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Herpetofaunal species richness responses to forest landscape structure in Arkansas

Craig Loehle [a,*], T. Bently Wigley [b], Paul A. Shipman [c], Stanley F. Fox [d], Scott Rutzmoser [e], Ronald E. Thill [f], M. Anthony Melchiors [g]

[a] *National Council for Air and Stream Improvement Inc., 552 S. Washington St., Suite 224, Naperville, IL 60540, USA*
[b] *National Council for Air and Stream Improvement Inc., PO Box 340317, Clemson, SC 29634-0317, USA*
[c] *Department of Biological Sciences, Rochester Institute of Technology, 85 Lamb Memorial Drive, Rochester, NY 14623, USA*
[d] *Department of Zoology, Oklahoma State University, Stillwater, OK 74078, USA*
[e] *School of Forestry and Wildlife Sciences, Auburn University, 108 M. White Smith Hall, Auburn, AL 36849, USA*
[f] *U.S. Forest Service, Southern Research Station, Wildlife Habitat and Silviculture Lab,*
506 Hayter Street, Nacogdoches, TX 75965-3556, USA
[g] *Weyerhaeuser Company, Western Timberlands Research, PO Box 9777, Federal Way, WA 98063-9777, USA*

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Abstract

Species accumulation curves were used to study relationships between herpetofaunal richness and habitat characteristics on four watersheds in Arkansas that differed markedly with respect to management intensity. Selected habitat characteristics were estimated for stands containing the sample points and within buffers with radii of 250, 500 m, and 1 km surrounding the sample points. Richness of all three herpetofaunal groups (amphibians, reptiles, and all herpetofauna) was greater in hardwood forests than in pine or mixed pine–hardwood. For all three groups, the youngest forest age class had the most species. For amphibians and total herpetofauna, richness declined as stand ages increased. Reptiles had the highest richness at sample points with the lowest class of stand basal area (BA), whereas amphibians were richest at points having the highest BA. In contrast to expectations, there was no effect of distance from water on richness of any taxa; however, we may have had incomplete data on the spatial distribution of small ponds outside the sample plots because they were not recorded in the GIS data. Results for distance to roads were ambiguous, but with more separation of compared curves as more plots were sampled, a positive influence of road proximity was suggested. There was a positive effect of buffer age diversity at the 250 m scale for all three herpetofaunal groups, but less so at scales >250 m except for amphibians, which also showed a positive effect at the 1 km scale. The two most intensively managed watersheds had higher species richness than the two less intensively managed watersheds for reptiles, amphibians, and both groups combined. In this study landscape, where urban and agricultural influences were minimal, we did not observe negative impacts of forest management and associated

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* Corresponding author. Tel.: +1 630 579 1190; fax: +1 630 579 1195.
E-mail address: craigloehl@aol.com (C. Loehle).

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activities, and local habitat heterogeneity created by silviculture often had a positive effect on herpetofaunal species richness.

Keywords: Herpetofaunal; Arkansas; Silviculture; Riparian; Fragmentation; Roads

1. Introduction

Many authors (e.g., Alford and Richards, 1999; Houlahan et al., 2000; Young et al., 2001) have reported that amphibians are in decline worldwide, although the reasons for this decline are not yet agreed upon (Collins and Storfer, 2003). Subsequently, it has been reported that reptiles also are in worldwide decline (Gibbons et al., 2000). Habitat fragmentation due to road construction (Saunders et al., 2002) and commercial forestry operations have been shown in some cases to negatively affect these species, at least locally and in the short-term (Ash, 1996; Enge and Marion, 1986; Gibbs, 1998a; Martin and McComb, 2003; Petranka et al., 1993). An alternative body of theory suggests that greater habitat diversity should increase species diversity (Rosenzweig, 1995). Therefore, commercial forestry, by creating a range of forest structural and microclimate conditions (Seymour et al., 2002), might help maintain herpetofaunal species diversity (Fox et al., 2004; Shipman et al., 2004). Thus, an open question is the extent to which commercial forestry promotes herpetofaunal diversity by creating a greater range of forest age classes, canopy structures, and types at the landscape scale, versus negatively affecting herpetofauna through impacts from roads, reduced amounts of older forest, altered stand structures, and fragmentation of suitable habitat.

Empirical data on effects of habitat fragmentation per se separate from area effects (Harrison and Bruna, 1999) are scant. To date, studies of herpetofauna and landscape structure have produced conflicting results. For example, land cover diversity was found by Nogués-Bravo and Martínez-Rica (2004) to weakly predict an increase in reptile but not amphibian species richness. Area-sensitivity of reptiles and amphibians on true islands has been demonstrated, but could not be predicted from traits such as body size, rarity, or dispersal ability (Hager, 1998). Russell et al. (2004) found that geology and topography were predictive of Columbia torrent salamander abundance and distribution, whereas age or composition of riparian forest was not predictive. In another study, Russell et al. (2002b) found no long-term difference in species richness or abundance of 15 of 17 species of reptiles and amphibians at isolated wetlands adjacent to unharvested or clearcut areas in South Carolina. Leiden et al. (1999) documented the presence of 72 species of herpetofauna in a heterogeneous, managed forest landscape in South Carolina including 7 species of special concern in South Carolina. Leiden et al. (1999) noted that this constituted the highest recorded biodiversity of amphibians and reptiles in South Carolina with the exception of the Savannah River Site, an area that was 10 times larger and had been studied since the 1950s. Renken et al. (2004) found that while timber harvesting produced local (mostly) negative effects on amphibians in Missouri Ozark forests, these effects could not be detected at larger scales for either amphibians or reptiles.

To further clarify relationships between herpetofaunal species richness and habitat structure, we studied these factors at multiple spatial scales on four Arkansas watersheds that differed markedly with respect to management intensity. Comparisons of herpetofaunal community structure among these same four watersheds and along presumed environmental gradients within them have been reported elsewhere for amphibians (Fox et al., 2004) and reptiles (Shipman et al., 2004). We estimated richness of reptiles, amphibians, and total herpetofauna for each of the four watersheds and as a function of stand type, age, and basal area; distance to roads and water; stand age heterogeneity at increasing distances from study plots; and watershed-level management intensity.

2. Methods

2.1. Study areas

The study was conducted on four 1500–4000 ha watersheds under different intensities of management in Garland and Saline counties near Hot Springs, Arkansas. The watersheds are located in Bailey Province 231, the Ouachita Mixed Forest, Meadow Province, characterized by mountains eroded from sedimentary rock formations with ridges reaching maximum altitudes of about 790 m. Major soils are ultisols that are often stony. Average annual temperature is about 17 °C. Average annual precipitation is about 1050 mm. At the time of the study, vegetation was dominated by oak–hickory–pine forest (*Quercus–Carya–Pinus*), and managed loblolly (*P. taeda*) and shortleaf (*P. echinata*) pine forests. Even in mixed stands, pine often constituted as much as 40% of the overstory cover. The four study watersheds differed markedly with respect to factors such as mean rotation lengths, forest type diversity, stand sizes and ages, and the amount of mature forest inclusions (Tappe et al., 2004a).

