

AMPHIBIAN COMMUNITIES UNDER DIVERSE FOREST MANAGEMENT IN THE OUACHITA MOUNTAINS, ARKANSAS

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Abstract—From May 1995 to March 1999, we censused amphibians in the Ouachita Mountains, Arkansas, on 60 plots on each of four forested watersheds five times per year, with new plots each year. We found negligible differences in species richness among watersheds, and community similarities were high, even though most pairwise comparisons were significantly different. The two most intensively managed watersheds were more similar to each other than to those less intensively managed, and the former had nominally higher overall species evenness and (beta) diversity. At the plot level, we found no significant differences in abundance, species richness, or (alpha) diversity, although the two most intensively managed watersheds had plots with fewer species and less diversity. Detrended correspondence analysis revealed that communities diverged on the basis of presumed gradients of terrestrial-aquatic, elevation, and canopy cover. Important communities that differed among watersheds were those of small, often ephemeral ponds and large, permanent ponds.

INTRODUCTION

Little is known about habitat parameters that influence amphibian communities, and even less is known about landscape-level environmental influences (Dodd and Cade 1998). Moreover, many species of amphibians are declining worldwide in abundance, and more baseline data on natural populations over time are needed to appraise the suspected causes.

Amphibian populations, particularly anurans, are catastrophically declining worldwide (Blaustein and Wake 1995, Houlahan and others 2000, Phillips 1990, Wake 1991). Habitat loss, or modification to the extent that it is only marginally suitable for amphibians, is considered by most biologists to be the principal cause for the decline of amphibian populations and species (Blaustein and Wake 1995). It has been suggested that local environmental degradation is insidiously reducing amphibian diversity (Delis and others 1996). Examples of human activities that might result in such alterations include impoundment of natural waterways, mining, agriculture, urbanization, and forest management.

We report results of pretreatment data collection for a large-scale, long-term, field study of amphibian communities and the influence of habitat and landscape environmental variables in four watersheds of the Ouachita Mountains of west-central Arkansas. Following the pretreatment stage, sections of the watersheds will be subjected to different forest management to achieve a variety of specific "desired future conditions." After treatment, data on amphibian communities will again be collected and used to quantify community changes and to compare with the predictions of multivariate community models that we are developing. This long-term study is one component of Phase III of the Ouachita

Mountains Ecosystem Management Research Project; the wildlife component of this cooperative effort involves Weyerhaeuser Company, the National Council of the Paper Industry for Air and Stream Improvement, Oklahoma State University, the Oklahoma Cooperative Fish and Wildlife Research Unit, the University of Arkansas Monticello, the Ouachita National Forest, and the Southern Research Station of the USDA Forest Service.

The objectives of our overall study are to: (1) characterize reptile and amphibian communities in four watersheds representing markedly different forest-management strategies in the Ouachita Mountains, Arkansas; (2) develop and validate models for predicting community composition based on site, stand, and landscape parameters; and (3) develop recommendations to promote maintenance of reptile and amphibian communities in managed forest landscapes. This report contains results for amphibians of the pretreatment data analysis performed at the end of four survey years.

METHODS

Study Areas

The study was conducted on four 1500- to 4000-ha watersheds under different intensities of management in Garland and Saline counties near Hot Springs, AR. The watersheds differed markedly with respect to factors such as mean rotation lengths, forest type diversity, stand sizes and ages, and the amount of natural second-growth coverage (Guldin and others, Tappe and others, in press).

Little Glazypeau, a watershed located some 22 km southwest of the other three watersheds (that were contiguous) and managed largely for sawlog production by Weyerhaeuser Company, represented our most intensively managed

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watershed. Much of the second-growth shortleaf pine (*Pinus echinata*)-hardwood forest that originally covered this watershed had been harvested and planted to loblolly pine (*P. taeda*) plantations of 9-142 ha. Typically, these plantations were thinned twice, pruned to 5-8 m high, fertilized, and harvested at 30-35 years old. The remaining, selectively-harvested acreage in the watershed occurred on rocky ridge-tops, steep slopes, and streamside management zones that were retained for watershed protection and to provide habitat diversity for wildlife. South Alum, an experimental section of the Ouachita National Forest that has received minimal logging for > 80 years, represented the least intense level of silviculture. South Alum was almost entirely USDA Forest Service and consisted of mature forest over most of the area. Bread Creek and North Alum fell in between these extremes of forest management. From independent records of forest management and present composition of number, age, and distribution of pine (mostly *Pinus echinata*) plantations, Bread Creek was considered less intensely managed than North Alum (Tappe and others, in press). Bread Creek was primarily USDA Forest Service 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 management and half under USDA Forest Service 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 intensity of forest management, ran South Alum, Bread Creek, North Alum, and Little Glazypeau. These same watersheds, in order of size, were South Alum (1500 ha), Bread Creek (1535 ha), Little Glazypeau (2273 ha), and North Alum (3961 ha).

