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RESEARCH ARTICLE

Reptile and Amphibian Responses to Restoration of Fire-Maintained Pine Woodlands

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Abstract

Fire-maintained woodlands and savannas are important ecosystems for vertebrates in many regions of the world. These ecosystems are being restored by forest managers, but little information exists on herpetofaunal responses to this restoration in areas dominated by shortleaf pine (*Pinus echinata*). We compared habitat characteristics and herpetofaunal communities in restored pine woodlands to relatively unmanaged, second-growth forests in the Ouachita Mountains of western Arkansas, USA. We found woodland restoration with periodic burning affected species differently; some species benefited, some species appeared negatively affected, but most species did not respond clearly either way. Overall reptile captures were significantly ($p = 0.041$) greater in pine-woodlands than in unrestored forest; one species of snake and three species of lizards were captured more often in woodlands than unrestored forests. Among anurans, we found no significant difference in captures between woodlands and unrestored forests for any species. Among salamanders, we captured western slimy salamanders (*Plethodon albagula*) almost exclusively in unrestored forest, but captures of other species did not differ between the two treatments. Historically, the Ouachita region likely consisted of a mosaic that included both fire-maintained habitats (woodlands, savannas, and prairies) and areas of denser forest on mesic sites that were less likely to burn. Consequently, landscapes that retain both open woodlands and denser, less-intensely burned forest (in the form of unharvested greenbelts or separate stands) would likely promote and maintain a greater diversity of herpetofauna.

Key words: **amphibians, Arkansas, burning, fire, habitat restoration, herpetofauna, Ouachita Mountains, reptiles, savanna, woodland.**

Introduction

Because reptile and amphibian populations are declining worldwide (e.g., Gibbons et al. 2000; Houlahan et al. 2000), there is increased interest in effects of forest management and habitat restoration on herpetofauna (deMaynadier & Hunter 1995). There is also increased interest in restoring fire-maintained ecosystems among land managers. Consequently, land managers need information on herpetofaunal responses to restoration of these fire-maintained habitats. Fire-maintained ecosystems, including savannas and open woodlands are important habitats for herpetofauna in many regions of the world, including North America, Africa, and Australia (Friend 1993; Trainor & Woinarski 1994; Russell et al. 1999; Means 2006). Studies that examined the interactions between burning and herpetofauna suggest that burning may restore the vegetative structure of fire-adapted ecosystems and herpetofaunal species that historically adapted to these ecosystems tolerate fire and may benefit from the resulting habitat (Russell et al. 1999). For amphibians, available data suggest that responses to fire are species-specific, poorly understood, and variable among habitats and regions (Pilliod et al. 2003).

Throughout the central and eastern United States, fires that were historically ignited by lightning and Native Americans maintained upland mosaics of grasslands, forests, and woodlands or savannas dominated by pine (*Pinus* spp.) or oak (*Quercus* spp.; e.g., Abrams 1992; Lorimer 2001; Frost 2006; Nowacki & Abrams 2008). European settlement and subsequent logging, agriculture, and fire suppression profoundly altered these landscapes during the 18th and 19th centuries (Lorimer 2001; Frost 2006; Nowacki & Abrams 2008). In the last 100 years, fire-suppression activities caused grasslands, savannas, and woodlands to succeed to closed-canopy forests, and fire-adapted plant species were replaced by shade-tolerant and fire-sensitive vegetation in many areas (Nowacki & Abrams 2008). In the Ouachita Mountains of western Arkansas and eastern Oklahoma (U.S.A.), many forests are now dense, with closed overstories, shade-tolerant hardwood midstories, and sparse understories dominated by woody plants (Masters 1991; Kreiter 1995). Historically, these pine-dominated forests were open, with herbaceous understories that were maintained by frequent (<10 year interval) ground-level fires (Foti & Glenn 1991; Masters et al. 1995; Bukenhofer &

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Figure 1. A typical second-growth pine-hardwood forest with dense canopy, abundant midstory, and sparse herbaceous vegetation in the Ouachita Mountains of Arkansas, U.S.A., prior to restoration (A) and a restored, fire-maintained pine woodland (B).

Hedrick 1997). These pine woodlands, also referred to as pine-grasslands, pine-savannas, or pine-bluestem (*Schizachrium* spp.) ecosystems, supported a unique suite of species, including the endangered red-cockaded woodpecker (*Picoides borealis*).

Land managers are currently implementing woodland and savanna restoration programs throughout North America. In the Ouachita National Forest (ONF), approximately 103,000 ha (about 14% of the ONF) have been targeted for restoration of pine woodlands. To restore this community, the overstories of mature (generally > 50 years old) forest stands are thinned, midstories are removed or reduced, and stands are subjected to prescribed burns at 3- to 5-year intervals (Fig. 1). Furthermore, age at harvest has increased from 70–80 years to 120 years. Implementation of this and other large-scale woodland restoration projects likely affects various floral and faunal communities across the landscape. However, responses of herpetofaunal communities to woodland restoration in areas dominated by shortleaf pine (*P. echinata*) are unknown.

Our objective was to determine reptile and amphibian responses to restoration of pine woodlands. We compared captures of herpetofauna in restored pine woodlands to captures in similar forests not subjected to restoration (generally unmanaged, second-growth forests of pine-hardwood). In addition, we compared habitat characteristics of woodlands with unrestored stands and investigated the relationship between these habitat components and captures of each species.

Methods

Study Area

We conducted the study on the Poteau Ranger District (lat 34°45′ N, long 94°15′ W) of the ONF, located in the Ouachita Mountains of western Arkansas, U.S.A. The Ouachita Mountain ecological subregion extends from central Arkansas into eastern Oklahoma and consists of a series of east- to west-oriented mountains. Throughout this region, elevation ranges from 100 to 800 m, mean annual precipitation ranges from 112 to 142 cm, mean annual temperature ranges from 16.0 to 17.0°C, and the growing season is 200–240 days (McNab & Avers 1994). Soils in the area are derived from shale and sandstone and are typically shallow, rocky, and drought prone (Masters et al. 1993). The predominant forest type in the area is mixed shortleaf pine-hardwood forests. The hardwood component in these forests is diverse and includes oaks (*Quercus* spp.), hickories (*Carya* spp.), and red maple (*Acer rubrum*).