Little Glazypeau, a 2273 ha watershed located 22 km southwest of the other three watersheds (that were contiguous) and managed largely for sawlog production by Weyerhaeuser Company, represented the most intensively managed watershed. Much of the second-growth shortleaf pine–hardwood forest that originally covered this watershed had been harvested and planted to loblolly pine plantations of 9–142 ha. During a typical even-aged rotation, these plantations would be thinned twice, pruned to 5–8 m high, fertilized, and harvested at 30–35 years. The remaining, selectively harvested forests in the watershed occurred on rocky ridgetops and steep slopes, and within streamside management zones (SMZs) that were retained for water quality protection and to provide habitat diversity for wildlife.

South Alum, a 1500 ha experimental section of the Ouachita National Forest that had not been harvested for >40 years, represented the least intense level of silviculture. Thus, South Alum consisted of mature forest over most of the area.

Bread Creek and North Alum fell between these extremes of forest management intensity and were 1535 and 3961 ha, respectively. Records of timber management activities and present composition of number, age, and distribution of pine (mostly shortleaf pine) plantations indicated that Bread Creek was less intensely managed than North Alum (Tappe et al., 2004a). Bread Creek was primarily USDA Forest Service (USFS) land, and had been managed according to prevailing Forest Service standards and guidelines for several decades, whereas North Alum was of mixed ownership, with about half of the area under Weyerhaeuser ownership (intensive pine plantation management) and half under USFS management. North Alum displayed characteristics of a diverse range of management activities, ranging from no management along steeper slopes and higher elevations to intensively managed pine plantations, mainly at lower elevations. Thus, the watersheds, in order of increasing intensity of timber management, were South Alum (M1), Bread Creek (M2), North Alum (M3), and Little Glazypeau (M4).

2.2. *Herpetofaunal sampling plots*

We surveyed amphibians and reptiles using area-constrained searches on a subset (56) of 75–235 circular plots/watershed that were established each year for breeding bird surveys (Tappe et al., 2004b). The herpetofaunal sampling plots, which also were circular with a 20 m radius (0.13 ha), were nested and centered within the 50 m radius bird sampling plots. Bird plots were located at 200 m intervals along >100 km of parallel transects (oriented approximately north–south across prevailing topography) that were established in 1995 over the four watersheds. These same transects were used in 1996, but new plots were established by shifting plot centers 100 m along the transects. In 1997, approximately 110 km of new transects were established between those of 1995, and in 1998 new plots were established along these new transects as in 1996. The subset of plots used for herpetofaunal surveys were selected to represent a cross-section of slopes, aspects, forest types, stand conditions, and aquatic habitats.

In each watershed, we annually selected hereptofaunal sampling plots to ensure that at least 12–15 of the 56 plots on the transects were in aquatic habitats, which consisted of springs, streams, and human-made ponds that had been established to benefit wildlife (USDA Forest Service wildlife ponds) or as sources of water for fighting fire. We established four additional plots per watershed per year off the transects at aquatic habitats (ponds or at wide pools in the high-order streams at the bottom of a watershed) to ensure that we had equivalent sampling effort for these aquatic habitats. Plots at ponds were established so that approximately half of each plot was over water and half over land.

2.3. *Herpetofaunal surveys*

Trained crews of 3–5 individuals surveyed all plots during daylight hours five times per year from May 1995 to March 1999 during early May, late May, mid-June, early October, and early the following March. Plots were surveyed thoroughly using standard methods (Heyer et al., 1994) by visually searching vegetation and the ground surface, and by lifting cover objects (rocks, logs, and debris); the latter were replaced to minimize impacts on subsequent surveys. We sampled plots in deep water by having one person move slowly through the water in chest waders and carefully scan the water and shoreline for animals. Some animals in the water were captured in this way by use of a dipnet. Animals that were seen and identified were tallied; those that required capture for identification were released at the point of capture before leaving the plot. Additionally, any anurans calling on the plot, but not seen, were identified by their call and counted. Sample design was not adequate to sample aquatic turtles, and the single individual encountered was not included.

We pooled amphibian and reptile count data across the five sampling periods within each year. Because plots were revisited five times and the data were pooled to increase reliability, the same individuals may have been recorded more than once. Therefore, we used only presence on a plot and made no attempt to evaluate abundance effects, although relative abundance has been reported elsewhere (Fox et al., 2004; Shipman et al., 2004). Unidentified individuals made up a small fraction of the observations and were dropped from all analyses. Data collected during the first year (1995) from South Alum and North Alum also were excluded from analyses due to differences in sampling effort by former collaborators, and data from other plots were discarded when five surveys per year were not attained. Thus, analyses presented here were based on data from 696 plots, each representing data from five pooled surveys per year.

2.4. *Habitat data*

For each sample point, we characterized habitat at the stand, neighborhood, and buffer scales using data from a variety of sources. We used Albers coordinates for plot locations and an Albers Equal Area projection for all data. Stand-level parameters were derived from landowner-provided inventory data collected for the stand containing the sample point. Thus, we defined stands operationally as forest management units and assumed that their inventory data were representative of the wildlife plots within them. The inventory data included forest age, forest type, and basal area (m^2/ha). Neighborhood parameters were computed over various distances from the plots using USGS 1:24,000 data layers analyzed with GIS (ArcView GIS 3.3 Spatial Analyst extension), and included distance to nearest road and distance to nearest water. At the buffer scale, we estimated area-weighted standard deviation of forest age (SDA) using Fragstats (McGarigal and Marks, 1995) and Patch Analyst 3.1 extension for ArcView GIS (Elkie et al., 1999) within 250, 500 m, and 1 km circular buffers centered on the plots.

We lacked forest inventory data for portions of some circular buffers that extended beyond the border of our study area. For such cases, we used aerial photographs (USGS National Aerial Photography Program) collected during the studies to estimate forest characteristics for all properties within 1 km of each study area. Although we were unable to extract BA from the aerial photographs, we were able to estimate age and dominant forest type by dividing the properties outside the study areas into units of homogeneous cover and visually comparing these units with known locations for which we had forest inventory data. By finding stands in the managed forest that were similar to the unknown forests we were able to estimate the age and dominant forest type. In rare cases the property surrounding the managed forest consisted of pastures or included residential development; these areas were classified as nonforest of age 0.