Sampling Plots

We surveyed amphibians and reptiles using area-constrained searches on a subset (56) of the 75-235 plots/watershed that were established each year for breeding bird surveys (Tappe and others, in press). Bird plots were established at 200-m intervals along > 100 km of parallel transects (oriented approximately north-south across prevailing topography) that were established in 1995 over the 4 watersheds. These same transects were used in 1996, but new plots were established by shifting plot centers 100 m. In 1997, approximately 110 km of new transects were established between those of 1995; new plots were established in 1998 along these new transects as in 1996. The subset of plots that were used for amphibian surveys were selected to represent a cross-section of slopes, aspects, forest types, stand conditions, and aquatic habitats. The center of our 20-m-radius (0.13-ha) plots also was the center of a bird sampling plot. Plastic flagging was used to delineate plot boundaries on all amphibian plots. In each watershed, we selected amphibian plots to make sure there were at least 12-15 of them in aquatic habitat, which consisted of springs, streams, and man-made ponds that had been established to benefit wildlife (Forest Service wildlife ponds) and/or as sources of water for fire fighting. An additional four plots per watershed per year were established off the transects at these ponds (or at wide pools in the high-order streams at the bottom of a watershed) to ensure that we had equivalent sampling

effort at these aquatic habitats. Plots at these aquatic sites were established so that the center of the plot was on land right next to the shore (roughly half of the plot was over water and half over land). Thus, we surveyed 60 plots per year per watershed, in total.

Amphibian Surveys

Trained crews of 3-5 individuals surveyed each set of 60 plots per watershed during daylight hours 5 times a year from May 1995 to March 1999: early May, late May, mid-June, early October, and early the following March. Plots were surveyed entirely 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 were captured in this way by use of a dipnet. Amphibians 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. Anuran species calling off-plot in similar habitat were recorded as present, but no attempt was made to count the number of individuals.

Data Analysis

Amphibian count data were pooled across the five sampling periods per year, but data from each plot served as separate samples. Data collected in the first year (1995) from South Alum and North Alum were excluded from analyses due to differences in sampling effort by former collaborators, and data from a few other plots were discarded when five surveys per year were not attained. Thus, analyses presented here are based on data from 833 plots, each censused five times, for a total of 4,165 censuses.

Watershed level—Community indices were first calculated at the watershed level: number of individuals by species for all years combined, amphibian abundance, species richness, (beta) species diversity [H' ; Shannon-Wiener diversity index (Shannon and Weaver 1949)], and species evenness [diversity divided by maximal diversity, or $H'/(ln \text{ number of species})$; Pielou 1966]. With only four watersheds to compare, no statistical tests were employed. Because the Shannon-Wiener diversity index is quite sensitive to sample size and because we did not have an equal effort among all watersheds (two watersheds with data from only three years; see previous statement), we randomly reordered the plots within each watershed, pooling years, and plotted the Shannon-Wiener diversity index of each watershed for cumulative sets of plots up to the total number of plots for each watershed. Such a plot would show if diversity approached an asymptote as cumulative plots increased and if our total number of plots per watershed was sufficient to adequately estimate species diversity.

We computed Morisita's index of community similarity (Morisita 1959) between all pairs of watersheds, pooling data for the entire study for each watershed. This index is desirable because sample sizes and species diversities of the communities being compared have little influence on its

calculation (Morisita 1959; Wolda 1981). Using additive tree cluster analysis (Sattath and Tversky 1977), we converted that matrix of similarities into a dendrogram of communities such that the total length of branches connecting any two communities was proportional to the compositional difference between those communities. To statistically compare the various Morisita's indices of community similarity, we conducted randomization tests (Biondini and others 1988). For each pair of watersheds, we randomly reassigned plots between them (retaining the sample size of each watershed) and computed Morisita's index for these two "synthetic" communities. We repeated this procedure 1,000 times and tabulated the number of times the recomputed index was smaller than or equal to the "actual" index. If less than 100 recomputed indices fell below or equal to the "actual" index, then those two watersheds were considered different ($p < 0.10$) in species composition.

Plot level—For analyses at the plot level, we used mixed model, two-way ANOVAs (ANOVAs with both random and fixed effects; PROC MIXED, SAS 1999) to test for differences among watersheds, years, and year * watershed interaction. We recognize that our sample of plots drawn from each of four watersheds is pseudoreplication (Hurlbert, 1984), but the large scale of this study preempted the sampling of a sufficient number of replicate watersheds per treatment class. While the results of our ANOVA must be interpreted with caution due to this pseudoreplication, we feel that the analysis nevertheless suggests likely ecological patterns that deserve attention. The response variables of the ANOVAs were (1) amphibian abundance per plot, (2) species richness per plot, and (alpha) plot diversity (Shannon-Wiener index). We first transformed the count variables (1 and 2) by the square root, SQR (count + 0.5), to make distributions within cells of the ANOVA more normally distributed. Even with those transformations, our data did not fully meet assumptions of normality and homogeneity of variances, but the Satterthwaite algorithm of the mixed model ANOVA is relatively robust to abuses of these assumptions, especially of homogeneity of variances (SAS 1999), and so we proceeded with these parametric analyses. We recognized differences in weather between years, not of interest to us here, and included year effects and year * watershed interaction as random effects, not to be statistically interpreted. The fixed factor (watersheds) was tested for statistical significance at $p < 0.10$. If a significant watershed effect was found, we used LSD to evaluate pairwise differences between any two watersheds.

