years, and ranged 158–341 per treatment unit each year.

We placed drift fence arrays randomly ≥ 100 m apart within treatment units. Arrays were constructed with 3, 7.6-m, 50cm high sections of aluminum flashing positioned at approximately 120° angles (in a Y configuration), with 1, 19-L bucket buried at the center, and at the end of each arm, for 4 pitfall traps per array. We placed a double-ended funnel trap, constructed from aluminum screening, along both sides of each arm for 6 funnel traps per array. We drilled holes in the bottoms of pitfalls to prevent flooding. We shaded all traps with a small board, and placed a sponge in pitfall traps

Table 2. Mean $(\pm SE)^a$ live tree density, canopy openness, shrub stem density, and leaf litter depth, and results of mixed-model analysis of variance (ANOVA) comparing treatment (trt), year, and treatment × year interaction effects at Green River Game Land, Polk County, North Carolina, USA, 2002–2016. Treatments were a mechanical understory removal followed by a high-severity burn (MB), and low-severity burn (B), each followed by 3 subsequent burns; a mechanical understory removal (M; 2 applications); and controls (C; n = 3 per treatment). In the treatment differences column, treatments with different superscripted letters within a row differ at the P < 0.05 level.

	Treatment						Mixed-model ANOVA results						
		C		М	[I	3	М	В	P _{trt}	Pyr	$P_{\mathrm{trt} imes \mathrm{yr}}$	Treatment differences
Habitat variable	Year	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE				
Live tree density (ha) ^b	2002-2003	642.0	28.0	646.0	16.4	653.3	31.0	598.0	46.5	0.002	< 0.001	< 0.001	C ^A M ^A B ^A MB ^B
	2004-2005	608.0	24.0	643.3	11.1	580.7	29.4	456.0	29.9				
	2006	593.0	15.9	629.3	11.1	561.7	29.4	406.0	29.9				
	2014	556.0	32.3	516.0	4.0	401.3	56.9	164.7	44.5				
	2015	545.1	22.6	505.8	3.1	399.8	54.4	159.9	42.3				
	2016	552.5	23.7	503.8	3.1	410.1	49.4	171.4	29.6				
Canopy openness (%) ^c	2003	1.6	0.4	3.0	0.8	2.7	1.0	12.8	5.0	0.061	< 0.001	0.729	C ^A M ^A B ^{AB} MB ^B
	2005	6.0	2.7	9.0	2.0	8.3	2.4	35.5	13.1				
	2006	0.9	0.3	3.1	1.6	3.3	2.3	25.9	13.3				
	2014	2.9	0.8	6.2	0.8	8.2	4.3	25.5	15.4				
	2015	2.7	1.3	5.2	0.1	7.2	4.0	34.4	21.4				
	2016	2.3	1.2	3.3	0.7	9.0	5.4	29.4	18.2				
Shrub stem density (ha) ^b	2002-2003	1,918.0	133.3	448.0	92.6	665.3	30.4	758.7	343.9	0.015	< 0.001	< 0.001	C ^{AB} M ^B B ^{AB} MB ^A
-	2004-2005	1,983.3	172.9	1,026.0	118.8	1,514.7	536.1	4,246.0	1,108.4				
	2006	1,716.7	187.0	1,211.3	161.3	850.0	235.0	2,434.7	708.3				
	2014	1,990.7	69.4	1,041.3	225.8	3,298.7	1,584.8	10,168.0	1,301.0				
	2015	1,110.3	81.7	865.0	218.0	1,828.7	840.4	6,047.7	1,049.1				
	2016	1,048.3	50.3	852.7	129.5	2,458.0	1,338.7	7,672.6	948.2				
Leaf litter depth (mm) ^d	2002-2003	4.3	0.5	5.6	0.2	1.0	0.0	0.4	0.1	< 0.001	< 0.001	< 0.001	$C^A M^A B^B MB^C$
	2004-2005	4.6	0.1	5.8	0.4	4.0	0.1	3.3	0.1				
	2006	5.5	0.2	6.1	0.4	1.1	0.4	0.5	0.0				
	2014	6.8	0.3	6.6	0.3	5.5	0.1	5.1	0.2				
	2015	7.8	0.7	7.8	0.4	2.0	0.9	1.1	0.3				

^a Means and standard errors are from raw data and do not represent Ismeans output from the statistical model.