Treatments

Prior to restoration, pine-woodland stands were typical of mature, second-growth, pine-hardwood forests in the western Ouachita Mountains (Fig. 1A; Guldin et al. 1994). Restoration of pine woodlands began with a wildlife stand improvement (WSI) harvest, whereby approximately 36% of the pine and 80% of the hardwood basal area (BA) was removed, which left residual pine BAs of 13.7–16.1 m^2/ha and residual hardwood BAs of 1.4–1.6 m^2/ha. Most midstory trees were felled, but a few smaller midstory species such as dogwoods (*Cornus florida*) were retained for mast production (for wildlife). Prescribed burns were then conducted at 2 to 5-year intervals, usually during winter.

We sampled 12 forest stands: nine restored pine woodlands and three unrestored controls (Fig. 1). All stands were 10.5–42.1 ha (mean 25.0 ha) in size, generally rectangular in shape, and had slopes less than 20%. Control stands were generally unmanaged, second-growth forests of pine-hardwood and were representative of pine-woodland stands prior to restoration. Burning records (after 1978) indicated no recent burns had occurred in these control stands.

We randomly selected nine previously restored pine-woodland stands from those available. These stands underwent initial WSI thinning nine or more years prior (1980–1990) and had undergone three or more (range 3–7, average = 5.4) prescribed burns prior to the beginning of our study. Unthinned 15 to 50-m wide buffers (greenbelts) were retained around drainages in restored stands for water-quality protection. Water flow in these drains was usually limited to heavy rain events. Forests in greenbelts were similar to controls but were burned when the surrounding woodlands were burned. During our study, all prescribed burns were conducted in March and April and all burned stands were part of larger burning units (64.8–1335.5 ha). Thus, most woodland stands were contiguous to large areas of burned forest.

During the 3 years of our study (1999–2001), restored woodland stands were burned on a 3-year burning cycle. Each year, three of the nine woodland stands (those burned 3 years prior) were burned during late winter or early spring following their third growing season. Thus, each year, we sampled three stands during their first growing season, three stands during their second growing season, and three stands during their third growing season after prescribed burning, and each stand was sampled during every phase of the 3-year burning cycle.

Herptofauna Sampling

We sampled herpetofauna using drift fence arrays. Each array consisted of four 15-m long fences (90° apart) constructed of steel hardware cloth (3.2-mm mesh) with a $1.2 \times 1.2 \times 0.46$-m high box trap in the center (Burgdorf et al. 2005). Bottoms of fences were buried 10–15 cm in the ground. A pitfall (18.9-l plastic bucket) was buried flush with the soil surface at the distal end of each drift fence. We placed elevated plywood covers over pitfalls to provide shade and deflect precipitation and we placed leaf litter in buckets to provide cover and microhabitat for captured animals. We provided a water dispenser in each trap.

In each stand, we installed three arrays. Each array was greater than 150 m apart, greater than 50 m from roads or stand edges, and greater than 75 m from permanent or intermittent streams, ponds, and greenbelts. We checked traps weekly from early April until late September, for 3 years (1999–2001); trapping effort was equal among all stands and years (24 weeks each year). We recorded all captured vertebrates and immediately released them greater than 50 m from the trap. We followed Collins and Taggart (2002) for all common and scientific names, with the exception of fence lizards (*Sceloporus undulatus*), whose taxonomy and distribution is under revision. We followed appropriate animal care guidelines (see Guidelines for Use of Live Amphibians & Reptiles in Field Research; American Society of Ichthyologists & Herpetologists; http://www.asih.org/files/hacc-final.pdf). We did not mark captured individuals because of safety concerns associated with lone field personnel marking venomous snakes in remote areas. Therefore, we assumed that recapture probabilities using drift fences and pitfalls were similar between the two treatments.

Habitat Sampling

We measured habitat in September and early October at four plots surrounding each array (12 plots in each stand). A plot was located 7 m beyond the distal end of each drift fence. At plot center, we measured canopy closure (%) with a spherical densiometer, and overstory and midstory (conifer and hardwood combined) BA using a prism. In three adjacent 2×2-m subplots, we visually estimated (±10%) down wood cover. In three nested 1×1-m subplots, we visually estimated percent cover of grass, herbaceous dicots (forbs), leaf litter, rock and bare ground, and woody understory vegetation ($\leq$ 2 m high). In the center of each 1×1-m subplot, we measured litter depth and assigned depth to one of six classes: $1 = 0$ cm, $2 = 0.1 - 2.0$ cm, $3 = 2.1 - 4.0$ cm, $4 = 4.1 - 6.0$ cm, $5 = 6.1 - 8.0$ cm and $6 =$ greater than 8.1 cm. Within an 11.3-m-radius semicircle, we measured the volume of each log with an average diameter 10 cm or greater using Smalian's cubic volume estimate (Avery & Burkhart 1994). We estimated horizontal vegetation density using a 0.5×0.5-m density board (Nudds 1977). For horizontal vegetation density, we measured the distance at which 50% of the density board was obscured by vegetation at three heights: ground level to 0.5-m high (Z1), 0.75–1.25 m above the ground (Z2), and 1.75–2.25 m above the ground (Z3). With this measure, denser vegetation resulted in lower numbers and sparse vegetation resulted in higher numbers. We measured overstory BA in 1999 and 2001 and all understory measures annually.

Data Analysis

For all analyses, we considered forest stands the experimental units. We compared means of each habitat variable in restored stands (averaged over the three post-burn growing years) with unrestored controls (all 3 years averaged) using t-tests. We tested each habitat variable for normality using Shapiro-Wilk tests (SAS Institute Inc. 2000) and applied various transformations to ensure each variable met assumptions of normality.

