

# THE ROLE OF REGIONAL FACTORS IN STRUCTURING OUACHITA MOUNTAIN STREAM ASSEMBLAGES

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**Abstract**—We used Basin Area Stream Survey data from the USDA Forest Service, Ouachita National Forest to evaluate the relationship between regional fish and macroinvertebrate assemblages and environmental variability (both natural and anthropogenic). Data were collected for three years (1990-1992) from six hydrologically variable stream systems in the Ouachita Mountains that were paired by management regime within three drainage basins. Most of the variability in regional fish assemblages was explained by the historically constrained drainage basins themselves rather than measured habitat variables. Macroinvertebrate assemblages also showed some historical constraint but were associated more closely with stream habitat conditions. Timber harvest regimes showed little effect on regional assemblages. At the basin-level, taxonomic assemblages of both fishes and macroinvertebrates were a better predictor of environmental variability than trophic assemblages, bringing into question the use of trophic groups as an ecological measure in large-scale studies. Regional analyses are critical for understanding how stream systems are organized at different spatial scales and are important for effective management of streams within an altered landscape.

## INTRODUCTION

Describing the interactions that determine distribution and abundance of organisms is a primary goal of ecologists (Andrewartha and Birch 1954, Townsend and others 2000) and has defined much of the field of stream ecology (Allan 1995, Gorman and Karr 1978, Tonn and others 1983). These relationships, however, are complex and vary depending on spatial, temporal, or taxonomic resolution (Schlosser 1987, Vinson and Hawkins 1998, Wiens and others 1986). The assembly of regional stream faunas differs from that of local assemblages (Tonn 1990). At larger space and time scales, biota are influenced more by historical events (e.g., biogeographical history and speciation events) and climatic factors (Cooper and others 1998, Huguency 1997, Lohr and Fausch 1997, Ricklefs and others 1999, Vinson and Hawkins 1998). These large-scale, historical influences act as “filters” for regional faunas and limit the total species pool available at smaller scales (Cueto and de Casenave 1999, Ricklefs and others 1999, Tonn 1990).

At smaller scales, local ecological processes (i.e., abiotic and biotic) act as a final “filter” in structuring assemblages (Tonn 1990). The role of both environmental factors (Gorman and Karr 1978, Grimm and Fisher 1989, Grossman and others 1982, Jackson and Harvey 1993) and biotic interactions (Dahl and Greenberg 1998, Gilliam and others 1989, Power and Matthews 1983) in structuring aquatic assemblages is well documented for stream systems. Because of the dependence on factors operating at larger space and time scales, it is overly simplistic to only consider the role of local processes in organizing assemblages. Knowledge of regional and historical influences are critical for refining hypotheses of community assembly and organization for streams at smaller scales (Angermeier and Winston 1998, Brooks and McLennan 1993, Caley and Schluter 1997).

We used a large data set from the USDA Forest Service to examine patterns of regional fish and macroinvertebrate assemblage structure. The data were collected from six hydrologically variable streams paired within three drainage basins in the Ouachita National Forest, AR. Because much of the flow in these streams is dependent on rainfall events, they are prone to flood in the spring and dry to isolated pools in the summer. Variable flow regimes can strongly influence the structure of stream assemblages (Boulton and others 1992, Capone and Kushlan 1991, Delucchi 1988, Stanley and others 1994, Taylor 1997).

In addition to the natural disturbance regime, streams in the Ouachita National Forest are impacted by anthropogenic disturbances, primarily activities associated with timber harvesting. The effects of timber harvesting practices on stream fishes in the central United States are poorly understood (Brown and Matthews 1995, Hicks and others 1991, Rutherford and others 1992). Macroinvertebrates inhabiting forested streams are particularly responsive to timber harvesting (Wallace and others 1997, Webster and others 1992), and responses may include short-term shifts in dominant functional groups and/or changes in community structure (Allan 1995, Campbell and Doeg 1989). Timber harvesting practices can have both short and long-term effects on stream biota, with most long-term effects resulting from persistent sedimentation (Campbell and Doeg 1989, Silsbee and Larson 1983).