^b We sampled live tree density and shrub stem density 1 growing-season after all initial treatments were implemented (2002 for M and C; 2003 for B and MB), and again after 3 growing-seasons (2004 for M and C; 2005 for B and MB); 5 growing-seasons after the mechanical thinning in M and 1 growing-season after a second burn in B and MB (2006; all treatments); 2 growing-seasons after a second mechanical thinning in M and 3 growing-seasons after a third burn in B and MB (2014; all treatments); and 3 and 4 growing-seasons after the second mechanical thinning in M, and 1 and 2 years after a fourth burn in B and MB (2015 and 2016; all treatments).

^c We sampled canopy cover during same years as herpetofaunal trapping.

^d We sampled leaf litter depth as outlined above through 2015.

moistened as needed to provide cover and humidity for captured animals; frequently flooded buckets also contained a small piece of sponge or styrofoam for flotation.

We checked all drift-fence arrays every 1–3 days and every day following a rain event. We identified and measured reptiles and amphibians (snout-vent [SV] and total length; mm). We identified individuals as juveniles based on the following SV length thresholds: five-lined skinks (Plestiodon *fasciatus*) \leq 52 mm (Vitt and Cooper 1986), eastern fence lizards (S. undulatus) ≤42 mm (Palmer and Braswell 1995), American toads (Anaxyrus americanus) ≤41 mm (Wright 2002), green frogs (Lithobates clamitans) \leq 51 mm (Wright 2002), plethodontid salamanders (*Plethodon* spp.) \leq 58 mm (Homyack and Haas 2009), and northern red salamanders (*Pseudotriton ruber*) \leq 52 mm (Bruce 1978). We marked individuals by year and treatment by toe-clips (lizards, frogs, and salamanders), scale-clips (snakes), or scute-notching (turtles; Swingland 1978) except in 2006-2007, when we instead marked amphibians using Visible Implant Elastomer (Northwest Marine Technology, Shaw Island, WA, USA; Davis and Ovaska 2001). We sterilized injection syringes and scissors between marking individuals. We recorded freeranging reptiles and amphibians observed within treatment units but did not mark or include them in data analyses. All capture and handling methods were approved by the North Carolina State University Institutional Animal Care and Use Committee (Projects 06-025-O, 14-001-O). Animal collection was permitted by the North Carolina Wildlife Resources Commission (Permits no. 0342, 0611, 1013, 1218, 0996, 1050, 13-SC00140, 14-SC00140, 15-SC00140, and 16-SC00472).

Data Analysis

We used repeated measures analysis of variance (ANOVA; PROC MIXED; SAS 9.3, SAS Institute, Inc., Cary, NC, USA) in a randomized block design with compound symmetry covariance structure to examine changes in habitat features and herpetofaunal communities in response to the fuel reduction treatments and controls over all sampled years and repeated treatments. In all repeated measures ANOVAs, we considered treatment, year, and their interaction to be fixed effects, and unit within treatment a random effect and the repeated subject factor. We natural-log transformed (+0.1) data to reduce heteroscedasticity, and square-root arcsine transformed percent data (canopy openness) as needed to approximate normality for ANOVAs.

We standardized all herpetofaunal capture data for differences in trapping effort among years by using captures per 100 array nights (1 array night included 4 pitfall and 6 funnel traps open for 1 night). Herpetofaunal response variables analyzed were species richness of all herpetofauna, reptiles, and amphibians, and total, adult, and juvenile capture rates of species having \geq 200 first-captures. We lumped the 2 captured plethodontid salamander species for data analyses because of possible confusion between them during 2003–2004, and because of their similar ecological habits; data beginning in 2006 indicated that the majority (91%) were white-spotted slimy salamanders (*P. cylindraceus*; northern slimy salamander [*P. glutinosis*] complex; Highton and Peabody 2000) and 9% were southern gray-cheeked salamanders (*P. metcalfi*; Jordan's salamander [*P. jordani*] complex; Highton and Peabody 2000).

We were unable to calculate detection probability accurately because of low recapture rates (Bailey et al. 2004). Because plethodontid salamanders spend most of their time underground or under cover objects (Bailey et al. 2004; O'Donnell et al. 2014, 2016), and because both vagility and detectability varies among herpetofaunal taxa, we considered our capture data to be a measure of relative surface activity, rather than relative abundance.