Detrended canonical correspondence analysis (DCA)—To appraise amphibian community composition, develop preliminary hypotheses of presumptive environmental gradients influencing these communities, and compare graphically the environments and amphibian communities of the four watersheds, we used DCA (ter Braak and Prentice 1988, ter Braak and Šmilauer 1998), pooling plots from all four watersheds and years. Application of DCA to our data allowed for a more detailed inspection of amphibian communities at the plot level and how they were distributed along inferred environmental gradients. DCA is probably the most widely employed eigenanalysis-based ordination technique used by community ecologists. It is an indirect ordination

method that orders plots with similar compositions of species along multiple axes simultaneously. The statistical algorithm is to calculate sample scores of each plot as a weighted average of the species scores, and species scores as a weighted average of samples scores; iterations are repeated until there is no further change in scores, at which time samples (plots) with similar animal communities appear clustered when plotted on multiple axes. Environmental gradients are inferred from the pattern of species and/or plots and the biologist's knowledge of the species. As a step beyond single-number summary statistics like diversity indices or Morisita's indices, DCA results in a cloud of points for separate species in n-dimensional space, conventionally viewed as centroids (averaged central tendency) in two dimensions at a time. In other words, DCA results in a pattern, not a number. For our analysis, rare species (less than three individuals encountered over all four watersheds for all four years) and plots where no amphibian species were found were excluded due to computational constraints.

RESULTS AND DISCUSSION

We found 4,214 individuals of 20 amphibian species during our four-year study (table 1). Total species diversity was 1.76 for all watersheds pooled. We found a mean of 5.06 amphibians per plot (median = 3.00, range = 0-64).

Watershed Level

Despite large differences in size of watersheds and substantial differences in management intensities, the amphibian communities of these four watersheds were fairly similar. Species richness was just 17-18 species per watershed, and 15 of the total set of 20 species (75 percent) were common to all four watersheds (table 1). The watersheds differed some in both overall species diversity and evenness; the order from lowest to highest by both measures was Bread Creek, South Alum, Little Glazypeau, and North Alum (table 1). Bread Creek and South Alum were virtually identical in these measures. Recalculated diversity indices against cumulative plots showed that diversity leveled off after about 40-100 plots (fig. 1), well below the lowest total of plots for any watershed. North Alum showed distinctly higher overall diversity than the other watersheds, and in rank order, the two watersheds most intensively managed had higher species diversity than the two least intensively managed, although Little Glazypeau was not that different from Bread Creek or South Alum.

By far, the dominant species found in all watersheds was the western slimy salamander (*Plethodon albagula*), representing on the average 60.0 percent of each watershed community. Additionally, species composition of the six most ubiquitous species of each watershed was strikingly similar (table 2).

We examined the overall set of species to see if there were any species absent from all but one watershed, or present in only one watershed. One species, the central newt (*Notophthalmus viridescens*), was absent from Little Glazypeau; and one species, the Strecker's chorus frog (*Pseudacris streckeri*), was present only in Little Glazypeau, although represented by only one observed individual (table 1).

Table 1—Amphibian abundance on four watersheds in the Ouachita Mountains, Arkansas, 1995-1999

Species	Little Glazypeau	North Alum	Bread Creek	South Alum
	----- number -----			
<i>Acris crepitans</i> Cricket frog	238	143	48	3
<i>Ambystoma annulatum</i> Ringed salamander	0	0	3	1
<i>Ambystoma maculatum</i> Spotted salamander	0	1	4	0
<i>Bufo americanus</i> American toad	44	56	189	49
<i>Bufo woodhousei</i> Woodhouse's toad	2	2	7	2
<i>Desmognathus brimleyorum</i> Ouachita dusky salamander	74	17	15	9
<i>Eurycea multiplicata</i> Many-ribbed salamander	17	33	68	48
<i>Gastrophryne carolinensis</i> Eastern narrowmouth toad	24	22	10	1
<i>Hemidactylium scutatum</i> Four-toed salamander	14	6	2	2
<i>Hyla chrysoscelis</i> Gray treefrog	39	17	43	15
<i>Hyla cinerea</i> Green treefrog	1	1	0	0
<i>Notophthalmus viridescens</i> Central newt	0	7	3	2
<i>Plethodon albagula</i> Western slimy salamander	642	355	890	368
<i>Plethodon serratus</i> Southern redback salamander	13	22	57	195
<i>Pseudacris crucifer</i> Spring peeper	11	39	11	2
<i>Pseudacris streckeri</i> Strecker's chorus frog	1	0	0	0
<i>Pseudacris triseriata</i> Upland chorus frog	33	26	20	10
<i>Rana catesbeiana</i> Bullfrog	6	6	2	3
<i>Rana clamitans</i> Green frog	53	30	70	38
<i>Rana utricularia</i> Southern leopard frog	7	9	12	1
Total	1,219	792	1,454	749
Species richness	17	18	18	17
Species diversity	1.65	1.94	1.50	1.53
Species evenness	0.58	0.67	0.51	0.53

Data are arrayed (left to right) from the most to the least intensively managed watersheds.