In this study, we used multivariate techniques to examine the relationship between regional fish and macroinvertebrate assemblages and environmental variability (both natural and anthropogenic) in these small, Ouachita Mountain stream systems. We were particularly interested in how the assemblages would differ in their response to

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*Citation for proceedings:* Guldin, James M., tech. comp. 2004. Ouachita and Ozark Mountains symposium: ecosystem management research. Gen. Tech. Rep. SRS-74. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 321 p.

this variability. Fishes are constrained to their historically defined drainage basins, and we predicted that this historical constraint would strongly influence their response to environmental variability. In contrast, many macroinvertebrates emerge from the aquatic environment as adults and choose future breeding sites based on environmental quality at a stream locality (Anderson and Wallace 1984). Macroinvertebrates have the ability to rapidly recolonize a site following a disturbance event (e.g., flood or drought; Stanley and others 1994). Because of their recolonization potential and the ability to cross basin barriers, macroinvertebrate assemblages are less constrained by large-scale processes, and their response to environmental variability should differ from that of fishes. Previous authors (Lammert and Allan 1999, Plafkin and others 1989) have suggested that macroinvertebrates should be more strongly associated with local habitat conditions and fishes influenced more by factors operating at larger spatial scales.

Finally, we were interested in how these patterns change with assemblage resolution (taxonomic versus trophic groupings). Because assemblages based on trophic groups would be less constrained by phylogeny and biogeographic history, we predicted that they may be more strongly associated with variability in habitat conditions than taxonomic assemblages.

## MATERIALS AND METHODS

### Study Area

The six streams in this study are located within the Saline, Cossatot, and Arkansas River basins in the Ouachita Mountains, Ouachita National Forest, AR (table 1). The Ouachita Mountains, located in southeastern Oklahoma and southwestern Arkansas, are a series of east-west oriented ridges and valleys. The mountains are composed of Paleozoic sedimentary rock, and streams are dominated by bedrock, boulder, and cobble substrata with some finer sediments interspersed (Robison 1986). Many small streams in the Ouachita Mountains have a highly variable flow regime throughout the year (Brown and Matthews 1995, Taylor 1997). As most of these streams are maintained primarily by rainfall events, they are prone to flooding in the spring and drying to isolated pools in the summer months.

Within each of the three drainage basins, streams were paired with one in a basin managed for timber and the other in a basin with no harvesting activities (Ponce and others 1982), (table 1). The extent of timber harvest activities over the last 100 years is reflected in age-class distributions of trees within the basins (table 1). Relative to reference basins, managed basins show higher areal percentages of forest in early succession (i.e., trees less than 50 years old) and a lower percentage of forest in mid to late-successional stages (Clingenpeel 1994). Because a variety of harvesting practices are used, managed basins in the Ouachita National Forest are a mosaic of stand-types ranging from small clearcuts to late-successional stands. Reference basins are also a mosaic of stand ages, but natural processes dictate the structure of these stands.

### Sampling Methods

All six study streams were sampled each summer (late May to early August) from 1990-1992 by Forest Service inventory teams (led by JAC). A mesohabitat classification system (McCain and others 1990) was used to divide each stream into habitat units (e.g., mid-channel pool, backwater pool, run, glide, high gradient riffle, cascade) from their headwaters to downstream reaches.

Physical stream features were measured within each classified habitat unit. Stream width was measured along a transect at the midpoint of each habitat unit, and depth was measured at four equidistant points and the thalweg along this same transect. Several instream variables were visually estimated as the percentage of area occupied within a habitat unit, including: substrate composition, embeddedness, undercut banks, large and small woody debris, white-water, boulder ledges, terrestrial vegetation overhanging the stream, vegetation clinging to substrate, rooted vegetation, and bank stability (i.e., percent of the bank not eroded). Bank angle and canopy closure were determined at the center of each habitat unit. Clingenpeel (1994) provided a detailed description of these methods.

Water samples were collected in 10 percent of each type of habitat unit (e.g., if 300 mid-channel pools were present, 30 were sampled). These collections were stratified along the length of each stream (Clingenpeel and Cochran 1992).

**Table 1—Streams sampled by the USDA Forest Service in 1990-1992**

Stream	Basin	Area	Mgmt.	Late	
				Early	successional
		<i>ha</i>		<i>percent</i>	
South Alum	Saline	1533	R	9	55
Bread	Saline	1517	M	40	20
Caney	Cossatot	2518	R	2	70
Brushy	Cossatot	3428	M	32	18
Dry	Arkansas	2170	R	8	30
Jacks	Arkansas	2938	M	25	20

Reference streams indicated by 'R' and managed by 'M', with this assignment based on the percentages of each basin in early (less than 50 years old) versus late successional (greater than 80 years old) forest.