We considered interaction differences significant when treatment, year, or treatment × year had an overall experimental α of ≤ 0.05 . Where significant treatment \times year interactions were present, we identified treatments or years warranting further examination ($P \le 0.05$ in tests of effect slices), and used the least square means for partitioned Ftests (SLICE option) in PROC MIXED (SAS 9.3) to examine the significance of treatments within identified years, and years within identified treatments. Because the large number of years tested increased the probability of a Type I error, we used a Bonferroni correction (Bland and Altman 1995) to adjust test statistics. For vegetation and herpetofauna, we considered individual lsmeans tests for treatment differences within years (6 comparisons) to be significant with an experimental α of ≤ 0.008 ; we considered tests for year differences within treatments to be significant with an experimental α of ≤ 0.003 (15 comparisons) for vegetation and α of ≤ 0.002 (21 comparisons) for herpetofauna.

RESULTS

Habitat

Live tree density differed among years, and was lower in mechanical + burn than other treatments; we detected a treatment \times year interaction effect (Table 2). Tests of effect slices indicated that tree density differed among treatments in 2006, 2014, 2015, and 2016, and changed over time in mechanical-only, burn-only, and mechanical + burn. Partitioned F-tests (SLICE option with Bonferroni adjustments) of treatment differences within years indicated that tree density was lower in mechanical + burn than mechanical-only in 2006, and lower in mechanical + burn than all other treatments in 2014, 2015, and 2016. Partitioned Ftests within treatments indicated that tree density did not differ among years in mechanical-only. Tree density in burn-only was lower in 2014, 2015, and 2016 than 2003, 2005, or 2006. In mechanical + burn, tree density was lower in 2006, 2014, 2015, and 2016 than 2003 or 2005. Percent canopy openness at the drift fence-level was marginally $(P \le 0.1)$ greater in mechanical + burn than control or mechanical-only and differed among years; we did not detect an interaction effect.

Shrub stem density differed among years, and was lower in mechanical-only (and marginally lower in burn-only) than

mechanical + burn; we detected a treatment \times year interaction effect (Table 2). Tests of effect slices indicated that shrub stem density differed among some treatments in all years, and changed over time in all treatments and controls. Partitioned F-tests of treatment differences within years indicated that shrub stem density was lower in mechanicalonly than control in 2003, higher in mechanical + burn than mechanical-only in 2005, and higher in mechanical + burn than all other treatments in 2014, 2015, and 2016. Partitioned F-tests within each treatment indicated that shrub stem density did not differ among years in control units. In burn-only, shrub stem density was greater in 2005, 2014, 2015, and 2016 than 2003, and greater in 2014 and 2016 than 2006. Shrub stem density was lower in 2003 than all subsequent years in mechanical-only. In mechanical + burn, shrub stem density was lower in 2003 than all subsequent years, higher in 2014 and 2015 than 2005 and 2006, and higher in 2015 than 2006.

Leaf litter depth differed among years, and was lower in mechanical + burn than other treatments; we detected a treatment \times year interaction effect. Tests of effect slices indicated that leaf litter depth differed among treatments in 2003, 2006, and 2015, and changed over time in control, burn-only, and mechanical + burn. Partitioned F-tests of treatment differences within years indicated that leaf litter depth was lower in mechanical+burn than all other treatments, and lower in burn-only than mechanical-only or control in 2003, 2006, and 2015. Partitioned F-tests within treatments indicated that leaf litter in control units did not differ among years. In burn-only, leaf litter was lower in 2003 than 2005 or 2014, and lower in 2006 and 2015 than 2005 or 2014. In mechanical + burn, leaf litter was lower in 2003 than 2005, 2014, or 2015, lower in 2006 than 2005 or 2014, and lower in 2015 than 2005, 2006, or 2014.

Reptile and Amphibian Captures

We captured 3,299 individuals (60 recaptures; 1.5%) of 15 amphibian species, and 1,307 individuals (127 recaptures; 9.7%) of 20 reptile species (Table 3). Frogs and toads represented 53.8% of total first-captures followed by lizards (22.8%), salamanders (17.9%), snakes (5.4%), and turtles (0.2%). We captured only 6 species with sufficient frequency (\geq 200 individuals) for statistical analyses: five-lined skink, eastern fence lizard, American toad, green frog, plethodontid salamanders, and northern red salamander.