Using Morisita's index of community similarity, watershed amphibian communities were quite similar, ranging from 0.84 to 0.98 (table 3). South Alum differed the most from the other watersheds, displaying an index of 0.84 with both Little Glazypeau and North Alum. The additive tree cluster analysis grouped the two most intensively managed watersheds (Little Glazypeau and North Alum) and the two least

intensively managed watersheds (Bread Creek and South Alum) (fig. 2). Despite generally high indices of community similarity, all of the indices [except that between North Alum and Little Glazypeau (0.98)] were statistically significant by the randomization tests; i.e., all watershed pairs except this one were significantly different from each other beyond that expected by chance.

Table 2—Six most common amphibian species found in each watershed in order of decreasing abundance

Little Glazypeau	n	North Alum	n	Bread Creek	n	South Alum	n
<i>Plethodon albagula</i> (Slimy salamander)	642	<i>Plethodon albagula</i> (Slimy salamander)	355	<i>Plethodon albagula</i> (Slimy salamander)	890	<i>Plethodon albagula</i> (Slimy salamander)	368
<i>Acris crepitans</i> (Cricket frog)	238	<i>Acris crepitans</i> (Cricket frog)	143	<i>Bufo americanus</i> (American toad)	189	<i>Plethodon serratus</i> (Redback salamander)	195
<i>Desmognathus brimleyorum</i> (Ouachita dusky salamander)	74	<i>Bufo americanus</i> (American toad)	56	<i>Rana clamitans</i> (Green frog)	70	<i>Bufo americanus</i> (American toad)	49
<i>Rana clamitans</i> (Green frog)	53	<i>Pseudacris crucifer</i> (Spring peeper)	39	<i>Eurycea multiplicata</i> (Many ribbed salamander)	68	<i>Eurycea multiplicata</i> (Many ribbed salamander)	48
<i>Bufo americanus</i> (American toad)	44	<i>Eurycea multiplicata</i> (Many ribbed salamander)	33	<i>Plethodon serratus</i> (Redback salamander)	57	<i>Rana clamitans</i> (Green frog)	38
<i>Hyla chrysoscelis</i> (Gray treefrog)	39	<i>Rana clamitans</i> (Green frog)	30	<i>Acris crepitans</i> (Cricket frog)	48	<i>Hyla chrysoscelis</i> (Gray treefrog)	15

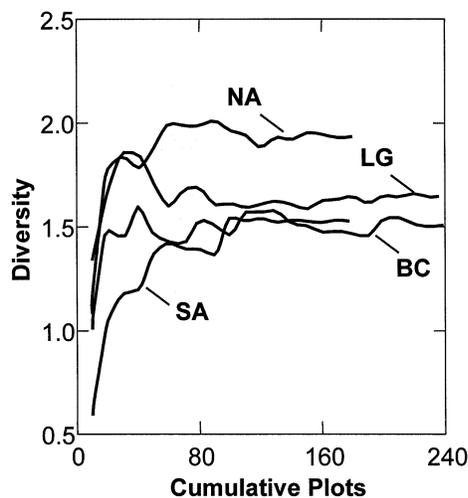


Figure 1—Diversity of each watershed against cumulative number of plots (in random order) included in recalculation (SA = South Alum, BC = Bread Creek, NA = North Alum, LG = Little Glazypeau).

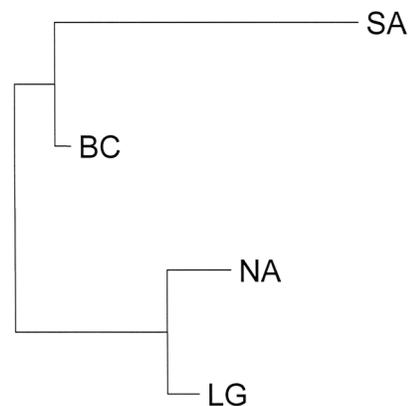


Figure 2—Additive tree dendrogram of amphibian community similarity of four watersheds constructed from pairwise Morisita Indices (SA = South Alum, BC = Bread Creek, NA = North Alum, LG = Little Glazypeau). Difference between any two communities is proportional to the total branch length connecting them.

Table 3—Morisita's index of community similarity for all pairs of watersheds

Watershed	Little Glazypeau	North Alum	Bread Creek	South Alum
Little Glazypeau	1.00			
North Alum	0.98	1.00		
Bread Creek	0.94 ^a	0.92 ^a	1.00	
South Alum	0.84 ^a	0.84 ^a	0.91 ^a	1.00

Index ranges from 0 to 1, where 1 means communities are identical.

^a Significantly dissimilar by Randomization test, $p < 0.10$.

Plot Level

We found no differences in total number of individuals per plot, species richness per plot, or species diversity per plot between the watersheds (table 4), as indicated by ANOVA. Consequently, we did not perform pairwise contrasts.