Our goal was to determine the overall effect of restoration on the herpetofaunal community regardless of responses to the three post-burn periods (first, second, and third growing season after burn) or potential changes throughout each season (e.g., months). Therefore, we summed yearly herpetofaunal captures across all 24 weeks in each stand, averaged those sums among the 3 years of sampling, and compared mean captures of each herpetofaunal species in restored woodlands ($n = 9$) to unrestored controls ($n = 3$) using t-tests or non-parametric equivalents. For each species, we tested data for normality using Shapiro-Wilk tests at $\alpha = 0.10$. We transformed data to meet the assumptions of normality or used exact tests on Wilcoxon scores (SAS Institute Inc. 2000) when data could not be normalized. We conducted analysis only on species with 15 or more captures that were captured in eight or more stands to reduce the likelihood of making inaccurate inferences from sparse data. For comparisons between treatments, we considered each species a separate experiment.

We hypothesized that distance to breeding sites (water sources) would affect amphibian abundance (e.g., Greenberg 1993; Schurbon & Fauth 2003). To test this assumption, we calculated distance (m) from the center of each stand (regardless of treatment) to the nearest semi-permanent water source (wildlife ponds and second-order streams) in a geographic information system (GIS). We found no significant correlations ($p \geq 0.05$) between distance to semi-permanent water and total captures of any amphibian species; thus, we did not include distance to water as a covariate in amphibian analyses. Although small, ephemeral pools are reproductive areas for many amphibians and the presence of these pools may affect spatial distribution of some amphibians (Greenberg 1993), we were not able to determine presence of these ephemeral pools within or adjacent to each stand.

We used redundancy analysis (RDA) (CANOCO version 4.54; ter Braak & Šmilauer 2002) in an exploratory analysis to examine relationships among captures of each herpetofaunal species and habitat parameters. Because both woodlands and controls were upland, mixed pine-hardwood forests that differed primarily in forest structure, the gradient of habitats which we examined was not broad. Therefore, we used RDA because we expected a more linear than unimodal response to our relatively short habitat gradient (ter Braak & Prentice 1988). We conducted separate RDAs for reptiles and amphibians. We used Monte Carlo permutation tests (499 permutations) to determine significance of the first RDA axes (ter Braak & Šmilauer 2002). We used a square-root transformation of species data, standardized habitat parameters (ter Braak & Šmilauer 2002), and only included species with 15 or more captures that were captured in eight or more stands.

Results

Structural Differences Between Woodlands and Controls

Out of 14 habitat variables, 10 differed significantly ($p < 0.05$) between controls and restored woodlands (Table 1). Although overstory BA did not differ between controls and woodlands, restored woodlands had less midstory BA, less canopy cover, less leaf litter cover, and shallower leaf litter, but greater grass, forb, and woody shrub cover, and more rock and bare ground cover. There was no difference in cover of down wood or volume of down logs between woodlands and controls. Horizontal distance at ground level not obscured by vegetation (Z1) was less and Z3 was greater in woodlands than controls, which indicated woodlands had more ground-level vegetation but less vegetation 2 m above the ground than controls.

Herpetofauna Captures

We captured 2,592 reptiles of 33 species (Table 2) and 2,493 amphibians of 18 species (Table 3). We captured 24 species of snakes; 46% of snake captures were southern copperheads (*Agkistrodon contortrix contortrix*) and southern black racers (*Coluber constrictor priapus*) (Table 2). We captured seven species of lizards, and fence lizards were the most abundant (30% of lizard captures). Turtle captures were relatively uncommon and three-toed box turtles (*Terrapene carolina triunguis*) were the only species commonly captured. Among amphibians, bronze frogs (*Rana clamitans clamitans*) and dwarf American toads (*Bufo americanus charlessmithi*) together comprised 73% of amphibian captures (Table 3). Salamander captures were relatively rare. Only 84 salamanders were captured and western slimy salamanders (*Plethodon albagula*) were the most-often captured salamander (29 captured).

Overall reptile captures were significantly greater in pine woodlands than in unrestored controls (Table 2). Capture rates for all snakes combined did not differ between controls and woodlands, but captures of Great Plains rat snakes (*Elaphe emoryi*) were significantly greater in restored woodlands, whereas captures of rough green snakes (*Opheodrys*

Table 1. Habitat characteristics of restored pine-woodland stands (averaged over a 3-year burning cycle, $n = 9$ stands) compared with characteristics of unrestored control stands (averaged over the same 3-year period, $n = 3$ stands) in the Ouachita Mountains of western Arkansas, U.S.A. (1999–2001).

	Control		*Woodland*		
Variable	$\bar{x}$	*SE*	$\bar{x}$	*SE*	p^a
Overstory BA (m^2/ha)	19.8	0.6	18.8	0.9	0.548
Midstory BA (m^2/ha)	4.2	0.7	1.6	0.1	< 0.001*
Canopy cover (%)	90.7	1.3	68.7	3.5	< 0.001*
Forb cover (%)	1.6	0.3	16.6	1.7	< 0.001*
Grass cover (%)	9.0	2.3	21.3	2.6	0.027*
Woody plant cover (%)	15.4	3.3	28.4	1.4	0.002*
Leaf litter cover (%)	98.4	0.2	95.1	0.5	0.004*
Rock and bare ground cover (%)	1.2	0.1	3.4	0.5	0.012*
Litter depth	2.93	0.02	1.82	0.06	< 0.001*
Down wood (%)	3.9	0.9	4.6	0.3	0.355
Z1	15.7	1.8	3.8	0.2	< 0.001*
Z2	24.6	2.8	23.3	1.0	0.615
Z3	31.6	4.7	82.2	3.7	< 0.001*
Log volume (m^3/ha)	36.8	14.8	33.8	6.9	0.844

Litter depth was measured in 2-cm class increments (see text for details). Z1 − Z3 = horizontal distance at which 50% of a density board was obscured by vegetation at ground level (Z1), centered at 1 m above the ground (Z2), and centered 2 m above the ground; shorter distances indicate denser vegetation.