For each of the stand, neighborhood, and buffer variables of interest, we divided the sample points into separate categories or "bins", and for each bin we then developed a separate species accumulation curve (see species richness methods below). The number of bins and thresholds used for each bin or category differed among habitat variables and were selected whenever possible to achieve approximate parity in plot numbers. Bins for forest age class were ≤ 20, >20 to ≤ 40, >40, and >80 years. Too few plots (only 39) were available to create an age class of ≤ 10 years and no recently clearcut stands were sampled (although some stands ≤ 5 years old were available). For total BA, we assigned plots to categories of ≤ 13.8, >13.8 to ≤ 18.4, and >18.4 m^2/ha BA. For forest type, we used three bins, including pine ($>75\%$ pine BA), hardwood ($<25\%$ pine BA), and mixed pine–hardwood forest types (25–75% pine BA). For distance from plot center to the nearest road and water we used bins of ≤ 70 and >70 m. At the buffer scale, we used bins of ≤ 20 and >20 years SDA (thresholds picked to achieve rough parity in group plot numbers) for 250 and 500-m buffers and bins of ≤ 30 and >30 years SDA for 1 km buffers. We also binned plots by watershed, i.e., separately for watersheds M1, M2, M3, and M4.

2.5. Species richness methods

Our particular interest in this study was the assessment of relationships between landscape structure and measures of biodiversity as represented by species richness of amphibians, reptiles, and total herpetofauna. In contrast to properties such as basal area, which can be measured with some precision on any given piece of ground, diversity is a function of scale of measurement and number of samples. For example, it is possible to evaluate treatment effects on richness at the plot scale, but these results may not represent responses at the landscape scale, particularly when there are few species per plot. Plot-level species counts do not allow consideration of the extent to which species are different from plot to plot. Thus, it is necessary to take into account the sampling properties of species on a landscape.

The consequence of sampling a larger area or more plots is typically to include more habitats, hence more species. This leads to the well-known species–area relationship, $S = cA^z$, where c and z are parameters, S is the number of species, and A the area. Typically this relationship is used with complete (or nearly complete) floral or faunal lists for areas (e.g., islands) of different size (for examples, see Rosenzweig, 1995). In this study, we instead used the related species accumulation function $S = cN^z$, where N is the number of sample plots because all plots were sampled using a standard method and were the same size.

We used the sample-based rarefaction method (Gotelli and Colwell, 2001; Koellner et al., 2004) to obtain the expected value for S for different-sized sets of plots (e.g., sets of 10, 11, 12, etc. plots up to the total available for each bin). For example, for the 10-plot group, we selected 30 samples of 10 plots at random (without replacement) from the entire universe of available plots and computed the mean number of species over these 30 replicates. This was repeated at each N. This approach smoothed the data, resulting in an excellent fit to the species accumulation model (Colwell and Coddington, 1994). The goal was not to estimate true S per se, but to develop species accumulation curves that could be overlaid for comparison. This approach allowed us to evaluate how species were added as sampled area encompassed more area within each bin. Potential abundance effects (i.e., more species because there are more individual animals per plot) did not affect our results. Thus, when two species accumulation curves were overlaid, we interpreted the higher curve to be more species rich. Curves for bins or watersheds that had a larger area, and subsequently more plots, extended further; however, we compared the curves only at the highest point of the shortest curve. Our null hypotheses were that species accumulation curves for each habitat variable bin would be coincident, with larger bins with more plots simply having a longer but not higher curve.

After rarefaction, we fitted the data and estimated asymptotic 95% confidence limits using nonlinear least squares with optimization software available in Mathematica (http://www.wolfram.com). This has been shown to be superior to using a linearized fitting method (Rosenzweig, 1995). Because of the large number of plots, the fit to the rarefaction curves usually was excellent ($R^2 > 0.94$) and even very small differences in c and z (and therefore in S) were statistically significant. However, if one habitat type had an accumulation curve predicting 8 species and another had a curve predicting 8.1 species, we would not consider this difference to be biologically meaningful. This is, of course, the common problem of distinguishing between statistical and biological significance. Therefore, we did not declare a difference between two habitats or classes of plots unless the critical distance between the curves (at the highest point of the shortest curve) was ≥ 2 species.

We also used the species accumulation curves to decipher the contribution of various habitat components to diversity (e.g., Olszewski, 2004). If each habitat type has a unique set of species, then plots for the individual types will fall below the plot utilizing samples from all the types. This represents additive diversity (Olszewski, 2004; Veech et al., 2002), which suggests that more habitat types will yield higher overall richness. In contrast, if some habitat types contain a subset of species found in another type, a combined sample or mixed landscape will be less diverse on a per unit area basis than the richest type alone and the combined sample curve will fall between the two individual curves. This is a dilution effect which suggests that more habitat types will not produce more diversity.

3. Results

For our analyses, we used 19 amphibian and 32 reptile species found on the plots used in our study, including 10 frog and toad, 8 salamander, 7 lizard, 2 turtle, and 23 snake species (Table 1).

Table 1
Amphibian and reptile species identified on the study watersheds

Scientific name	Common name
Frogs and toads	
Acris crepitans	Cricket frog
Bufo americanus	American toad
Bufo woodhousei	Woodhouse's toad
Gastrophryne carolinensis	Eastern narrowmouth toad
Hyla chrysoscelis	Gray treefrog
Pseudacris crucifer	Spring peeper
Pseudacris streckeri	Strecker's chorus frog
Pseudacris triseriata	Upland chorus frog
Rana clamitans	Green frog
Rana utricularia	Southern leopard frog
Salamanders	
Ambystoma annulatum	Ringed salamander
Ambystoma maculatum	Spotted salamander
Desmognathus brimleyorum	Ouachita dusky salamander
Eurycea multiplicata	Many-ribbed salamander
Hemidactylium scutatum	Four-toed salamander
Notophthalmus viridescens	Central newt
Plethodon albagula	Western slimy salamander
P. serratus	Southern redback salamander
Lizards	
Anolis carolinensis	Green anole
Eumeces anthracinus	Coal skink
Eumeces fasciatus	Five-line skink
Eumeces laticeps	Broadhead skink
Scincella lateralis	Ground skink
Sceloporus undulatus	Northern fence lizard
Cnemidophorus sexlineatus	Six-line racerunner
Turtles	
Terrapene carolina	Eastern three-toe box turtle
Terrapene ornata	Ornate box turtle
Snakes	
Agkistrodon contortrix	Copperhead
Agkistrodon piscivorus	Cottonmouth
Carphophis vermis	Western worm snake
Coluber constrictor	Black racer
Crotalus horridus	Timber rattlesnake
Diadophis punctatus	Western ringneck snake
Elaphe emoryi	Great Plains ratsnake
Elaphe obsoleta	Black ratsnake
Heterodon platirhinos	Eastern hognose
Lampropeltis getula	Speckled kingsnake
Lampropeltis triangulum	Milksnake
Masticophis flagellum	Coachwhip
Nerodia erythrogaster	Yellowbelly water snake
Nerodia rhombifer	Diamondback water snake
Nerodia sipedon	Midland water snake
Opheodrys aestivus	Rough green snake
Sistrurus miliarius	Western pigmy rattlesnake
Storeria dekayi	Brown snake
Storeria occipitomaculata	Northern redbelly snake
Tantilla gracilis	Flathead snake
Thamnophis sirtalis	Red-sided garter snake
Virginia striatula	Rough earth snake
Virginia valeriae	Smooth earth snake

3.1. Stand scale

The mean age of plots in the hardwood type (60.4 years) and mixed pine–hardwood type (65.9 years) did not differ significantly, but the pine plot mean age (46.1 years) differed from the other two based on Mann–Whitney U-tests at the 0.05 significance level.