Detrended Correspondence Analysis

Detrended correspondence analysis indicated relatively long environmental gradients along the first three axes for amphibian communities in the four watersheds (table 5). The fourth and additional axes contributed little to the pattern of community organization since each additional

Table 4—Number of plots surveyed (1995–1999), mean amphibian abundance per plot, mean species richness per plot, and mean species diversity per plot by watershed

Watershed	<i>n</i>	Mean abundance ^a	Mean species richness ^b	Mean species diversity ^c
Little Glazypeau	236	5.17	1.35	0.25
North Alum	180	4.40	1.51	0.32
Bread Creek	239	6.08	1.90	0.43
South Alum	178	4.21	1.70	0.41

^a ANOVA: $F_3 = 1.73$, $p = 0.25$.

^b ANOVA: $F_3 = 2.61$, $p = 0.14$.

^c ANOVA: $F_3 = 2.56$, $p = 0.14$.

Table 5—Eigenvalues of first 4 axes of detrended correspondence analysis of 18 amphibian species distributed among a pooled total of 681 plots on the 4 watersheds^a

Axis	Eigenvalue
One	0.795
Two	0.513
Three	0.430
Four	0.282

^a An eigenvalue is the correlation coefficient between the plot scores and species scores along a given axis where each axis is orthogonal (independent) to all previous axes in the analysis.

axis explains only residual variation not already incorporated into the DCA. In other words, plots and species scores were relatively tightly correlated with each other along an appreciable stretch of at least the first three axes (eigenvalues range from 0 to 1: high eigenvalues mean that clouds of points are spread linearly along each axis, and low eigenvalues mean that points are clustered at the center of each axis). Species' centroids plotted against axes two vs. one (fig. 3) and against axes three vs. one (fig. 4), showed strong separation of species.

The pattern of species' centroids along axis one suggested that it was a moisture gradient from terrestrial (left) to aquatic conditions (right) (fig. 3). Those species scoring the lowest on this axis were the very terrestrial woodland salamanders, *Plethodon serratus* (southern redback salamander) and *P. albagula* (western slimy salamander). Further to the right were the more aquatic salamanders, *Desmognathus brimleyorum* (Ouachita dusky salamander) and *Eurycea multiplicata* (many-ribbed salamander), which frequently were found in small streams or shallow backwaters of larger water courses. Next to the right along axis one were the community of amphibians of small, generally fishless, often ephemeral, ponds (*Bufo americanus*, *Hyla chrysoscelis*, *Ambystoma maculatum*, *Notophthalmus viridescens*, and

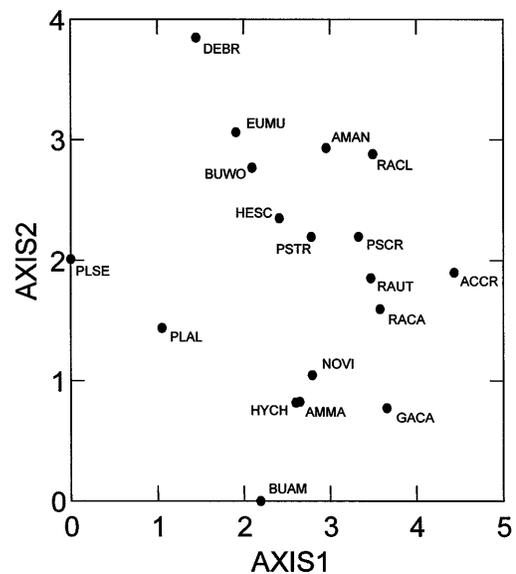


Figure 3—Centroids of species' scores from detrended correspondence analysis (DCA) of censused plots on all four watersheds pooled: DCA axis two vs. one (ACCR = *Acris crepitans*; AMAN = *Ambystoma annulata*; AMMA = *A. maculatum*; BUAM = *Bufo americanus*; BUWO = *B. woodhousei*; DEBR = *Desmognathus brimleyorum*; EUMU = *Eurycea multiplicata*; GACA = *Gastrophryne carolinensis*; HESC = *Hemidactylium scutatum*; HYCH = *Hyla chrysoscelis*; NOV = *Notophthalmus viridescens*; PLAL = *Plethodon albagula*; PLSE = *P. serratus*; PSCR = *Pseudoacris crucifer*; PSTR = *P. triseriata*; RACA = *Rana catesbeiana*; RAUT = *R. utricularia*).