Dissolved oxygen and temperature were measured in the field. Water samples were analyzed for conductivity, pH, bromide, nitrate, phosphorus, manganese, magnesium, sodium, cobalt, calcium, and sulfate at Berea, KY, with 1983 EPA Methods for Chemical Analysis of Water and Wastes.

Fishes and macroinvertebrates also were collected in 10 percent of each habitat unit type, arrayed longitudinally in each stream. Fishes were collected with multiple-pass electro-fishing and block nets (Clingenpeel and Cochran 1992) and preserved for identification. Macroinvertebrates were collected at each locality with a kick-net and substrate washing into a net (5-min each). These samples were pooled and preserved for later identification.

### Statistical Methods

We summarized stream habitat and water chemistry variables for each stream by year and computed means for each. An overall mean and coefficient of variation were calculated for depth measurements (transect and thalweg). We used 39 physical variables in a principal components analysis (PCA) to reduce the dimensionality of these data to a few significant axes. We were not attempting to interpret these axes; rather, we used PCA to objectively select a small subset of the original data that would represent the major gradients in the study streams. We retained six variables (conductivity, percent canopy cover, percent boulder substrate, CV depth, percent cover of rooted vegetation, and bank stability) for further analyses. These variables had the highest component loadings for the first five axes, which accounted for about 72 percent of the total variance. We retained conductivity and canopy cover because they both had equally high loadings on the first axis.

We also summarized fish and macroinvertebrate data for each stream by year. For taxonomic analyses, we used fish species and macroinvertebrate genera (or order or family when genus was not determined). We classified fishes and macroinvertebrates into trophic groups according to Horwitz (1978) and Merritt and Cummins (1984), as summarized by Allan (1995).

We used Canonical Correspondence Analysis (CCA), (ter Braak 1986, 1990) to examine the relationship between regional fish and macroinvertebrate assemblages (taxonomic and trophic) and the reduced set of environmental variables. We also included dummy environmental variables for the individual river basins (i.e., Arkansas, Cossatot, Saline) and presence or absence of timber harvesting within a watershed. These analyses allowed us to simultaneously examine effects of the historically defined drainage basins, presence or absence of logging activities, and measured environmental variables on assemblage structure. Based on assemblage structure and the environmental variables modeled, we plotted the site scores for each stream by year in multivariate space and grouped them by drainage basin. We constructed these graphs separately for fish and macroinvertebrate trophic and taxonomic assemblages. We used Monte Carlo tests (1000 permutations) to estimate the significance of each CCA performed.

We used the Mantel test (Fortin and Gurevitch 1993) to examine the association between assemblage structure

(taxonomic and trophic) and measured environmental variables. We were interested specifically in how strongly the trophic matrices were associated with both taxonomic and habitat matrices. We tested the prediction that trophic matrices would be associated more strongly with environmental variability than taxonomic matrices because of their relative freedom from phylogenetic and historical constraint. For the Mantel test, we used rectangular  $n \times n$  matrices (e.g., fish taxa by site) to construct triangular correlation matrices. The Mantel test determines the association between pairs of the triangular correlation matrices at a time, testing the null hypothesis that there is no association within elements of the matrices. Thus, for these data we tested the association between trophic assemblages and both taxonomic assemblages and environmental variability (i.e., trophic vs. taxonomic and trophic vs. habitat). We also performed partial Mantel tests (Manly 1997), where a given test between two matrices is constrained by removing association with a third matrix (e.g., trophic vs. habitat with the effects of taxonomy removed). Partial Mantel tests are comparable in function and interpretation to partial correlation analyses (Manly 1997, Zar 1996). We repeated these Mantel tests for both fish and macroinvertebrate assemblages.

## RESULTS AND DISCUSSION

### Summary of Collections

A total of 30 species of fishes (9 families) and 152 genera of macroinvertebrates (65 families, 20 orders) were collected over the 3-year study period from the six streams. Examples of all major trophic groups (Horwitz 1978, Merritt and Cummins 1984, Allan 1995) were represented in these data. For both fishes and macroinvertebrates, overall number of individuals collected was highest in streams of the Cossatot River basin (table 2). For fishes, species richness was higher in the managed streams than in their paired reference for all three basins (table 2). In two of three cases (Saline and Arkansas basins), richness of macroinvertebrate taxa was greater in the managed streams than the paired reference (table 2). However, because of high variability among basins, there were no significant differences (T-test,  $p > 0.05$ ) between managed and reference watersheds with respect to number of individuals collected or richness of fishes or macroinvertebrates.