Capture rates of American toads, green frogs, plethodontid salamanders, and northern red salamanders differed among years but not among treatments, and we did not detect a treatment \times year interaction effects (Table 3; Fig. 1). Capture rates of five-lined skinks (44% of all lizard captures) differed among years, and were greater in mechanical + burn than burn-only or control. Eastern fence lizard (44% of all lizard captures) capture rates also differed among years, and were greater in mechanical + burn than control; we did not detect a treatment \times year effect for either species (Table 3; Fig. 2). None of the snake species captured were sufficiently common for statistical analyses. Adult American toad, plethodontid salamander, and northern red salamander capture rates differed among years but not among treatments ($P \ge 0.2734$), and we did not detect a treatment × year interaction effect; adult green frogs were not sufficiently abundant for statistical analyses (Table 4). Juvenile American toad ($\le 41 \text{ mm SV}$) and juvenile green frog ($\le 51 \text{ mm SV}$) capture rates differed among years but not among treatments, and we did not detect a treatment × year interaction effect; juvenile plethodontid salamanders ($\le 58 \text{ mm SV}$) and northern red salamanders ($\le 52 \text{ mm SV}$) were not sufficiently abundant for statistical analyses (Table 4).

Adult five-lined skink capture rate differed among years, and was greater in mechanical + burn than other treatments; we did not detect a treatment × year interaction effect (Table 4; Fig. 3). Adult eastern fence lizard capture rate differed among years, and was greater in mechanical + burn than control; we did not detect a treatment \times year interaction effect (Table 4; Fig. 3). Juvenile five-lined skink (\leq 52 mm SV) capture rate differed among years but not among treatments, and we did not detect a treatment × year interaction effect (Table 4; Fig. 3). Juvenile eastern fence lizard (\leq 42 mm SV) capture rate differed among years and was marginally greater in mechanical + burn than control; we did not detect a treatment × year interaction effect (Table 4; Fig. 3). Tests of effect slices indicated that the capture rate of juvenile eastern fence lizards changed over time in mechanical + burn, and differed among treatments in 2014, 2015, and 2016. Partitioned F-tests of treatment differences within identified years indicated that the juvenile capture rate was greater in mechanical + burn than all other treatments in 2014, and marginally greater in 2015 and 2016. Partitioned F-tests within mechanical + burn indicated that the juvenile capture rate was lower in 2003 and 2004 than 2014, 2015, and 2016 (P=0.005), and lower in 2006 and 2007 than 2014 and 2015 ($P \le 0.0207$).

Species richness of amphibians, reptiles, and total herpetofauna differed among years but not among treatments; we did not detect a treatment \times year interaction effect for total species richness (Table 3). Tests of effect slices indicated that total species richness differed among treatments only in 2003 and 2004, and changed over time in all treatments and controls. Partitioned *F*-tests of treatment differences within years indicated that total herpetofaunal species richness in 2003 and 2004 was lower in control than burn-only or mechanical + burn. Partitioned *F*-tests within each treatment indicated that total species richness was lower in 2003 and 2004 than all subsequent years in control and mechanical-only, all subsequent years except 2015 in burnonly, and all subsequent years except 2006, 2015, and 2016 in mechanical + burn.

DISCUSSION

Our findings indicate that capture rates of 2 common lizard species were consistently greater in mechanical + burn, but capture rates of other common herpetofauna, including

Table 3. Number first-captured (and recaptured) reptiles and amphibians (all years and units combined; 20,772 array nights), and results of mixed-model analysis of variance (ANOVA) comparing treatment (trt), year, and treatment × year interaction effects on first-captures of common (\geq 200 first-captures) species/100 array-nights (AN), and species richness at Green River Game Land, Polk County, North Carolina, USA, 2003–2016. Treatments were a mechanical understory removal followed by a high-severity burn (MB), and low-severity burn (B), each followed by 3 subsequent burns; a mechanical understory removal followed by a high-severity burn (MB), and low-severity burn (B), each followed by 3 subsequent burns; a mechanical understory removal (M; 2 applications); and controls (C; n = 3 per treatment). We sampled all treatment units after all initial treatments were implemented (2003–2004), after a second burn (2006–2007), 2 years after a third burn and second mechanical thinning (2014), and after a fourth burn (2015–2016). In the treatment differences column, treatments with different superscripted letters within a row differ at the P < 0.05 level.