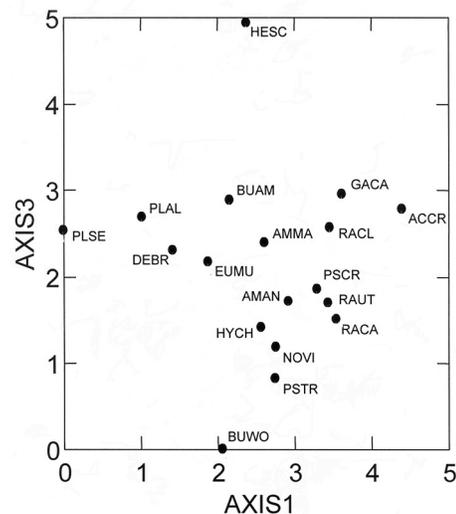


Figure 4—Centroids of species' scores from detrended correspondence analysis (DCA) of censused plots on all four watersheds pooled: DCA axis three vs. one (ACCR = *Acris crepitans*; AMAN = *Ambystoma annulata*; AMMA = *A. maculatum*; BUAM = *Bufo americanus*; BUWO = *B. woodhousei*; DEBR = *Desmognathus brimleyorum*; EUMU = *Eurycea multiplicata*; GACA = *Gastrophryne carolinensis*; HESC = *Hemidactylium scutatum*; HYCH = *Hyla chrysoscelis*; NOV = *Notophthalmus viridescens*; PLAL = *Plethodon albagula*; PLSE = *P. serratus*; PSCR = *Pseudoacris crucifer*; PSTR = *P. triseriata*; RACA = *Rana catesbeiana*; RAUT = *R. utricularia*).

Gastrophryne carolinensis; American toad, gray treefrog, spotted salamander, central newt, and eastern narrowmouth toad). Aligned vertically with this community but extending toward more extreme values of axis one were mapped the community of salamanders and frogs that were most aquatic and associated with small to large ponds and quiet pools of larger streams (*Ambystoma annulata*, *B. woodhousei*, *Rana clamitans*, *R. utricularia*, *R. catesbeiana*, and *Acris crepitans*; ringed salamander, Woodhouse's toad, green frog, southern leopard frog, bullfrog, and cricket frog), and small frogs commonly associated with wet to flooded brushy areas (*Pseudacris triseriata* and *P. crucifer*; upland chorus frog and spring peeper).

Axis two was interpreted as an elevational gradient, with higher-elevation sites with low scores on this axis, and lower-elevation sites with high scores (fig. 3). The most upland community was that of the small, generally fishless, often ephemeral ponds, which were often artificially created wildlife ponds, shallow roadside ditches, or scooped-out depressions next to a road berm and were often found near roads at the boundary ridges of the watersheds (American toad, gray treefrog, spotted salamander, central newt, and eastern narrowmouth toad). *Bufo americanus*, a member of this group, also was frequently found at dry, ridge-top sites away from ponds. Next in the ordination of axis two fell the terrestrial salamanders (*P. albagula* and *P. serratus*), who were found on terrestrial sites at all elevations and so whose centroids fell out in the center of the gradient. Species found lower down in the watersheds included those of medium-to-large ponds and flooded wetlands, habitats characteristic of lowlands (ringed salamander, Woodhouse's toad, green frog, southern leopard frog, bullfrog, cricket frog, upland chorus frog, and spring peeper). Finally, those salamanders that frequented small streams or shallow backwaters of larger water courses (*D. brimleyorum* and *E. multiplicata*) were plotted; frequently their habitat adjoined the largest streams at the bottom of the watershed.

Axis three was more difficult to interpret (and had less statistical explanatory power) (table 5), but knowledge of the species sorting out at the extremes of this presumed gradient led us to conclude that it reflected differences in canopy cover, low to high on the vertical axis (fig. 4). *Bufo woodhousei* breeds along the shores of rather large ponds and is rarely encountered in other habitats. Such sites have zero to low canopy cover. *Pseudacris triseriata* generally was found in or near water in flooded, brushy areas with sparse overstory. The central newt usually was found swimming in small, open ponds with limited canopy cover, and gray treefrog frequented ridge-top hardwoods, also with limited canopy cover. On the opposite extreme, we found the rather rare four-toed salamander (*Hemidactylium scutatum*) on dark plots with maximal canopy cover, either in closed-in pine plantations or very dense hardwoods. The centroids of the rest of the species fell out in the middle of this axis, implying that these species were limited to intermediate levels of canopy cover, or they were found on plots with both low and high canopy cover (thus, their centroids would fall out along the middle of this axis).

Scattergrams of plot scores onto the same three axes, aggregating the plots of the separate watersheds, offered

additional support for our interpretation of the environmental gradients that the axes represented. Ellipses enclosing 95 percent of the plots of the more intensively managed watersheds, Little Glazypeau and North Alum, were a bit larger than those enclosing 95 percent of the plots of their less intensively managed counterparts, Bread Creek and South Alum (figs. 5 and 6). In fact, ellipses for Little Glazypeau and North Alum completely enclose those for Bread Creek and South Alum for axes three vs. one (fig. 6). In DCA, broader extent of plots along axes means that those plots offer more varied habitat (plot to plot) for more varied communities of the organisms; i.e., greater beta diversity. Thus, even though plots of the four watersheds were not strongly separated (which meant communities were not all that different), there was the suggestion that North Alum and Little Glazypeau offered a more heterogeneous, patchy habitat mosaic than Bread Creek and South Alum. The former watersheds, in addition to plots with intermediate DCA scores, had more extreme aquatic plots (axis one) and both open and closed-canopy plots (axis three) than the latter. This enhanced patchiness appeared to have furnished suitable habitat conditions for a greater diversity of amphibians; i.e., greater between-site, or beta, diversity.