[a] Probability based on Student's t-test. To meet the assumptions of normality, data for midstory BA and litter depth were 1/x-transformed, data for canopy cover and rock and bare ground cover were log-transformed ($\ln[x + 1]$), and data for Z1 were $1/x^2$-transformed.

*Significant at $\alpha = 0.05$.

Table 2. Common and scientific names of reptiles, total reptiles captured during 3 years of sampling, and mean number of reptiles captured during 24 weeks of sampling each year in nine restored pine woodlands (averaged over a 3-year burning cycle) compared with captures in three unrestored control stands (averaged over the same 3-year period) in the Ouachita Mountains of western Arkansas, U.S.A. (1999–2001). Only species with 15 or more captures that were captured in at least eight stands were compared statistically.

		Control		*Woodland*		
Species	*Total*	$\bar{x}$	*SE*	$\bar{x}$	*SE*	p[a]
Reptiles (all)	2,592	54.22	5.84	77.93	4.29	0.041[b]*
Snakes (all)	1,159	25.44	3.38	34.44	3.25	0.157
Southern copperhead (*Agkistrodon contortrix contortrix*)	314	8.78	2.48	8.70	1.23	0.969[b]
Southern black racer (*Coluber constrictor priapus*)	219	4.22	0.59	6.70	1.81	0.510[b]
Western rat snake (*Elaphe obsoleta*)	81	2.33	0.19	2.22	0.40	0.520
Western pygmy rattlesnake (*Sistrurus miliarius streckeri*)	72	1.11	0.40	2.30	0.34	0.155
Great Plains rat snake (*Elaphe emoryi*)	62	0.44	0.11	2.15	0.72	0.014[c]*
Eastern coachwhip (*Masticophis flagellum flagellum*)	57	0.44	0.29	1.96	0.53	0.060
Eastern garter snake (*Thamnophis sirtalis sirtalis*)	56	1.22	0.91	1.67	0.42	0.582
Eastern hognose snake (*Heterodon platirhinos*)	46	0.56	0.29	1.52	0.26	0.129
Speckled kingsnake (*Lampropeltis getula holbrooki*)	39	0.67	0.19	1.22	0.24	0.164
Western ribbon snake (*Thamnophis proximus proximus*)	37	1.56	0.91	0.85	0.22	0.541
Prairie kingsnake (*Lampropeltis calligaster*)	29	0.44	0.29	0.93	0.13	0.259
Northern scarlet snake (*Cemophora coccinea copei*)	28	0.22	0.11	0.96	0.37	0.564[d]
Redbelly snake (*Storeria occipitomaculata*)	23	1.11	0.56	0.48	0.16	0.291[d]
Louisiana milk snake (*Lampropeltis triangulum amaura*)	17	0.33	0.33	0.52	0.11	0.547
Red milk snake (*Lampropeltis triangulum syspila*)	17	0.11	0.11	0.59	0.12	0.091[d]
Rough green snake (*Opheodrys aestivus*)	17	1.00	0.33	0.30	0.09	0.032[d]*
Yellow-bellied water snake (*Nerodia erythrogaster flavigaster*)	12	0.22	0.22	0.37	0.13	
Western worm snake (*Carphophis vermis*)	6			0.22	0.08	
Brown snake (*Storeria dekayi*)	6			0.22	0.08	
Blotched water snake (*Nerodia erythrogaster transversa*)	5			0.19	0.08	
Ringneck snake (*Diadophis punctatus*)	4	0.22	0.22	0.07	0.05	
Western cottonmouth (*Agkistrodon piscivorus leucostoma*)	2	0.11	0.11	0.04	0.04	
Flathead snake (*Tantilla gracilis*)	2	0.11	0.11	0.04	0.04	
Western earth snake (*Virginia valeriae elegans*)	1			0.04	0.04	
Unknown snake	7					
Lizards (all species)	1,400	28.11	5.64	42.48	3.04	0.032[d]*
Fence lizard (*Sceloporus undulatus*)	421	3.89	1.83	14.30	1.58	0.014[d]*
Broad-headed skink (*Eumeces laticeps*)	361	10.00	2.40	10.04	1.53	0.967
Ground skink (*Scincella lateralis*)	353	7.00	0.51	10.74	1.47	0.047*
Five-lined skink (*Eumeces fasciatus*)	201	6.00	0.69	5.44	0.72	0.450
Northern green anole (*Anolis carolinensis carolinensis*)	31	0.78	0.62	0.89	0.53	
Six-lined racerunner (*Aspidoscelis sexlineatus*)	12			0.44	0.18	
Southern coal skink (*Eumeces anthracinus pluvialis*)	11	0.33	0.19	0.30	0.10	
Unknown lizard/skink	10					
Turtles (all)	33	0.67	0.33	1.00	0.10	0.379[d]
Three-toed box turtle (*Terrapene carolina triunguis*)	32	0.67	0.33	0.96	0.10	0.419[d]
Mississippi map turtle (*Graptemys pseudogeographica kohnii*)	1			0.04	0.04	

[a] Unless noted otherwise, probability based on Student's t-test on log-transformed data (ln [x + 1]).
[b] Data were square-root transformed.
[c] Data were 1/(x + 0.5) transformed.
[d] Probability based on exact tests of Wilcoxon scores.
*Significant at $\alpha = 0.05$.

aestivus) were significantly greater in controls. Among species with sample sizes too small for analysis, western worm snakes (*Carphophis vermis*), brown snakes (*Storeria dekayi*), blotched water snakes (*Nerodia erythrogaster transversa*), and western earth snakes (*Virginia valeriae elegans*) were captured only in restored woodlands, whereas ringneck snakes (*Diadophis punctatus*), western cottonmouths (*A. piscivorus leucostoma*), yellow-bellied water snakes (*N. erythrogaster flavigaster*), and flathead snakes (*Tantilla gracilis*) were captured in both woodlands and controls.