After rarefaction, species accumulation curves of amphibian, reptile, and total herpetofauna for the three forest types and for all forest types combined fit with $R^2 > 0.98$ in all cases. For amphibians, reptiles, and total herpetofauna, species richness was greatest in the hardwood type (Fig. 1). However, we had fewer plots in hardwood forests than in other forest types, so this result is not robust. For reptiles and amphibians (Fig. 1a and b), the species accumulation curves suggested equivalence of the pine and pine–hardwood no recently clearcut stands were sampled (although some stands ≤5 years old were available). For total BA, we assigned plots to categories of ≤13.8, >13.8 to ≤18.4, and >18.4 m^2/ha BA. For forest type, we used three bins, including pine (>75% pine BA), hardwood (<25% pine BA), and mixed pine–hardwood forest types (25–75% pine BA). For distance from plot center to the nearest road and water we used bins of ≤70 and >70 m. At the buffer scale, we used bins of ≤20 and >20 years SDA (thresholds picked to achieve rough parity in group plot numbers) for 250 and 500-m buffers and bins of ≤30 and >30 years SDA for 1 km buffers. We also binned plots by watershed, i.e., separately for watersheds M1, M2, M3, and M4.

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The mean age of plots in the hardwood type (60.4 years) and mixed pine–hardwood type (65.9 years) did not differ significantly, but the pine plot mean age (46.1 years) differed from the other two based on Mann–Whitney *U*-tests at the 0.05 significance level.

After rarefaction, species accumulation curves of amphibian, reptile, and total herpetofauna for the three forest types and for all forest types combined fit with $R^2 > 0.98$ in all cases. For amphibians, reptiles, and total herpetofauna, species richness was greatest in the hardwood type (Fig. 1). However, we had fewer plots in hardwood forests than in other forest types, so this result is not robust. For reptiles and amphibians (Fig. 1a and b), the species accumulation curves suggested equivalence of the pine and pine–hardwood

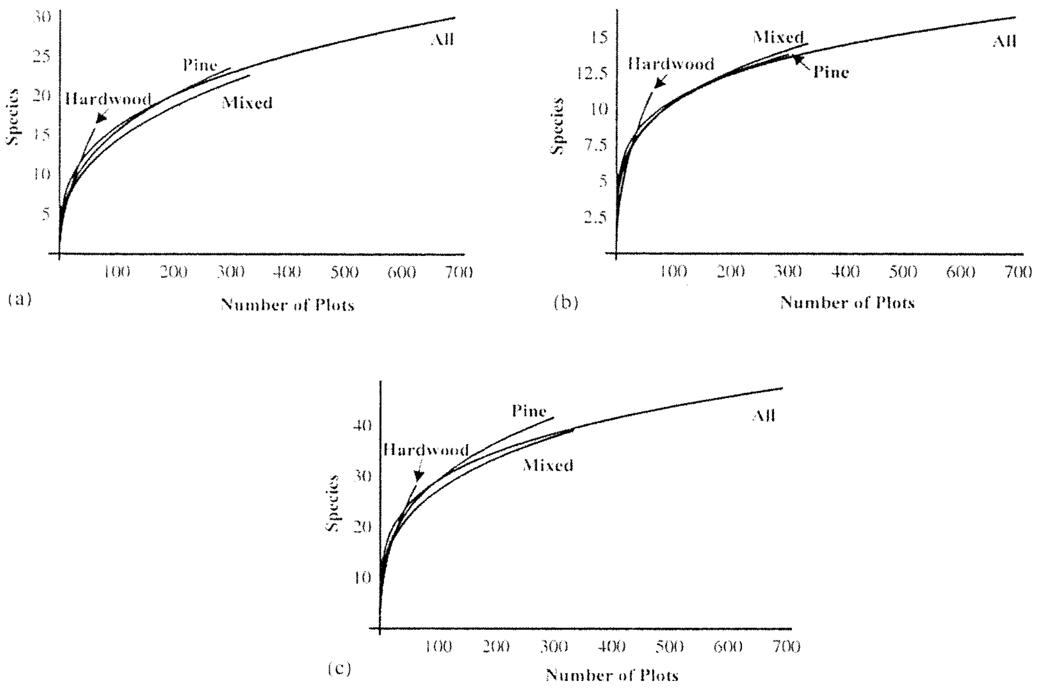

Fig. 1. Stand type effects on (a) reptiles, (b) amphibians and (c) herpetofauna.

types as the curve for all forest types combined overlapped the curves for the individual forest types (differences were <2 sp.). For total herpetofauna, the pine type was more species rich than the mixed pine–hardwood type, and dilution was evident (Fig. 1c).

After rarefaction, species accumulation curves for the forest age classes (≤20, 20–40, >40, and >80 years) fit with $R^2 > 0.98$ in all cases except one curve with $R^2 = 0.96$ (Fig. 2). For reptiles, the ≤20-year age class had the most species, followed by the >80- and >40-year classes (which did not differ from each other) (Fig. 2a). The intermediate age class had the lowest richness. For amphibians, the curves for the age classes did not differ by the minimum two species except that the ≤20-year class was richer than the two older classes (Fig. 2b). For total herpetofauna, curves differed with a strict ordering of diversity by age class (≤20 most diverse, then >20 to ≤40 years, then >40 and >80 years; Fig. 2c). Thus, the ≤20-age class was richest for all three herpetofaunal groups.

After rarefaction, species accumulation curves for the BA bins fit with $R^2 > 0.98$ in all cases even though fewer plots were available for the analysis due to the lack of inventory data on some plots. Reptiles were more species rich in the lowest-BA stands (≤13.8 m^2/ha; Fig. 3a), amphibians more rich in the highest-BA (>18.4 m^2/ha; Fig. 3b) stands, and richness of total herpetofauna was equivalent in the highest- and lowest-BA stands, both of which were richer than the intermediate category (>13.8 to ≤18.4 m^2/ha; Fig. 3c).