CONCLUSIONS

Although watershed sizes varied more than two-fold, there was no relationship between species richness and watershed area. Likewise, there was no relationship between species richness and intensity of management. There is the suggestion, however, that species diversity and species evenness may relate to intensity of management. The two most intensively managed watersheds (Little Glazypeau and North Alum) showed overall species diversity higher

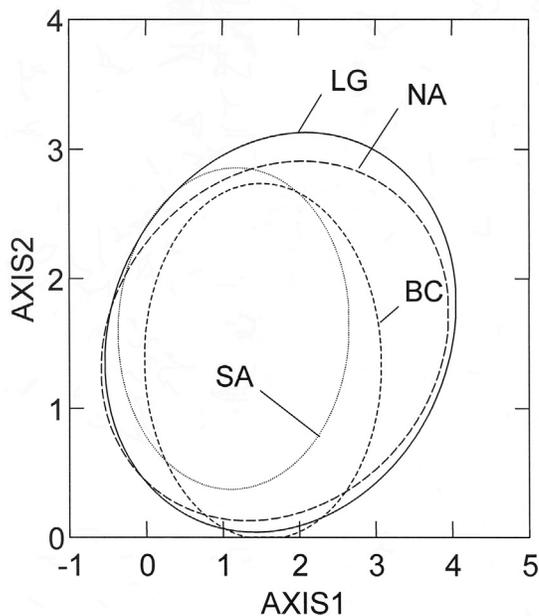


Figure 5—Ninety-five percent sample probability ellipses of the plot scores from detrended correspondence analysis (DCA) of the four watersheds: DCA axis two vs. one (SA = South Alum, BC = Bread Creek, NA = North Alum, LG = Little Glazypeau).

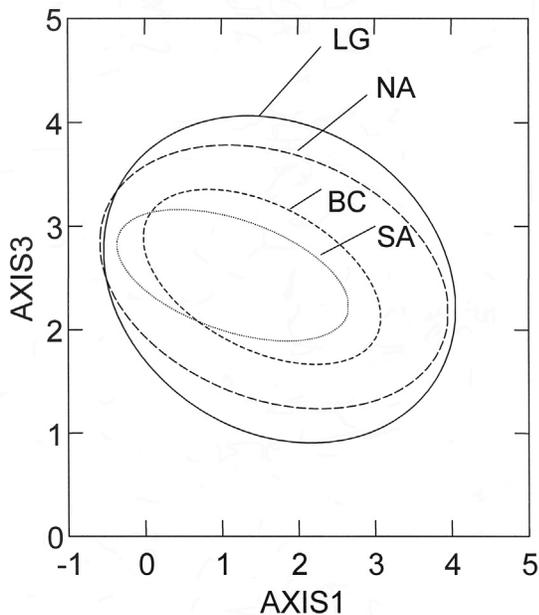


Figure 6—Ninety-five percent sample probability ellipses of the plot scores from detrended correspondence analysis (DCA) of the four watersheds: DCA axis three vs. one (SA = South Alum, BC = Bread Creek, NA = North Alum, LG = Little Glazypeau).

than that of the least intensively managed watersheds (Bread Creek and South Alum), with the diversity of North Alum distinctly higher than the rest. Recall that North Alum had large areas of relatively undisturbed middle and upper slope forests along with intensively managed Weyerhaeuser plantations (representing a diversity of successional stages) on the lower slope and valley topographic positions. Since species richness of all four watersheds was almost identical, the pattern of species diversity came about because the most intensively managed watersheds had a more even distribution of species. Cluster analysis of community similarity using Morisita's index, which incorporates Simpson's index of dominance (Simpson 1949), resulted in the same pattern. The most divergent watershed was the one least intensively managed, South Alum, and the two most intensively managed watersheds, Little Glazypeau and North Alum, grouped together. In fact, of all the pairs, only little Glazypeau and North Alum fell out statistically indistinguishable based on Morisita's index. This high degree of similarity was due primarily to the higher species evenness in both these watersheds.

At the plot level, no relationship to silviculture was strongly evident. None of our community parameters (total number, species richness, and species diversity) differed significantly among watersheds, although the least disturbed watersheds (Bread Creek and South Alum) had plots with nominally higher species richness and species diversity, unlike the tendency observed at the watershed level.

All told, the amphibian communities on the four watersheds did not appear to be that different, even though the level of similarity of most pairwise comparisons was gauged to be less than that expected by chance. However, when classifying the four watersheds into just two levels of intensity of

management, there is the qualitative suggestion that whereas alpha diversity (within-plot diversity) was related negatively to intensity of forest management, beta diversity (among-plot diversity) was related positively to intensity of forest management. Both tendencies, however, were only weakly demonstrated. At face value, it would appear that whereas the individual plots on the more intensively managed watersheds harbored perhaps somewhat less diverse assemblages of amphibians, the overall diversity of the watershed was putatively higher for these than the less intensively managed watersheds. These tendencies suggest that forest management applied at a large scale in the Ouachita Mountains of Arkansas may increase overall amphibian diversity (almost completely through increased evenness), probably because such habitat manipulation increases the diversity of habitat patches (timber stands of different ages and plant species distributions). Along with an increase of diversity of habitat patches comes increased diversity of canopy, litter, understory, down wood, soil moisture, stream hydrology, and various other habitat features that impact amphibians. This suggested increased beta diversity, which was not demonstrated statistically, comes at a cost of decreased alpha diversity, however (also not demonstrated statistically).