Overall captures of lizards were significantly greater in woodlands than controls, primarily because captures of fence lizards were nearly four times greater in woodlands (Table 2). Captures of ground skinks (*Scincella lateralis*) were also significantly greater in restored woodlands. No species of lizard or skink was captured more often in controls than woodlands. Among infrequently captured species, six-lined racerunners (*Aspidoscelis sexlineatus*) were captured exclusively in woodlands, whereas northern green anoles (*Anolis carolinensis carolinensis*) and southern coal skinks (*Eumeces anthracinus pluvialis*) were captured in both controls and woodlands. Although we captured 31 northern green anoles, they were only captured in five stands (two controls and three woodlands). We found no differences in captures of three-toed box turtles between controls and woodlands.

We found no significant difference between restored woodlands and controls in captures of all amphibians combined, all anurans combined, or any species of anuran (Table 3). Among rarely captured frogs, all were captured in both controls and woodlands except northern spring peepers (*Pseudacris crucifer crucifer*); the single northern spring peeper was captured in a control stand. Although we captured 20 green frogs (*R. clamitans melanota*), they were only captured in six of the stands (one control and five woodland stands).

Captures of all species of salamanders combined did not differ significantly between restored woodlands and controls. However, western slimy salamanders (the most often captured species) were captured almost exclusively in controls (28 of 29 were captured in controls), but we did not conduct statistical analysis because of this sample distribution. Among individual species, only captures of central newts (*Notophthalmus viridescens louisianensis*) and spotted salamanders (*Ambystoma maculatum*) were great enough for analyses, but captures of neither of the species differed significantly between controls and woodlands. Among infrequently captured amphibians, Ouachita dusky salamanders (*Desmognathus brimleyorum*) and many-ribbed salamanders (*Eurycea multiplicata multiplicata*) were captured only in woodlands, whereas marbled salamanders (*A. opacum*) were captured in both controls and woodlands.

Species-habitat Associations

The association between habitat variables and reptile captures (Via RDA) was significant for Axis 1 (permutation test; $p = 0.004$) and explained 28.1% of the variation among captures of different species and habitat parameters. Axis 2 explained an additional 18.9% of the variation. In general, Axis 1 represented a gradient with the right side of Axis 1 (Fig. 2A) more representative of unmanaged controls with dense canopy cover ($r = 0.54$), greater midstory BA ($r = 0.48$), deeper leaf litter ($r = 0.52$), and less overall vegetation 0–0.5 m above the ground ($r = 0.51$). Axis 2 generally represented a gradient with the top of Figure 2A representing areas with greater grass cover ($r = 0.44$), less overstory BA ($r = -0.36$), fewer down logs ($r = -0.43$), and less down wood ($r = -0.31$). The eastern coachwhip, eastern hognose snake (*Heterodon platirhinos*), Great Plains rat snake, red milk snake (*Lampropeltis triangulum syspila*), fence lizard, and three-toed box turtle were associated mostly with areas having greater down wood and ground-level vegetation (forb cover, woody cover, Z1), but less midstory BA, less litter cover, and less canopy cover than other species (Fig. 2B). Alternatively, rough green snakes, southern copperheads, western rat snakes (*Elaphe obsoleta*), speckled kingsnakes (*Lampropeltis getula holbrooki*), and redbelly snakes (*Storeria occipitomaculata*) were associated more with areas having dense canopy cover, more midstory BA, deeper leaf litter, and less ground-level vegetation (Z1) than other species.

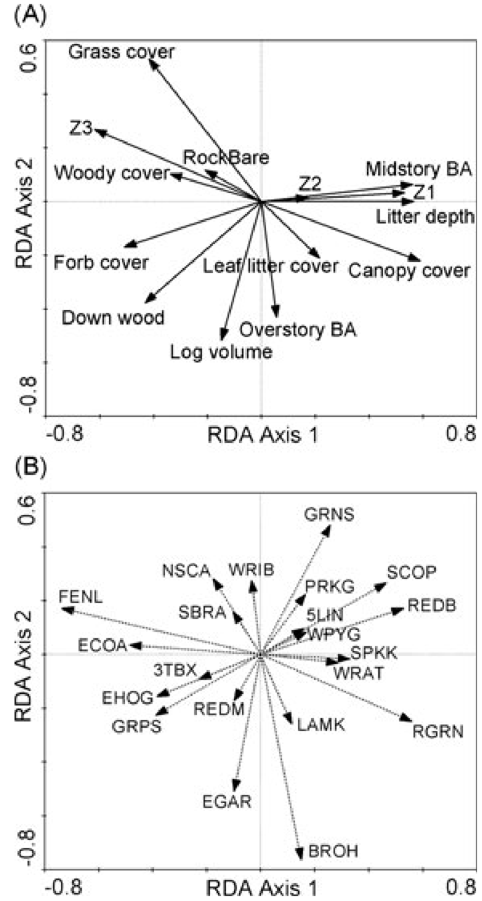

Figure 2. Relationships among 14 habitat variables (A) and position of 21 reptile species (B) on RDA Axis 1 and 2, derived from nine restored pine woodlands and three unrestored controls sampled over 3 years (1999–2001) in the Ouachita Mountains of western Arkansas, U.S.A. See text for descriptions of habitat variables. Species were 3TBX, three-toed box turtle; 5LIN, five-lined skink; BROH, broad-headed skink; ECOA, eastern coachwhip; EGAR, eastern garter snake; EHOG, eastern hognose snake; FENL, fence lizard; GRNS, ground skink; GRPS, Great Plains rat snake; LAMK, Louisiana milk snake; NSCA, northern scarlet snake; PRKG, prairie kingsnake; REDB, redbelly snake; REDM, red milk snake; RGRN, rough green snake; SBRA, southern black racer; SCOP, southern copperhead; SPKK, speckled kingsnake; WPYG, western pygmy rattlesnake; WRAT, western rat snake; and WRIB = western ribbon snake.