3.2. Neighborhood scale

After rarefaction, species accumulation curves for different distances to water and roads (≤70 and >70 m) fit with $R^2 > 0.98$ for all three herpetofaunal groups. Plots ≤70 m from water did not have more species in any of the three analyses than plots >70 m from water (Fig. 4). Results for roads, however, were ambiguous as the species accumulation curves for all three herpetofaunal groups crossed (Fig. 5). Thus, plots farther from roads were more diverse when only a few plots were sampled; however, when >120 plots were sampled the zone near roads was more diverse by at least 2 species at the largest number of plots. The

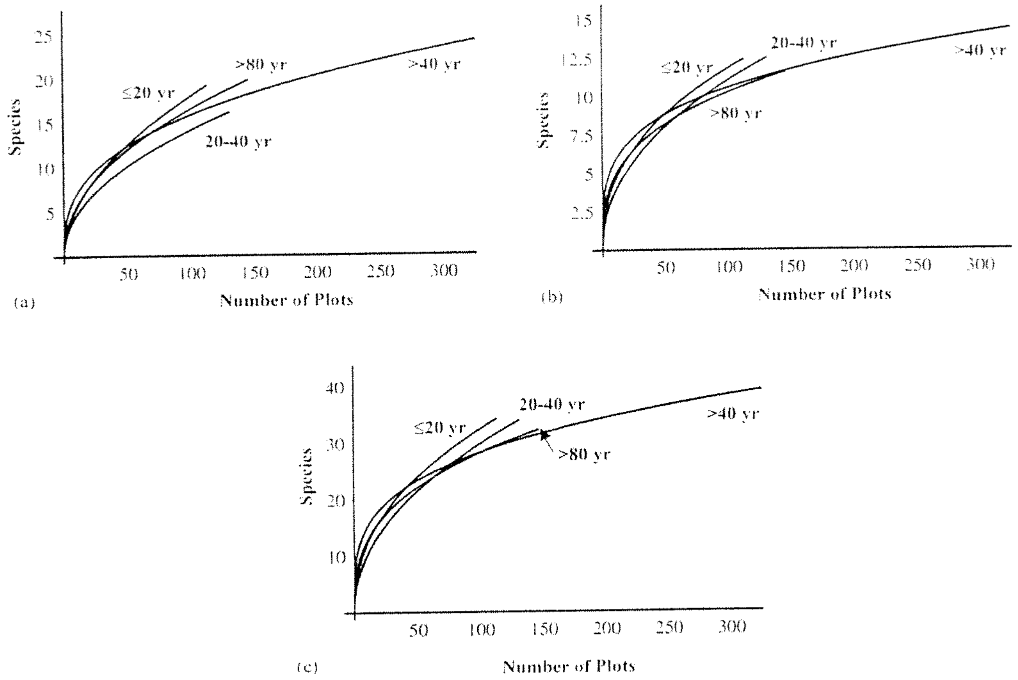

Fig. 2. Stand age effects on (a) reptiles, (b) amphibians and (c) herpetofauna.

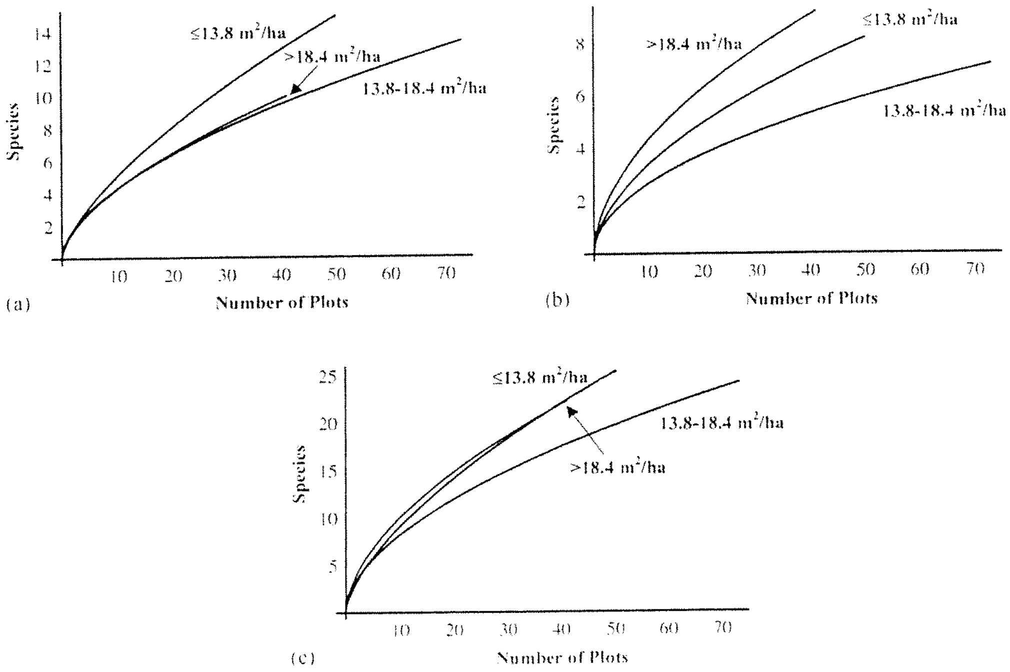

Fig. 3. Effect of total basal area (ft^2/ac) species richness on (a) reptiles, (b) amphibians and (c) herpetofauna.

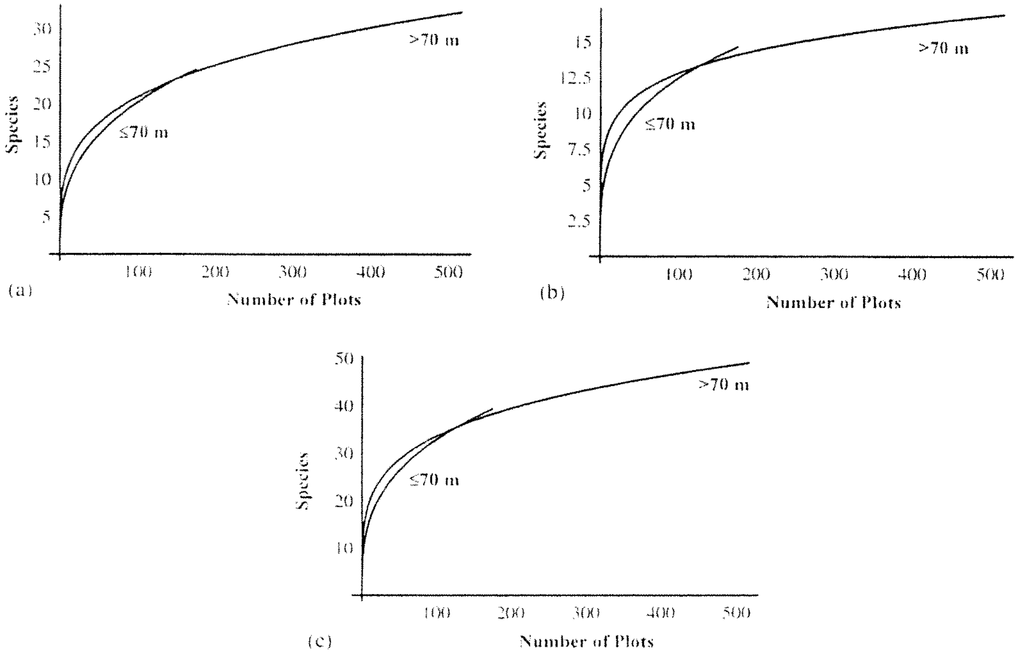

Fig. 4. Distance to water effects on (a) reptiles, (b) amphibians and (c) herpetofauna.