		Mixed-model ANOVA results				
	Total	P _{trt}	$P_{\rm yr}$	$P_{ m trt imes yr}$	Treatment differences	
Amphibians	3,299 (60)					
Frogs and toads, Anura	2,476 (49)					
American toad (Anaxyrus americanus)	2,040 (42)	0.345	< 0.001	0.854		
American bullfrog (Lithobates catesbeianus)	12 (0)					
Narrowmouth toad (Gastrophryne carolinensis)	1 (0)					
Gray treefrog (Hyla versicolor chrysoscelis)	3 (0)					
Green frog (L. clamitans)	395 (7)	0.891	< 0.001	0.795		
Pickerel frog (L. palustris)	13 (0)					
Wood frog (L. sylvaticus)	12 (0)					
Salamanders, Caudata	823 (11)					
Blue Ridge two-lined salamander (Eurycea wilderae)	71 (1)					
Eastern newt (Nothophthalmus viridescens)	183 (1)					
Plethodontid salamanders ^a	326 (3)	0.206	0.003	0.710		
Northern red salamander (Pseudotriton ruber)	236 (6)	0.341	0.004	0.215		
Northern dusky salamander (Desmognathus fuscus)	1 (0)					
Seal salamander (D. monticola)	5 (0)					
Blackbelly salamander (D. quadramaculatus)	1 (0)					
Reptiles	1,307 (127)					
Lizards, Lacertilia	1,050 (114)					
Green anole (Anolis carolinensis)	1 (0)					
Broad-headed skink (Plestiodon laticeps)	55 (9)					
Coal skink (P. anthracinus)	53 (0)					
Five-lined skink (P. fasciatus)	464 (57)	0.025	< 0.001	0.363	$C^A M^{AB} B^A M B^B$	
Eastern fence lizard (Sceloporus undulatus)	463 (48)	0.032	< 0.001	0.559	C ^A M ^{AB} B ^{AB} MB ^B	
Ground skink (Scincella lateralis)	14 (0)					
Snakes, Serpentes	250 (11)					
Copperhead (Agkistrodon contortix)	14 (0)					
Eastern worm snake (Carphophis amoenus)	145 (7)					
Black racer (Coluber constrictor)	2 (0)					
Timber rattlesnake (Crotalis horridus)	2 (0)					
Ring-necked snake (Diadophis punctatus)	47 (3)					
Eastern hog-nosed snake (Heterodon platirhinos)	5 (0)					
Milk snake (Lampropeltis triangulum)	5 (0)					
Northern water snake (Nerodia sipedon)	3 (0)					
Corn snake (Pantherophis guttatus)	1 (0)					
Eastern rat snake (P. alleghaniensis)	3 (0)					
Redbelly snake (Storeria occipitomaculata)	3 (0)					
Common garter snake (Thamnophis sirtalis)	20 (1)					
Turtles, Testudinides	7 (2)					
Snapping turtle (Chelydra serpentina)	1 (0)					
Eastern box turtle (Terrapene carolina)	6 (2)					
Total amphibian richness ^b	14	0.319	< 0.001	0.058		
Total reptile richness	20	0.067	< 0.001	0.653		
Total richness ^b	34	0.597	< 0.001	0.015		

^a Includes white-spotted slimy salamander (*Plethodon metcalfi*) and southern gray-cheeked salamander (*Plethodon jordani*) (91% and 9% of plethodontid salamanders captured, respectively, based on all plethodontid salamander captures 2006, 2007, 2014–2016 (*n* = 295, all positively identified).

^b Richness counts lump both plethodontid salamanders.

plethodontid salamanders, were not affected by any fuel reduction treatment even after repeated applications over several years. The changes in vegetation structure following the initial high-severity burn in mechanical + burn, and maintained by subsequent burns, likely explain the changes in the lizard community. Initial (2003) burns were hotter in mechanical + burn than burn-only because of cut fuels left in place for a year prior to burning, resulting in tree mortality (on average, 23% of trees died by 2005, and 71% by 2016) and associated increased canopy openness within 2 growing seasons post-burn. Repeated burns likely prevented stump sprouts or seedlings from growing to canopy closure, maintaining a young forest condition in mechanical + burn. Some delayed tree mortality was also evident in burn-only, likely due to hotspots or repeated burning. Leaf litter depth was reduced after the initial and each repeated burn in both burn (burn-only and mechanical + burn) treatments but recovered rapidly as leaves dropped from deciduous trees each fall. In contrast, tree density and associated canopy cover, and leaf litter depth in control and mechanical-only



Figure 1. Mean (μ [±SE]) number of first-captured American toads (A), plethodontid salamanders (B), green frogs (C), and northern red salamanders (D) per 100 array nights in repeated dormant-season fuel reduction treatments and controls at Green River Game Land, Polk County, North Carolina, USA, 2003–2016. Treatments were a mechanical understory removal followed by a high-severity burn (MB), and low-severity burn (B), each followed by 3 subsequent burns; a mechanical understory removal (M; 2 applications); and controls (n = 3 per treatment). We sampled all treatment units after all initial treatments were implemented (2003–2004), after a second burn (2006–2007), 2 years after a third burn and second mechanical thinning (2014), and after a fourth burn (2015–2016).

remained relatively constant, and higher than in burn-only or mechanical + burn. Shrub stem density was reduced after each fuel reduction treatment in mechanical-only, burn-only, and mechanical + burn but recovered rapidly. Stem density increased in mechanical + burn because of heavy basal or stump sprouting by stem-killed trees, averaging 73% more shrub stems in mechanical + burn than control in 2016.