The association between habitat variables and amphibian captures (via RDA) indicated Axis 1 was significant (permutation test; $p = 0.004$) and explained 41.6% of the variation among captures of different species and habitat parameters. Axis 2 explained an additional 25.5% of the variation. In general, Axis 1 represented a gradient of greater down wood ($r = 0.44$) and less woody shrub cover ($r = -0.38$; right side

Table 3. Common and scientific names of amphibians, total amphibians captured during 3 years of sampling, and mean number of amphibians captured during 24 weeks of sampling each year in nine restored pine woodlands (averaged over a 3-year burning cycle) compared with captures in three unrestored control stands (averaged over the same 3-year period) in the Ouachita Mountains of western Arkansas, U.S.A. (1999–2001). Only species with 15 or more captures that were captured in at least eight stands were compared statistically.

		Control		*Woodland*		
Species	*Total*	$\bar{x}$	*SE*	$\bar{x}$	*SE*	p[a]
Amphibians (all)	2,493	58.89	21.65	72.70	17.41	0.567[b]
Anurans (all)	2,409	54.78	22.22	70.96	16.75	0.556
Dwarf American toad (*Bufo americanus charlessmithi*)	1,536	29.67	15.20	47.00	11.70	0.367
Bronze frog (*Rana clamitans clamitans*)	279	8.56	6.23	7.48	2.67	0.762[b]
Southern leopard frog (*Rana sphenocephala utricularius*)	146	6.78	5.28	3.15	0.37	0.767[b]
Pickerel frog (*Rana palustris*)	121	2.00	0.51	3.81	0.66	0.091
Bullfrog (*Rana catesbeiana*)	82	1.33	0.69	2.59	0.88	0.456[b]
Eastern narrowmouth toad (*Gastrophryne carolinensis*)	46	0.78	0.29	1.44	0.33	0.473[c]
Fowler's toad (*Bufo fowleri*)	25	0.44	0.22	0.78	0.18	0.390
Green frog (*Rana clamitans melanota*)	20	0.56	0.56	0.56	0.24	
Gray treefrogs (*Hyla versicolor* and *Hyla chrysoscelis*)	12	0.22	0.11	0.37	0.12	
Blanchard's cricket frog (*Acris crepitans blanchardi*)	9	0.56	0.56	0.15	0.08	
Chorus frog (*Pseudacris* spp.)	3	0.11	0.11	0.07	0.07	
Northern spring peeper (*Pseudacris crucifer crucifer*)	1	0.11	0.11			
Unknown frog	129					
Salamanders (all)	84	4.11	2.11	1.74	0.67	0.146[c]
Western slimy salamander (*Plethodon albagula*)[e]	29	3.11	1.79	0.04	0.04	
Central newt (*Notophthalmus viridescens louisianensis*)	20	0.44	0.29	0.59	0.17	0.674
Spotted salamander (*Ambystoma maculatum*)	18	0.11	0.11	0.63	0.22	0.146[d]
Marbled salamander (*Ambystoma opacum*)	9	0.11	0.11	0.30	0.23	
Ouachita dusky salamander (*Desmognathus brimleyorum*)	3			0.11	0.11	
Many-ribbed salamander (*Eurycea multiplicata multiplicata*)	1			0.04	0.04	
Unknown salamander	4					

[a] Unless noted otherwise, probability based on Student's t-test on log-transformed data ($\ln[x + 1]$).

[b] Data were $1/(x + 0.5)$ transformed.

[c] Probability based on exact tests of Wilcoxon scores.

[d] Data were square-root transformed.

[e] Only captured in four stands (three controls and one restored stand); therefore, data were not analyzed.

of Axis, Fig. 3A). Axis 2 represented a gradient with more leaf litter cover ($r = 0.43$), greater overstory BA ($r = 0.26$), and less rock and bare ground cover ($r = -0.40$) at the top of Axis 2 (Fig. 3A). Fowler's toads (*B. fowleri*) and pickerel frogs (*R. palustris*) were associated more with abundant rock and bare ground and less vegetation above 0.5 m (Z2 & Z3) than other species (Fig. 3B). Southern leopard frogs (*R. sphenocephala utricularius*) were associated with abundant midstory trees and down wood compared with other species. Bullfrogs (*R. catesbeiana*) and bronze frogs were associated with abundant leaf litter cover, canopy cover, and overstory BA more than other species. Dwarf American toads and spotted salamanders were associated with abundant grass cover and more woody shrub cover, but less overstory canopy cover than other species.

Discussion

Widespread fire suppression resulted in the development of forests with substantially different vegetative structure from those of 100 years ago, and present abundance of many species is likely a result of those recent changes. Woodland restoration presumably forms amphibian and reptile communities more similar to those that occurred prior to widespread fire suppression. Throughout the southeastern United States and elsewhere, forests have been shaped by frequent fires for thousands of years (e.g., Sharitz et al. 1992; Lorimer 2001), and changes in habitat that result from fire suppression, including succession, encroachment of shrubs, and encroachment of hardwoods in pine-dominated ecosystems may lead to declines or extirpation of some herpetofaunal species (Means & Moler 1979; Means & Campbell 1982; Fellers & Drost 1993; Greenberg 1994). Pine woodlands provide a habitat that once dominated the more xeric south- and west-facing slopes in the Ouachita Mountains (Masters et al. 1995; Bukenhofer & Hedrick 1997), and woodland restoration benefits many other species that were historically adapted to this ecosystem (e.g., Wilson et al. 1995; Masters et al. 1998). Similar to studies of herpetofaunal responses to fire in other regions of the world (e.g., Lunney et al. 1991; Bramford 1992; Singh et al. 2002), our study suggests that woodland restoration and prescribed burning may alter the herpetofaunal community from that of fire-suppressed forests by affecting each species differently; some species may benefit, some species may be negatively affected, but most species do not respond clearly either way.