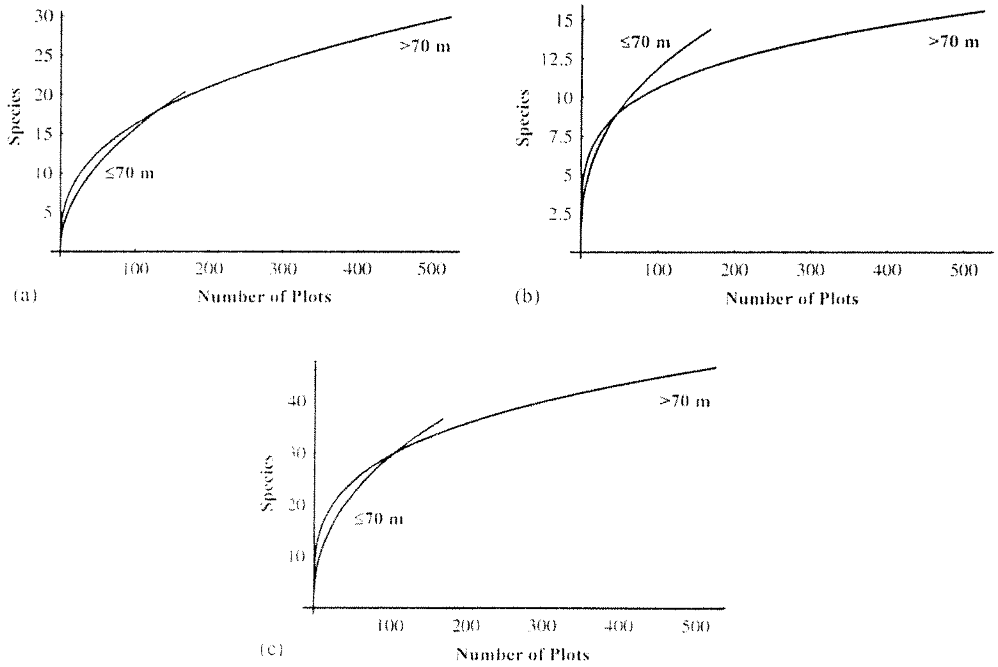

Fig. 5. Distance to roads effects on (a) reptiles, (b) amphibians and (c) herpetofauna.

Table 2
Effect on species richness of reptiles, amphibians, and total herpetofauna of standard deviation of forest age (SDA) within buffers with different radii from plot centers

Taxa	Buffer radius[a]		
	250 m	500 m	1 km
Reptiles	>20	Equal	Equal
Amphibians	>20	Equal	>30
All herpetofauna	>20	Equal	Equal

For each buffer, high or low SDA is listed if it had higher richness (>2 species difference at the highest point of the shorter curve) or equal is listed if the two curves were <2 species apart.

[a] SDA classes were <20 and >20 years for neighborhoods with radii of 250 and 500 m and <30 and >30 years for 1 km radius neighborhoods.

mean age of plots close to roads (53.9 years) did not differ ($p > 0.1$) from those farther from roads (57.8 years). The mean age of plots close to water (52.6 years) did not differ from those farther from water (58.0 years) based on a Mann–Whitney U-test at the 0.05 level. However, only 1.3% of the plots close to water were in hardwood stands, versus 11% of the plots in the zone farther from water.

3.3. Buffer scale

After rarefaction, species accumulation curves for the SDA bins fit with $R^2 > 0.98$ in all cases. For all three species groups at the 250 m scale, the buffer with a higher SDA had higher species richness (Table 2). At the 500 m scale, species accumulation curves for the two SDA categories were equivalent for amphibians, reptiles, and total herpetofauna. At the 1 km scale, amphibians were richer in the higher SDA class, but reptile and total herpetofauna richness was equivalent in the two SDA classes.

3.4. Watershed scale

For amphibians, curves for all four watersheds fit with $R^2 > 0.94$, while for reptiles and total herpetofauna, the curves fit with $R^2 > 0.98$. Because plots were laid out on similar grids, similar sampling methods were used, and the number of plots was equivalent in each watershed, no adjustment for watershed area was necessary. For reptiles, amphibians and total herpetofauna, M3, M4, or both M3 and

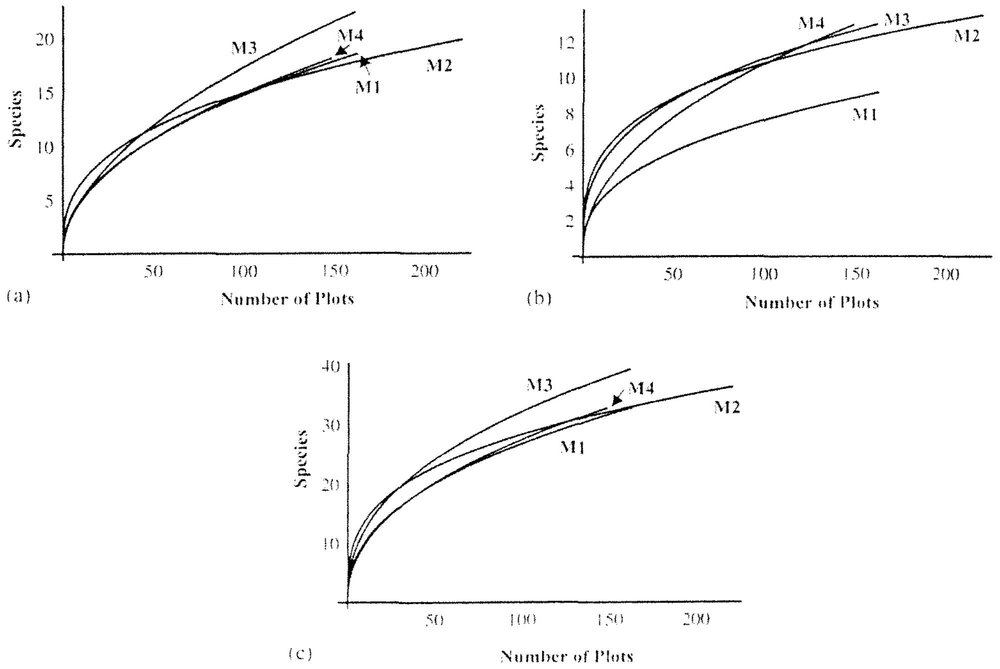

Fig. 6. Species accumulation curves for the four watersheds: (a) reptiles, (b) amphibians and (c) herpetofauna. M1–M4 indicate least to most managed watershed.