### Fish Assemblage Structure

Based on taxonomic and trophic assemblages of fishes, streams within individual drainage basins were closely associated and separated from other basins in multivariate space (fig. 1). Thus, most of the variation in regional fish assemblages was explained by differences among the historically defined drainage basins rather than measured environmental variables or timber harvesting activities. For both groups of assemblages, variation in the first CCA axis was dominated by the individual drainage basins (table 3), indicating that assemblages differed strongly among the historically defined basins. The second CCA axis was associated with the percentage of boulder substrate and the drainage basins (table 3). Logging regime was correlated weakly with both axes, indicating little effect in structuring fish assemblages at the regional scale.

**Table 2—Total number of individuals collected and taxa richness for each of the six study streams over the 3-year study period**

Measure	Stream/Basin					
	S. Alum Saline	Bread* Saline	Caney Cossatot	Brushy* Cossatot	Dry Arkansas	Jacks* Arkansas
<b>Fishes</b>						
No. Individ.	1,694	849*	6,320	7,020*	921	1,550*
Richness	18	19*	16	19*	4	13*
<b>Invertebrates</b>						
No. Individ.	2,402	4,821*	11,648	10,962*	2,185	3,611*
Richness	38	47*	43	40*	28	44*

\* = managed streams.

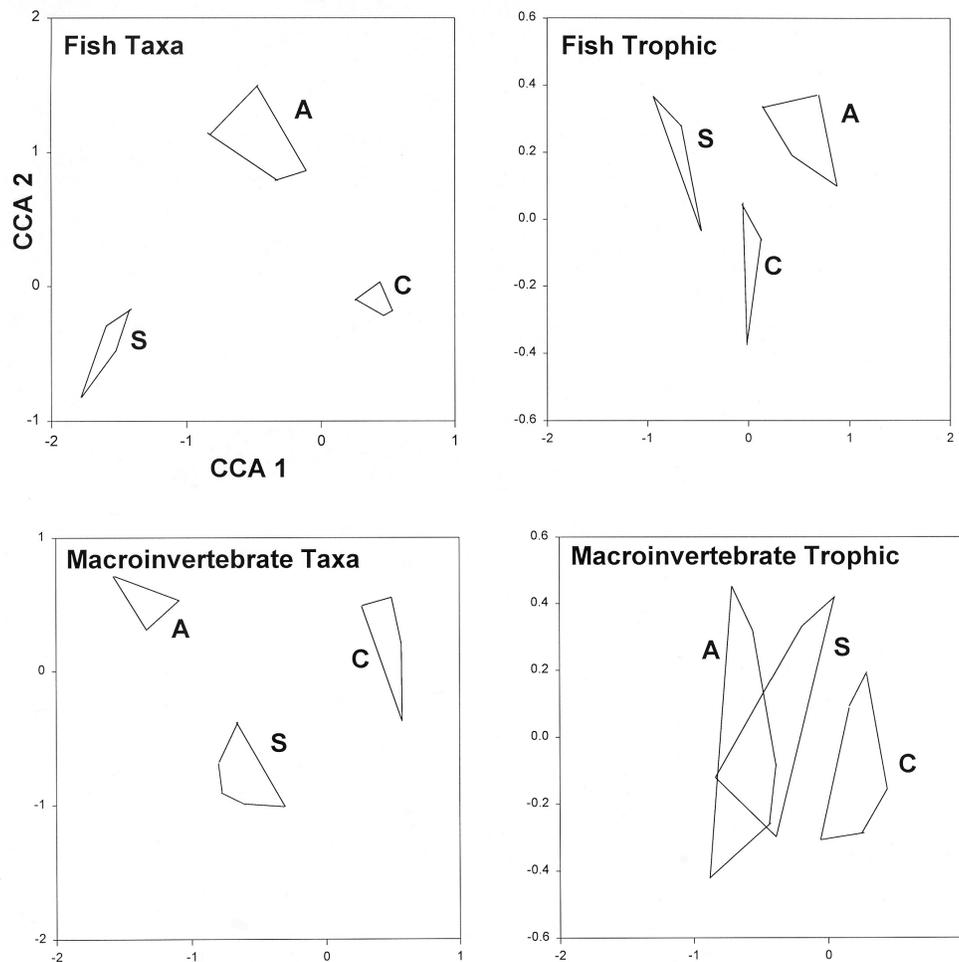


Figure 1—The distribution of site scores in multivariate space for fish and macroinvertebrate assemblages (taxonomic and trophic). Streams within a given year are grouped with polygons by drainage basin. A = Arkansas basin; C = Cossatot basin; S = Saline basin. Shown are the first (x-axis) and second (y-axis) canonical correspondence analysis axes.