The predicted increase in five-lined skinks and eastern fence lizards in the mechanical + burn treatment was likely due to the open forest structure created by the high-severity burns, with increased light and temperatures at ground level providing opportunity for thermoregulation, and suitable sites for egg deposition. Other studies in upland hardwood or mixed pine-hardwood forest showed that capture rates and (or) recruitment of fence lizards and (or) five-lined skinks increases following disturbances with heavy overstory removal such as clearcut or shelterwood harvests (McLeod and Gates 1998, Greenberg et al. 2016), thin-with-burn treatments (Sutton et al. 2013, 2014), open woodland restoration (Perry et al. 2009), or large canopy gaps (Greenberg 2001). Fouts et al. (2017) reported a relationship between canopy openness and abundance of northern fence lizards (S. undulatus hyacynthinus) and skinks (Plestiodon spp.), and modeled longer daily activity periods by fence lizards in burned than unburned xeric pine-oak forest. Our results showed a marginally greater capture rate of juvenile eastern fence lizards in mechanical + burn, and a similar, but nonsignificant, trend for juvenile five-lined skinks. Additionally, the capture rate of juvenile eastern fence lizards increased in mechanical + burn during 2014-2016, 2 growing-seasons after the third burn and continuing after the fourth burn. Our long-term results show that highseverity burns with heavy canopy reduction, followed by repeated low-intensity burns, increases habitat suitability for five-lined skinks and eastern fence lizards, and may promote greater juvenile recruitment.

We documented no treatment differences in capture rates of total, adult, or juvenile American toads, or total or juvenile green frogs, although capture rates varied considerably among years and variability was high within treatments and



Figure 2. Mean (μ [±SE]) number of first-captured five-lined skinks (A), and eastern fence lizards (B) per 100 array nights in repeated dormant-season fuel reduction treatments and controls at Green River Game Land, Polk County, North Carolina, USA, 2003–2016. Treatments were a mechanical understory removal followed by a high-severity burn (MB), and low-severity burn (B), each followed by 3 subsequent burns; a mechanical understory removal (M; 2 applications); and controls (n = 3 per treatment). We sampled all treatment units after all initial treatments were implemented (2003–2004), after a second burn (2006–2007), 2 years after a third burn and second mechanical thinning (2014), and after a fourth burn (2015–2016).

years. We captured a large proportion of juvenile American toads and green frogs from a single burn-only (34% and 26%, respectively) and mechanical + burn (35% and 11%, respectively) experimental unit in block 1 (an additional 21% of juvenile green frogs also came from a single mechanical-only unit, block 3), suggesting that capture rates for these aquatic breeders were related to proximity to breeding sites. However, radio-tracked individual adult American toads captured within our study area migrated an average of 994 m to a breeding pond complex on adjacent private land, from the burn-only and mechanical + burn unit in block 1 but also from an mechanical-only and control unit in block 2, a similar distance away (Pitt et al. 2013). Pitt et al. (2013) did not track juvenile recruits, but their results indicated that recruits could potentially emigrate from the pond complex to all similarly distant units. Thus, an explanation for why we captured more juvenile recruits in just 2 or 3 experimental

units is elusive, unless additional, undetected breeding sites occurred nearby. Shorter-term results from the same study site indicated that that distance from known water sources (large puddles, streams, and seepages) was not a significant covariate for total anurans or American toad captures (Matthews et al. 2010). However, American toad (Wilbur 1977) and green frog (Martof 1956, Ashton and Ashton 1988) tadpoles can metamorphose within 6 or 10 weeks, respectively, and thus could potentially reproduce successfully in ephemeral water sources that were not identified.