M4 had higher species accumulation curves than the two less intensively managed watersheds (M1 and M2; Fig. 6).

4. Discussion

4.1. Stand scale

In our study, hardwood forests had the most species for all three species groups, but this type had the fewest plots, rendering our finding somewhat equivocal. For reptiles and amphibians, the pine type and mixed pine–hardwood type were equivalent in richness. For total herpetofauna, the pine type was richer than the pine–hardwood type. Others have also reported higher abundances of herpetofauna in hardwood than in coniferous forests. For example, Mitchell et al. (1997) reported that amphibians were significantly more abundant in forest stands consisting of mature hardwoods than in a recent clearcut stand and a white pine plantation. DeGraaf and Rudis (1990) found that northern hardwood and red maple (*Acer rubrum*) forest supported more species than balsam fir (*Abies balsamea*) forest. They found that both diversity (H') and evenness (J') were correlated with litter depth, and both were higher in hardwood than in balsam fir stands.

The Ouachita Mountains are strongly dominated by east–west ridges. Thus, in our study landscape, many hardwood stands were on more mesic north-facing slopes or near water while pine stands were typically on drier south-facing slopes. Sampled hardwood stands were almost all not near water (although stringers of hardwoods could exist in a stand that is otherwise classified as pine or mixed). As a result, high herpetofaunal richness in this type may reflect site-specific abiotic factors more than forest composition per se; alternatively, it may reflect a combination of abiotic factors and forest composition. For example, differences among forest types in herpetofaunal assemblages in Texas were related to differences in moisture availability (Lewis et al., 2000), with greater abundances of amphibians and snakes occurring in more mesic forest types at the lower elevations. Similarly, Fleet and Autrey (1999) observed (also in Texas) that change in elevation created a natural moisture gradient across forest types that accounted for observed differences in amphibian, snake and turtle assemblages.

It might be expected that a landscape with more habitat types (as defined here) would have more species. If so, then a rarefaction graph of sample plots from all types would be above those for the individual types, indicating an additive effect. However, for amphibians we found equivalence, indicating no partitioning by forest type. For reptiles and total herpetofauna, dilution was evident. Both cases suggest that richness of these species groups would not be enhanced in a landscape containing more forest types, in contrast to usual expectations. This conclusion is qualified by our use of broad forest types (pine, hardwood, pine–hardwood), which may not adequately partition habitat attributes important to herpetofauna.

We found that the youngest and oldest forest age classes had the most reptile species. Of stands sampled, pine plots were younger than those in hardwood or mixed stands. Some reptiles are associated with open-canopy or disturbed habitats. Recently, Crosswhite et al. (2004) reported that in the Ouachita Mountains reptiles were most abundant in young, xeric clearcuts, while amphibians were most abundant in selectively harvested stands and unharvested mature forests. Four habitat parameters (canopy coverage, litter depth, woody plant cover, and large, woody debris) explained much of the variation in species composition among sample sites used by Crosswhite et al. (2004). Of course, some reptile species (e.g., arboreal lizards) are associated with structurally complex forests. Thus, a landscape composed of both old and young and, therefore, structurally variable forests would be expected to provide high levels of reptile diversity.

For amphibians we found that the youngest stands had the highest richness. The overall trend, while below the two species difference cutoff, was a ranking of richness correlating with the inverse of stand age, with a similar but stronger result for total herpetofauna. This would seem to contradict a pervasive assumption and empirical evidence that older forests provide higher quality habitat for amphibians. For example, Petranka et al. (1993) found that salamander abundance in high elevation forests of North Carolina increased with forest age up to 51–70 years after which the two variables appeared to be independent.

In mid-elevation forests, salamander richness and abundance increased with age until stands were about 120 years of age (Petranka et al., 1994). Herbeck and Larsen (1999) found that plethodontid salamander density in the southeastern Ozarks of Missouri was lowest in newly regenerated forests (<5 years old) and highest in forests >120 years old. Furthermore, terrestrial salamanders were reduced to very low numbers when mature forests (>70 years old) were intensively harvested. Not all studies show this effect, however (deMaynadier and Hunter, 1995).

Several considerations may at least partially explain our results for total herpetofauna (richer in young stands). First, we had more reptile species than amphibian species on our study landscape. Therefore, results for total herpetofauna may have been disproportionately affected by results for reptiles which were richest in young and old forests. Second, we did not have any recently clearcut stands in our sample, making the "young" class not as young as in some other studies. Third, our study landscape was historically subjected to frequent low-intensity fires and other disturbances (e.g., wind and ice storms) that promoted a shortleaf pine-bluestem (*Andropogon* spp.) type in some physiographic settings within the Ouachita Mountains. Because of this history of natural disturbance, herpetofauna communities in our landscape may be relatively resilient to disturbance, including forest harvesting, even though some species such as southern redback salamander (*Plethodon serratus*) were primarily associated with older forests (Fox et al., 2004). Regardless, our results suggest that a mix of stand ages likely will be required if land managers are to maintain all herpetofaunal species in the landscape.

Reptiles had the highest richness in the lowest-BA stands. Recently Ross et al. (2000) reported that snake abundance and species richness increased significantly with increasing removal of tree BA in hardwood forests in Pennsylvania. Adams et al. (1996) found that abundance and species richness of reptiles were significantly higher in harvested stands with reduced BA than in no-harvest stands. Because BA is typically correlated with leaf area and canopy cover, lower-BA stands typically have less shade and warmer forest floors, and thus warmer temperatures and ample basking sites. Stands with open canopies also may have increased abundance of small mammals and other prey items eaten by reptiles (e.g., Dickson and Michael, 1986; Pagels et al., 1991; Miller et al., 2004).

Amphibians responded in the opposite manner to BA probably for the same reason. Ross et al. (2000) observed that relative abundance and species richness of salamanders increased significantly with increasing BA and that >15 m^2/ha live tree BA appeared to be a threshold level for high salamander abundance. Adams et al. (1996) reported lower diversity of amphibians in stands with low BA than in no-harvest stands. Less dense stands typically are drier and warmer, and some amphibians, particularly salamanders, likely avoid them (e.g., Hicks and Pearson, 2003).

4.2. Neighborhood scale

Many species of southeastern herpetofauna have fundamental associations with moist environments and use both terrestrial and aquatic habitats during their annual cycles (Gibbons and Semlitsch, 1991). Furthermore, on managed forest landscapes, areas close to water also are typically treated as SMZs and therefore reserved from management or managed lightly. Thus, we hypothesized that plots closer to water would have higher species richness. However, at the scale of analysis possible with these data, which did not include all small water bodies (unless they fell on a sample plot) and were limited to a threshold of 70 m from water, we observed no effect of proximity to water on species richness. Of course, water bodies outside the plots that were too small to appear on the USGS maps may have affected our results, especially for amphibian species richness (e.g., Semlitsch and Bodie, 1998; Ross et al., 2000; Russell et al., 2002a). A larger sample size also might have permitted use of a smaller buffer width (≤70 m) and yielded different results. This result was not confounded by stand ages, which did not differ between the two bins.