Overall, streams within individual basins differed in environmental conditions. For example, streams in the Saline basin had greater aerial canopy cover and more rooted vegetation. Streams in the Arkansas basin were characterized by

a higher percentage of boulder substrate and greater bank stability, and streams in the Cossatot system had higher conductivity and greater variability in stream depth (L.R. Williams and others. Environmental variability, historical

**Table 3—Correlations between canonical correspondence axes (1 and 2) and environmental variables for fish and macroinvertebrate assemblages (taxonomic and trophic)**

Variable	Fish taxa		Fish trophic		Macroinvertebrate taxa		Macroinvertebrate trophic	
	1	2	1	2	1	2	1	2
Axis	(0.01)	(0.01)	(0.01)	(0.02)	(0.01)	(0.02)	(0.01)	(0.01)
P-value								
Conductivity	0.42	0.03	0.10	-0.16	0.43	-0.17	0.35	0.08
Boulder	-0.33	-0.68	0.42	0.63	-0.78	0.42	-0.81	-0.28
Canopy	-0.56	-0.30	-0.51	0.40	-0.29	-0.25	-0.19	-0.04
CV depth	0.55	0.09	0.40	-0.01	0.60	0.09	0.60	0.42
Vegetation (rooted)	-0.43	-0.37	-0.62	0.13	0.07	-0.87	-0.06	0.48
Stability (bank)	-0.28	0.34	0.22	0.27	-0.53	0.35	-0.43	-0.10
Basin								
Alum	-0.89	-0.42	-0.80	0.33	-0.41	-0.74	-0.38	0.41
Cossatot	0.91	-0.38	0.15	-0.71	0.94	0.28	0.85	-0.26
Logging	0.03	0.17	-0.03	0.11	-0.05	-0.41	-0.15	0.27

contingency, and the structure of regional fish and macroinvertebrate assemblages in Ouachita Mountain stream systems. Manuscript in preparation). Based on the relationships we found, regional fish assemblages are likely influenced by combinations of spatially constrained environmental variability (i.e., habitat conditions unique to individual basins) and the historical biogeography of individual drainage basins.

### Macroinvertebrate Assemblage Structure

Taxonomic assemblages of macroinvertebrates showed a similar pattern to fish assemblages, but the separation of streams into their respective basins was not as evident for macroinvertebrate trophic groups (fig. 1). For macroinvertebrate taxa, the first CCA axis was again dominated by differences among the historically defined drainage basins and the percentage of boulder substrate (table 3). The second axis was correlated with drainage basins and percent cover of rooted vegetation (table 3). Macroinvertebrate trophic groups were also associated with drainage basins; the Cossatot basin clearly separated from the other two in multivariate space (fig. 1). Percentage of boulder substrate and variability in stream depth also had a strong influence on trophic assemblages (table 3). Logging regime was not associated strongly with regional macroinvertebrate assemblages.

The weak relationship between macroinvertebrate trophic assemblages and drainage basins, and stronger associations with individual environmental variables, indicates that historical constraint may be less important in structuring regional macroinvertebrate assemblages. In contrast with fishes, macroinvertebrate assemblages were associated more strongly with environmental variability not associated with the drainage basins (i.e., habitat conditions that are unrelated to basins). Despite these stronger correlations with individual environmental variables, historical contingency still had some influence on macroinvertebrate assemblages when grouped by taxa (table 3).

### Trophic Patterns

For fish assemblages particularly, patterns for taxonomic and trophic assemblages were quite similar (fig. 1). This was in contrast to our prediction that trophic assemblages would be less constrained by historical contingency than taxa. Mantel tests indicated that fish and macroinvertebrate trophic groups were associated with both environmental variables and the taxonomic composition of assemblages (table 4). Because the trophic matrices are constructed from species matrices, we focused on the strengths of the relationships ( $r$ ) and not associated p-values. As expected, the strongest correlations were between trophic and taxonomic assemblages (table 4). Correlations between trophic groups and habitat were not as strong, and when the effect of taxonomy was removed, there was little correlation left between trophic assemblages and environmental variables (table 4). Thus, correlations between trophic and habitat matrices were confounded by their strong relationships with the taxonomic matrices. This indicates that taxonomic assemblages were associated more strongly with environmental variability than the trophic assemblages, and this pattern was evident for both fishes and macroinvertebrates.