Contrary to what we predicted, we documented no significant change in capture rates of plethodontid salamanders or northern red salamanders immediately after repeated burns when leaf litter was reduced, or in the longerterm after multiple burns in either burn treatment (burn-only and mechanical + burn). Earlier, short-term results from the study site (Greenberg and Waldrop 2008) immediately following initial treatments (2003-2004) also showed no change in plethodontid salamander or northern red salamander capture rate. Subsequent results following a second burn in burn-only and mechanical + burn (2006-2007) showed no difference in plethodontid salamanders in 2006 but fewer in mechanical + burn than burn-only or control in 2007 (Matthews et al. 2010). Several other studies showed that 1 or 2 low-intensity, dormant-season burns do not adversely affect terrestrial salamanders (Ford et al. 2010, O'Donnell et al. 2015, Raybuck et al. 2015, Seiboldt 2015, Greenberg et al. 2016). Importantly, the long-term results from this study indicate that, despite some variability among some treatments within individual years (Matthews et al. 2010), terrestrial salamander abundance did not decline overall, even after 4 repeated burns in burn-only and mechanical + burn, and further canopy cover reduction in mechanical + burn.

The absence of a significant salamander response to mechanical + burn was somewhat surprising because initial high-severity burns eventually reduced live tree density and associated canopy cover to levels analogous to those following shelterwood harvests, and an open canopy was maintained through repeated burning. Most studies indicate that plethodontid salamander capture rates decrease within 1-3 years after silvicultural treatments with substantial canopy removal, such as shelterwood or clearcut regeneration harvests, relative to controls or treatments involving understory manipulations where the forest canopy remains intact (Ash 1988, Harpole and Haas 1999, Homyack and Haas 2009, Perry et al. 2009, Greenberg et al. 2016). A decrease in salamander capture rate after regeneration harvests is usually attributed to increased light, and decreased leaf litter, moisture, and temperature moderation at the forest floor (O'Donnell et al. 2014), which have been suggested to promote evacuation, mortality from desiccation or starvation, retreat underground (Semlitsch et al. 2008, 2009), or reduced fecundity (Homyack and Haas 2009). We were unable to address salamander fecundity because we captured few juveniles in any treatment or controls. However, the long-term monitoring and continued capture of salamanders in all treatment units indicates

Table 4. Number of individual (first-captures) adults (A) and juveniles (J) of species having \geq 200 captures (all years and units), and results of mixed-model analysis of variance (ANOVA) comparing treatment (trt), year, and treatment × year interaction effects on adult or juvenile captures/100 array-nights (AN) at Green River Game Land, Polk County, North Carolina, USA, 2003–2016. Treatments were a mechanical understory removal followed by a high-severity burn (MB), and low-severity burn (B), each followed by 3 subsequent burns; a mechanical understory removal (M; 2 applications); and controls (C; n = 3 per treatment). We sampled all treatment units after all initial treatments were implemented (2003–2004), after a second burn (2006–2007), 2 years after a third burn and second mechanical thinning (2014), and, after a fourth burn (2015–2016). In the treatment differences column, treatments with different superscripted letters within a row differ at the P < 0.05 level.

			Mixed-model ANOVA results						
	A or J	Total	P _{trt}	$P_{\rm yr}$	P _{trtxyr}	Treatment differences			
Five-lined skink	А	276	0.004	0.001	0.411	$C^A M^A B^A M B^B$			
(Plestiodon fasciatus)	J	188	0.173	0.011	0.534				
Eastern fence lizard	A	404	0.033	< 0.001	0.736	$C^A M^{AB} B^{AB} MB^B$			
(Sceloporus undulatus)	J	59	0.092	0.003	0.005				
American toad	A	512	0.276	< 0.001	0.728				
(Anaxyrus americanus)	J	1,528	0.795	< 0.001	0.910				
Green frog	A	24							
(Lithobates clamitans)	J	371	0.904	< 0.001	0.732				
Plethodontid salamander ^a	A	287	0.244	0.001	0.827				
	J	39							
Northern red salamander	A	212	0.330	0.001	0.064				
(Pseudotriton ruber)	J	24							

^a Includes white-spotted slimy salamander (*Plethodon metcalfi*) and southern gray-cheeked salamander (*Plethodon jordani*) (91% and 9% of plethodontid salamanders captured, respectively, based on all plethodontid salamander captures 2006, 2007, 2014–2016 (*n* = 295, all positively identified).



Figure 3. Mean (μ [±SE]) number of first-captured adult (A and B) and juvenile (C and D) five-lined skinks and eastern fence lizards per 100 array nights in repeated dormant-season fuel reduction treatments and controls at Green River Game Land, Polk County, North Carolina, USA, 2003–2016. Treatments were a mechanical understory removal followed by a high-severity burn (MB), and low-severity burn (B), each followed by 3 subsequent burns; a mechanical understory removal (M; 2 applications); and controls (*n* = 3 per treatment). We sampled all treatment units after all initial treatments were implemented (2003–2004), after a second burn (2006–2007), 2 years after a third burn and second mechanical thinning (2014), and after a fourth burn (2015–2016).

that adult salamanders did not evacuate or die in substantial numbers in response to repeated prescribed burning, higher fire severity, or repeated mechanical understory reduction. Hence, we suggest that terrestrial salamanders, plethodontid salamanders and northern red salamanders in particular, may be resilient to low- and high-severity dormant-season burns and repeated burning in upland hardwood forests.