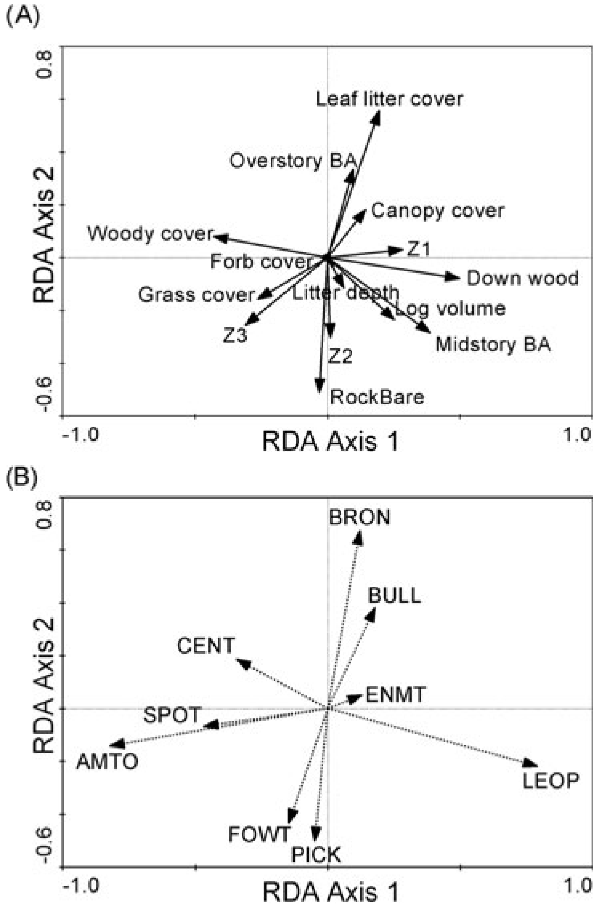

Figure 3. Relationships among 14 habitat variables (A) and position of nine amphibian species (B) on RDA Axis 1 and 2, derived from nine restored pine woodlands and three unrestored controls sampled over 3 years (1999–2001) in the Ouachita Mountains of western Arkansas, U.S.A. See text for complete descriptions of habitat variables. Species were BRON, bronze frog; BULL, bullfrog; CENT, central newt; AMTO, dwarf American toad; ENMT, eastern narrowmouth toad; FOWT, Fowler's toad; LEOP, southern leopard frog; PICK, pickerel frog and SPOT = spotted salamander.

Reptiles

We found overall reptile captures were greater in restored woodlands than controls. Other studies have found greater abundance or diversity of reptiles in forests subjected to moderate, ground-level burns (e.g., Means & Campbell 1982; Mushinsky 1985; Moseley et al. 2003). The physiology of reptiles is dependent on ambient temperature and physiological performance for many species is maximized within a narrow range of temperatures (e.g., Waldschmidt & Tracy 1983; Grant & Dunham 1988). Woodland stands in our study had less midstory BA and less canopy cover that allowed more sunlight to reach the forest floor, which may influence abundance of some reptiles (Lunney et al. 1991). The more open conditions of woodlands combined with shady areas created by residual trees provided a patchwork of warm sunny areas and cooler shady spots, and these conditions may have provided thermoregulatory benefits by providing two thermal microhabitats in the same forest stand.

The greater numbers of reptiles we captured in woodlands than in controls were partially attributed to greater captures of fence lizards in woodlands (four times greater). In hardwood forests, Greenberg and Waldrop (2008) found that high-intensity burns also resulted in greater reptile and fence lizard abundance compared with unburned stands. Although sample size was not adequate for analysis ($n = 12$ individuals) we captured six-lined racerunners exclusively in restored stands (five of the nine woodland stands). Six-lined racerunners are generally associated with open, xeric habitats throughout their range (e.g., Fitch 1958) and have been found to be most abundant in stands that are burned frequently, including annually (Means & Campbell 1982; Mushinsky 1985).

Among snakes, the southern copperhead was the most frequently captured species in both woodlands and controls. Similarly, Ford et al. (1991) found that southern copperheads were the most abundant species in upland pine habitats of eastern Texas. We found captures of Great Plains rat snakes significantly greater in restored stands than controls. However, we found no significant differences in captures between woodlands and controls for 22 of 24 snake species, although captures were just above significant ($p = 0.05–0.10$) for eastern coachwhips and red milk snakes. Nevertheless, habitat associations indicated eastern coachwhips, eastern hognose snakes, southern black racers, and Great Plains rat snakes were associated with areas having less canopy cover, less midstory BA and more ground-level vegetation; these habitat conditions were consistent with restored woodlands. Therefore, these large vertebrate-consuming snakes are likely to benefit from restoration of pine woodlands.

For some larger, vertebrate-consuming snakes, woodlands may not only provide thermal benefits but may provide more abundant prey. Reducing BAs of second-growth forests (via partial harvesting) in the Ouachita Mountains led to increased soft and hard mast production, increased down woody material, and increased understory vegetation, which contributed to a 4- to 6-fold increase in small mammal abundance (Perry & Thill 2005). Furthermore, Masters et al. (1998) found a 2- to 4-fold increase in total small mammal abundance in restored pine woodlands compared to unrestored control stands similar to the ones in our study. The greater abundance of small mammals not only provides more prey but also the burrowing of small mammals likely provides more burrows for fossorial reptiles and amphibians to occupy. Thus, woodlands likely provide greater prey resources for the larger snakes and may provide more burrows for semi-fossorial species such as northern scarlet snakes (*Cemophora coccinea copei*).