**Table 4—Correlations between trophic assemblages for fishes and macroinvertebrates and taxonomic and habitat matrices**

Matrix comparison	$r$
Fish trophic groups x taxa	0.701
Fish trophic groups x habitat	0.343
Partial Mantel (taxonomy effects removed)	0.012
Macroinvertebrate trophic groups x taxa	0.659
Macroinvertebrate trophic groups x habitat	0.212
Partial Mantel (taxonomy effects removed)	0.133

Correlations derived from Mantel and partial Mantel tests.

## CONCLUSIONS

Overall, we found that timber harvesting regime had little influence on number of individuals collected, taxonomic richness, or assemblage structure of fishes and macroinvertebrates at the regional scale. The lack of an effect seems to indicate that these systems are somewhat resistant to such perturbations, and we believe this is related to the dynamic natural disturbance regime of these streams. At the large scale of this study, the seasonal flooding and drying of these streams appears to override effects of timber harvesting activities as practiced in the Ouachita National Forest. However, land-use activities often have a stronger effect on stream biota at local rather than regional scales (Campbell and Doeg 1989, Lammert and Allan 1999, Rutherford and others 1992). Because of limitations in sampling design, we were unable to test this prediction at smaller spatial scales.

As we predicted for fishes, historical constraint had the strongest influence on the structure of regional assemblages. This historical explanation, however, has two components that are difficult to separate. First, biogeographical history influences the potential biota of a stream (Brooks and McLennan 1993, Matthews and Robison 1988, Tonn 1990). Second, habitat conditions within individual streams are constrained by the underlying geology of individual basins (Brown and Matthews 1995, Brussock and others 1985); basin geomorphology determines substrate composition and channel characteristics. Both of these historical components (i.e., biogeography and habitat variability unique to individual basins) are important in structuring regional fish assemblages in the six streams that we examined.

In contrast, regional macroinvertebrate assemblages were structured both by historical factors and also environmental variability that was not associated with the individual basins. We did not expect such a high degree of historical constraint on macroinvertebrate taxa. As above, this may relate to the inherent differences in habitat characteristics of the individual basins.

Regional studies of stream systems are critical for understanding the structure of their biotic assemblages. Huston (1999) argued that unraveling the interrelationships between local and regional processes is critical to understanding global patterns of species diversity. How these ecological processes are linked at different spatial scales is a fundamental question in the field of ecology (Levin 1992, Lohr and Fausch 1997). Because of the inherent difficulty in managing small stream systems (Poff and Ward 1989), detailed studies at multiple spatial and temporal scales are necessary to conserve and manage their biological diversity. An understanding of the effects of disturbance is also necessary for effectively managing aquatic ecosystems (Resh and others 1988). One of the basic tenets of ecosystem management is that disturbance is a vital attribute of ecological systems and native species have evolved within the context of this natural disturbance regime (Hessburg and others 1999, Landres and others 1999). The effects of anthropogenic disturbances cannot be fully understood unless the natural disturbance regime has been taken into

consideration (Landres and others 1999). Because many government agencies are using basin-level survey methods (Clingenpeel 1994, Hankin and Reeves 1988) to assess effects of anthropogenic disturbances, it is important to evaluate their efficacy. Given the intensive sampling methodologies and expense of these basin-level studies, it is important to consider the strengths and limitations of these methods in elucidating ecological relationships.

## ACKNOWLEDGMENTS

Research support was provided through two projects "Fish Community and Habitat Stability under Different Forest Management Regimes" dated September 1, 1997 through September 30, 1999 of Cooperative Agreement 33-CA-97-190 and "Community Dynamics in Small Ouachita Mountain Streams" dated August 1, 1999 through February 28, 2002 of Cooperative Agreement 33-CA-99-622. Financial support for this work was provided by the USDA Forest Service, Southern Research Station, Ouachita Mountains Ecosystem Management Research Project, Ouachita National Forest and the Department of Biological Sciences at Mississippi State University.

We thank personnel provided by the Forest Service, Northeast Louisiana University, and Arkansas State University for their assistance with field and laboratory work. This work was completed in partial fulfillment of the doctoral degree requirements for L.R. Williams.

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