One obvious environmental difference among the watersheds that affected beta diversity along axis one was the presence or absence of large ponds, which represented important habitat for the more aquatic frogs. South Alum lacked these large, permanent ponds; Bread Creek also lacked them but had some moderate-sized ponds; North Alum had some large ponds; and Little Glazypeau had the most, primarily because they were constructed as "heli-ponds" to supply water for fire control. Consequently, Bread Creek and especially South Alum lacked plots with high scores along DCA axis one (an environmental gradient from terrestrial to aquatic) and were relatively impoverished in species like bullfrog, southern leopard frog, and cricket frog. The DCA suggests roughly the same pattern of beta diversity among the watersheds as that implied from the watershed-wide Shannon-Wiener diversity indices (table 1), but neither analysis implies a strong difference among watersheds.

Our data weakly suggest that the more intensively managed watersheds held a greater diversity (greater evenness of about the same number of species) of amphibians than the less intensively managed watersheds. But such a difference may not relate to management at all. There may be other characteristics of Little Glazypeau and North Alum that favor a greater diversity of amphibians. For example, both these watersheds are larger than either Bread Creek or South Alum. North Alum is over three times larger than Bread Creek. It is well known that number of species increases with area of study plots, the familiar species-area curves of islands and mainland sites (Pianka 2000). Although we did not observe more species on the largest watershed, perhaps area alone furnished conditions that promoted higher species evenness, hence higher species diversity. The large size of North Alum means that it may have offered a greater variety of habitats that might have favored a greater variety of amphibians, and it was North Alum that held the highest overall species diversity and evenness of all four watersheds

(table 1), even though it was not the most intensively managed watershed. There also may be other characteristics that relate to the amphibian communities found on the watersheds. These are just four watersheds picked to vary along a management continuum, but they also may vary in other ways. Without a suitable set of replicate watersheds representing various levels of forest management, it is impossible to randomize all these other variables and to assess the relative effect of forest management on amphibian communities.

One example from our study illustrates that concern. We found no central newts on Little Glazypeau, but we found them on the other watersheds, especially North Alum (also rather intensively managed). Little Glazypeau lacked small, permanent, fishless ponds whereas the other three watersheds had them, mostly man-made ones established for wildlife. Predatory fish and newt species often do not coexist (Beebee 1997, Hecnar and M'Closkey 1997). Both are predatory and have high prey overlap. Apparently, fish are more efficient predators and can outcompete the newts; introduced centrarchids can quickly eradicate *N. viridescens* from small ponds (Hecnar and M'Closkey 1997). Without the refuge of small, permanent, fishless ponds in which *N. viridescens* breeds, Little Glazypeau may not support this species, and the lack of these ponds may have nothing to do with commercial forest management. In fact, most of the small ponds were established artificially in the other watersheds for the benefit of wildlife, but this was not done at Little Glazypeau. In contrast, permanent heliponds established by Weyerhaeuser in Little Glazypeau were occasionally stocked with fish by local residents or fishermen, who released catches from nearby lakes or ponds for recreational fishing.

MANAGEMENT IMPLICATIONS

Our study qualitatively suggests that intensive forest management may decrease local, plot-wise (alpha) amphibian species diversity, but in turn may increase overall, watershed (beta) amphibian species diversity, perhaps by increasing the diversity of available habitats. However, neither tendency was statistically demonstrated because plots were not distinctly different among watersheds, and overall amphibian communities of the four watersheds were extremely similar. Taken together, our data suggest that intensive silviculture as practiced in the Ouachita Mountains of west-central Arkansas is not detrimental to landscape-level amphibian communities. This is probably true because even under the most intensive forest management, stand sizes are large, riparian zones are largely left intact, and ponds are created either for the benefit of wildlife or for a water supply for fire control. It is important to maintain those practices to conserve and maintain existing amphibian diversity. We recommend that land managers construct and/or maintain both large and small ponds, critical breeding habitat for many species of amphibians. Especially small, often ephemeral, vernal ponds are important for amphibians (Dodd and Cade 1998, Semlitsch and others 1996, Semlitsch and Bodie 1998). Because fish are important predators of amphibian eggs and larvae (Bradford 1989, Denton and Beebee 1991, Grubb 1972, Webb and Joss 1997) and are known to completely eliminate some species from permanent ponds (Fisher and Shaffer 1996, Hecnar and M'Closkey 1997),

some attempt should be made to maintain some small, permanent, fishless ponds on managed watersheds. In addition to mostly terrestrial species and those characteristic of small lowland streams and backwaters, we found two large amphibian communities associated either with small, often ephemeral, often upland ponds, or large, permanent, more lowland ponds. Presence and maintenance of these two classes of ponds should be part of forest-management practices in the Ouachita Mountains.

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