It is possible, of course, that proximity to water may have influenced attributes of herpetofaunal communities other than species richness. Fox et al. (2004), in an ordination analysis of amphibian communities on these same four watersheds, demonstrated that both large, permanent ponds and small, often ephemeral ponds were important determinants of community structure. They concluded that amphibian community structure diverged among these four watersheds on the basis of presumed gradients of terrestrial–aquatic, elevation, and canopy cover, and that amphibian communities associated with small, often ephemeral ponds and large, permanent ponds differed in particular. Therefore, specific ways amphibian communities were structured may have differed along a terrestrial–aquatic gradient even though we found no such response for species richness.

Theory (Bissonette, 2002; Strittholt and Dellasala, 2001) and some empirical data suggest that roads should have a detrimental effect on some components of biological diversity, including herpetofauna. Roads can potentially affect herpetofauna in many ways such as through elimination of habitat, roadkill, and constraints on movements. For example, deMaynadier and Hunter (1995) noted that traffic on most forest roads was too light to elicit concerns about direct mortality of amphibians, but that forest roads could serve as physical or psychological barriers to movement. Gibbs (1998b) reported that the relative permeability of forest-road edges in southern Connecticut was much reduced in comparison to the forest interior and to edges between forest and open land. In Maine, deMaynadier and Hunter (2000) found that anuran habitat use and movements were unaffected even by 12 m-wide heavily traveled logging roads. However, salamander captures in roadside traps were only 25.9% of similarly oriented captures in paired forested controls, suggesting that the 12 m-wide road inhibited movement and perhaps occurrence. Marsh and Beckman (2004) showed that some species, but not others, had decreased density at gravel road edges in a Virginia forest, which they attributed to drier conditions.

Our results for roads, however, were ambiguous for all three taxonomic groups in spite of adequate sample size. It is unclear why we failed to find any clear negative impact on species richness from roads, particularly for amphibians, except that few plots were located exactly on a road margin. Our results were not affected by stand age. Traffic volume can significantly influence mortality and roadside populations of some amphibian species (Fahrig et al., 1995; Mazorelle, 2004). In many cases, however, road density is associated with degree of urbanization, agriculture, or eutrophication of water bodies, factors that had little to no influence in our study landscape. Most roads on our study areas were constructed primarily to support commercial forestry activities, were unpaved, and supported little traffic. Unpaved roads with low traffic volumes, which do not necessarily function as barriers for some fauna (e.g., Brock and Kelt, 2004), including selected amphibian species in some locales (e.g., Mazorelle, 2004), perhaps do not function as such for herpetofauna on our study area.

It also is possible that road density on our study areas was not great enough to cause community- and landscape-level effects for herpetofauna. For example, in a recent modeling exercise, Gibbs (2003) predicted that only in urban areas was road mortality predicted to cause significant effects for amphibians migrating <100 m from breeding sites (>10% additional mortality/year). In Ohio, Mazerolle (2004) did not detect any decreasing trend in abundance for amphibian roadside populations over an 8-year period. Interestingly, some authors (e.g., Adam and Lacki, 1993; Cromer, 1999) have documented ruts in small forest roads serving as breeding habitat for amphibians. We observed the same. Nevertheless, it is possible that with a smaller threshold for distance to nearest road (<70 m), we may have observed a road effect. And, other community parameters such as relative abundance, productivity, or specific community assemblage may have been affected even though richness was not.

4.3. Buffer scale

For buffers of 250 m radius, increased stand age diversity was associated with greater richness of all three taxonomic groups. At this scale, some species may have used more than one forest age class over daily to monthly movements. At larger scales, however, there was little benefit of forest age class diversity, which is not surprising given the limited daily movements of most reptile and amphibian species on our study area.

4.4. Watershed scale

Some authors (e.g., Petranka et al., 1993) have hypothesized that forest management activities negatively impact herpetofaunal communities. Indeed, deMaynadier and Hunter (1995) concluded that clearcut harvesting, a practice commonly used in some of our study watersheds, generally has negative short-term impacts on local amphibian populations, especially salamanders. They summarized results from 18 studies that on average documented 3.5-fold more amphibians in control sites than in recently clearcut sites. Although deMaynadier and Hunter (1995) reported that the long-term relationships between harvesting practices and amphibians were variable and could be mitigated by retention of adequate microhabitat structure, they did suggest that long-term effects in forest plantations could be significant.

In contrast to results from stand-level studies, we found that one or both of our more intensively managed watersheds had higher species richness than the two less intensively managed watersheds for reptiles, amphibians, and total herpetofauna. Many of the managed stands in these more intensively managed watersheds were pine plantations. This suggests that at the watershed scale, forest management (including plantation management) did not diminish and perhaps enhanced habitat diversity for herpetofauna. Fox et al. (2004) used a sample-based rarefaction technique with data from these same watersheds to sequentially calculate Shannon–Wiener diversity indices instead of species richness, and also concluded that forest management activities on this study area probably had no negative impact on amphibians. In a companion study of reptiles, Shipman et al. (2004) found that the larger and more intensively managed watersheds had higher species diversity indices (adjusted for the dominance of the two most common species) than the less intensively managed watersheds. Additionally, the least intensively managed watershed (South Alum) had significantly lower per-plot reptile abundances, species richness, and diversity (Shipman et al., 2004). Morisita's indices of community similarity for amphibian and reptile communities also were quite similar among the four watersheds, ranging from 0.84 to 0.98 for amphibians and from 0.89 to 0.98 for reptiles (a value of 1.00 means identical communities) (Fox et al., 2004; Shipman et al., 2004). Of course, the number of watersheds here is small, so we encourage additional studies involving more watersheds.

5. Conclusions

Species richness is not the only indicator of management impacts, positive or negative. It is, however, certainly relevant to sustainability, however. Within the limitations imposed by our data, we did not find a negative impact on herpetofauna from forest management in these Ouachita Mountain watersheds. In fact, characteristics such as young stands and high stand age diversity seemed to promote diversity. Obviously, forestry practices can negatively affect local habitat quality for selected herpetofaunal species, at least in the short-term (deMaynadier and Hunter, 1995). Some studies (Petranka et al., 1993, 1994) even have suggested long-term effects on herpetofaunal diversity. However, even within bins homogeneous with respect to a specific variable, our study plots encompassed a wide variety of environmental conditions, stand structures, times since harvest, and other factors that potentially influence biological diversity in forested ecosystems. Thus, our results are consistent with hypotheses by others (e.g., Connell, 1978; Rosenzweig, 1995) that a seral sequence resulting from an intermediate level of disturbance will support higher levels of diversity than an area composed of fewer seral stages.

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