Not all reptiles respond favorably to woodland restoration or burning (e.g., Lunney et al. 1991; McLeod & Gates 1998). Some snake species, including western worm snakes, redbelly snakes, western ribbon snakes (*T. proximus proximus*), western cottonmouths (*A. piscivorus leucostoma*), and brown snakes, may be associated mostly with aquatic, mesic, or cool and moist microhabitats (Trauth et al. 2004). For example, McLeod and Gates (1998) found that western worm snakes, brown snakes, and garter snakes (*Thamnophis sirtalis sirtalis*) were more abundant in unburned stands than burned stands. Without burning, some species of small litter-dwelling snakes, such as redbelly snakes and ringneck snakes may be more abundant in thinned forests than in unthinned forests or clearcuts (Todd & Andrews 2008). However, we could not distinguish effects of thinning on reptiles from effects of burning because woodland restoration entailed both treatments. We found captures of rough green snakes significantly greater in controls than in woodlands. This arboreal species lays eggs in hollows of small trees and typically perches about 2 m above the ground while hunting in highly branched vegetation (Plummer 1981, 1990). The lower density of midstory trees in woodlands and possible reductions of small hollow trees from midstory removal and burning may have contributed to lower captures of rough green snakes in woodlands.

Amphibians

Although some studies suggested burning negatively affects amphibians (e.g., Jones et al. 2000; Schurbon & Fauth 2003), others found either positive effects, failed to detect significant effects, or found mixed effects whereby some species benefit and others decline (e.g., Means & Campbell 1982; Greenberg 1994; Ford et al. 1999; Moseley et al. 2003). We found no difference between controls and woodlands in captures of all amphibians combined, anurans, or all salamanders combined. Furthermore, for every amphibian species with a sufficiently large sample size, we found no significant differences in captures between woodlands and controls.

Compared to reptiles, many amphibians (especially salamanders) prefer moist sites such as northern or eastern aspects (Harper & Guynn 1999), lower slopes (Ford et al. 1999) or areas of deep leaf litter (Pough et al. 1987), and dry conditions may impair respiratory function in some salamanders (Duellman & Trueb 1994). Dense leaf litter maintains moisture and decreases in leaf litter may contribute to reduced salamander abundance (e.g., Ash 1997). Some amphibian species associated with moist and cool microclimates with abundant leaf litter may be less abundant in burned stands (McLeod & Gates 1998; Jones et al. 2000). Although we found leaf litter cover was significantly less in woodlands than controls, the difference was only 3%, and down wood cover and volume of down logs did not differ between controls and woodlands. However, litter depth in controls was 61% greater than in woodlands. Pough et al. (1987) found that above-ground activity of salamanders was positively correlated with both litter depth and density of understory vegetation. Thus, the greater ground-level vegetation (grass cover, forb cover, Z1) in woodlands may have compensated for less litter depth by providing cover and retaining ground-level moisture.

We found woodland restoration did not appear to negatively affect captures of central newts and spotted salamanders. Furthermore, all species of salamanders we captured were present in burned stands. However, evidence suggested western slimy salamanders may have been negatively affected by woodland restoration. Although we captured 29, they were captured in only four stands (three unmanaged controls and one stand that was burned 3 years prior), which did not allow analysis, but 97% of captures were in the three control stands. Similarly, Means and Campbell (1982) compared herpetofauna captures in fire-maintained longleaf pine stands with captures in forests that had succeeded to hardwood due to fire suppression; they found slimy salamanders were captured almost exclusively in the hardwood forests. The western slimy salamander does not have an aquatic stage; they lay their eggs in moist sites, such as underground or under rotting logs (Trauth et al. 2004). Thus, they may be more susceptible to dry conditions than many other amphibians. Regardless, the western slimy salamander is considered common, widespread, and abundant in Arkansas (NatureServe 2007).

Nearly all of our restored woodland stands contained greenbelts that surrounded ephemeral stream drains. Although these greenbelts were burned when the surrounding stands were burned, they were neither thinned nor subjected to midstory reduction and they provided denser canopy cover than the surrounding stands. Furthermore, greenbelts were typically in lower elevation portions of stands and were typically bowl-shaped in topography; thus, they were likely more mesic than the surrounding stand. Greenbelts frequently do not burn as intensely as the surrounding treated stand because of moist and/or shadier conditions. Ford et al. (1999) suggested woodland salamanders were not affected by prescribed burns because they occurred primarily in riparian and midslope areas where leaf litter burned only slightly. Thus, greenbelts may act as refugia for some amphibians that cannot tolerate drier conditions in the surrounding woodland stand.

Other studies suggest that amphibian species richness decreases with increasing distance to the nearest permanent or intermittent water source (e.g., Greenberg 1993; Schurbon & Fauth 2003). We found no significant correlation between the distance to semi-permanent water sources (ponds and second-order streams) and abundance of any amphibian species. However, we could not ascertain the presence of small ephemeral pools within or adjacent to our study stands.

Fires that burn across topographically diverse landscapes are subjected to varying slopes, aspects, and moisture content of vegetation, which can lead to varying fire intensities and contribute to heterogeneous landscape conditions. Historically, the Ouachita region likely consisted of a mosaic that included both fire-maintained habitats (woodlands, savannas, and prairies) and areas of denser forest on mesic or north-slope sites that burned less frequently or less intensely. This diversity of communities likely contributed to herpetofaunal diversity. Consequently, a landscape that retains both pine woodlands and some component of denser, less-intensely burned forest (in the form of greenbelts or separate stands) would likely maintain greater overall herpetofaunal diversity across the landscape. Large, landscape-level prescribed fires (2000–5000 ha) that are ignited by helicopters, as currently implemented in the Ouachita Mountains, may also contribute to this habitat diversity by burning heterogeneous patterns, which are influenced by topography.

Implications for Practice

- Woodland restoration creates more open forest habitats that are favored by many reptiles but may not be optimal for all herpetofaunal species, including some salamanders. Thus, decisions regarding woodland restoration depend on which species management is targeting.
- If maintaining herpetofaunal diversity across landscapes is the goal of management, woodland restoration, while retaining unharvested or unthinned patches of forest in the form of buffers around stream drains or separate unthinned forest stands, would likely contribute to greater herpetofauna diversity across a landscape.

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