We observed a clear, non-significant trend of higher salamander capture rates in burn-only that remained consistent throughout 4 repeated, low-intensity burns; this trend was not evident in mechanical + burn. Notably, several other studies using drift fences with pitfall traps in upland hardwood forest have also reported a greater capture rate of terrestrial salamanders immediately following low-intensity dormant-season burns (Matthews et al. 2010, Greenberg et al. 2016). This could be due to higher activity levels associated with decreased litter depth or cover and associated changes in microclimate, changes in prey availability, or expanded foraging areas (Homyack et al. 2011). In contrast, other studies reported short-term decreased surface activity and abundance, and increased use of cover objects after 1 (O'Donnell et al. 2015, 2016) or 2 (Ford et al. 2010) lowintensity dormant-season prescribed burns in upland hardwood forest, based on diurnal plot searches or coverboard methods.

Perceived changes in reptile and amphibian capture rates are potentially confounded by behavioral changes following disturbances, weather, and sampling methods. For example, salamanders may retreat belowground or under cover objects (Grover 1998, O'Donnell and Semlitsch 2015, O'Donnell et al. 2015), American toads may increase their use of coarse woody debris (Pitt et al. 2013), and lizards may increase surface activity in response to reduced leaf litter or warmer temperatures (Fouts et al. 2017) following burns or other forest disturbances. Snapshot survey methods, including coverboards (Hocking et al. 2013, Pough et al. 1987) or active searches (O'Donnell et al. 2015), can provide insight into behavioral shifts, or changes in microdistribution by herpetofauna in response to disturbances (Marsh and Goicochea 2003) but may not accurately measure overall surface activity, a metric of relative abundance, within a longer activity window. In contrast, drift fences with pitfall traps that are continuously and concurrently open in all treatment units for an entire season can more accurately sample relative abundance of surface-active animals among disturbance treatments that encompass diel surface activity patterns, and changing weather conditions (Heatwole 1962, O'Donnell et al. 2014). In addition, drift fences with pitfall traps provide insight into herpetofaunal response at the community level by effectively sampling relative capture rate of more amphibian and reptile species than other survey methods.

Changes in surface activity, or changes in the relative number of individuals above and below ground, following some fuel reduction treatments could have influenced capture rates. Presumably, under this condition, recapture rates also should increase. However, recapture rates of commonly captured species remained negligible (range 0.9% to 12% for plethodontid salamanders and five-lined skinks, respectively) across all years and treatments; additionally, our analyses included only first-captures, or new individuals. Thus, we suggest that changes in relative capture rates among treatments, within (not among) a species, reflected the relative abundance of the local population actively moving on the forest floor surface, and was not simply a metric of change in surface activity levels by the same individuals.

MANAGEMENT IMPLICATIONS

None of the repeated fuel reduction treatments adversely affected any of the commonly captured reptile or amphibian species sampled, including terrestrial salamanders. Increased capture rates of five-lined skinks and eastern fence lizards in mechanical + burn suggests that the open conditions, created initially by high-severity fire and heavy tree mortality, then maintained by repeated burning, likely improved conditions for thermoregulation and successful reproduction. A trend of increased five-lined skink and eastern fence lizard capture rates over time in mechanical + burn suggested that response may be delayed, or repeated burning enhances habitat conditions for these species over time. Increased capture rates of juvenile eastern fence lizards after a third and fourth prescribed fire in mechanical + burn indicates that repeated burns may further increase habitat suitability for successful recruitment. We caution that our results cannot be generalized to all salamander, lizard, or other herpetofaunal species, as we could not address effects on species that were captured infrequently, including snakes and some fossorial and litter-dwelling species that could be more sensitive to disturbances affecting microhabitat and microclimate (Sutton et al. 2014). Our study highlights the importance of longterm studies that can address potentially delayed responses to forest disturbances, and potential additive effects of repeated disturbances. Different responses among species highlight the importance of including multiple taxa when assessing effects of forest disturbances on wildlife, and give perspective on how the perception of forest health may vary depending on target taxa (Harper et al. 2016).

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