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Environmental variability, historical contingency, and the structure of regional fish and macroinvertebrate faunas in Ouachita Mountain stream systems

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Synopsis

In 1990-1992, the United States Forest Service sampled six hydrologically variable streams paired in three different drainage basins in the Ouachita Mountains, Arkansas, U.S.A. Fishes, macroinvertebrates, and stream environmental variables were quantified for each stream. We used these data to examine the relationship between regional faunas (based on taxonomy and trophic affiliation of fishes and macroinvertebrates) and measured environmental variables. Because fishes are constrained to their historically defined drainage basins and many insect taxa are able to cross basin barriers, we anticipated that both groups would respond differently to environmental variability. Fishes were influenced more by environmental variability that was unique to their historical drainage basins, but macroinvertebrates were associated more strongly with environmental variability that was independent of drainage basins. Thus, the individual drainage basins represented a historical constraint on regional patterns of fish assembly. For both fishes and macroinvertebrates, groupings based on taxonomy and trophic affiliation showed a similar response to environmental variability and there was a high degree of association between taxonomic and trophic correlation matrices. Thus, trophic group structure was highly dependent on the taxonomic make-up of a given assemblage. At the basin-level, fish and macroinvertebrate taxa were associated more strongly with environmental variability than the trophic groups, and these results have implications for basin-level studies that use trophic groupings as a metric to assess ecological patterns. Trophic categories may not be a useful ecological measure for studies at large spatial scales.

Introduction

Quantifying the relationship between stream organisms and their environment is an important area of research in aquatic ecology (Gorman & Karr 1978, Tonn et al. 1983, Allan 1995). The importance of biotic and abiotic features in structuring stream fish and macroinvertebrate assemblages is well known or amply demonstrated (Gorman & Karr 1978, Lancaster et al. 1990, Jackson & Harvey 1993, Richards & Host 1994, Clenaghan et al. 1998, Vinson & Hawkins 1998). These relationships, however, are highly dependent on the spatial and temporal scales examined (Wiens et al. 1986, Lohr & Fausch 1997, Vinson & Hawkins 1998, Lammert & Allan 1999). In the past decade, ecologists broadened their perspectives concerning ecological processes across large space and time scales (e.g., the macroecological approach). The longstanding paradigm that community-level properties arise from ecological interactions that are resolved quickly and

within small areas and habitats has shilted (Schluter & Ricklefs 1993). Practitioners in the field of macroecology now embrace a more balanced view that patterns of diversity and community structure are caused by a variety of ecological and historical processes.

Biota in aquatic systems pass through a number of spatial filters; thus, the assembly of regional faunas differs from that of local communities (Tonn 1990). At large space and time scales, biota are influenced mostly by historical events (e.g., geomorphology, biogeographic history) and climatic factors (Hugueny 1997, Lohr & Fausch 1997, Cooper et al. 1998, Vinson & Hawkins 1998, Ricklefs et al. 1999). These large-scale, historical influences act as 'filters' for regional faunas and limit the total species pool available at smaller scales (Tonn 1990, Cucnto & de Casenave 1999, Ricklcfs et al. 1999). Although regional factors and historical events undoubtedly influence assemblage structure (Matthews 1987, Brazner & Reals 1997, Lohr & Fausch 1997, Cooper et al. 1998, Vinson & Hawkins 1998, Ricklefs et al. 1999), the specific role of these processes and their interactive effect on the structure of aquatic faunas are understood poorly (Hildrew & Giller 1994, Vinson & Hawkins 1998).

In this paper, we used a large data set from the United States Forest Service to examine the influence of environmental variability across a biogeographical scale on fish and macroinvertebrate regional faunas. These data were collected from six small, hydrologically variable streams paired within three drainage basins of the Ouachita Mountains, Arkansas, U.S.A. Because much of the flow in these streams is dependent on rainfall, they are exposed to flood events in the spring and fall, and they dry to isolated pools in the summer months (Taylor & Warren 2001). These periodic oscillations in flow can have strong effects on stream biota (Delucchi 1988, Boulton et al. 1992, Taylor et al. 1993, Taylor 1997, Taylor & Warren 2001, Williams et al. 2002) and may limit the ability to detect species associations (Angermeier & Schlosser 1989) and species-environment relationships (Braaten & Berry 1997). Assemblage structure after a perturbation event reflects differential dispersal ability and growth rates of colonists or survivors (Power 1992), but the specific response of assemblages to a disturbance is highly dependent on the extent of the perturbation and the spatial scale examined by the investigator (Taylor et al. 1993, Williams et al. 2002).

We were particularly interested in how regional fish and macroinvertebrate faunas were associated with environmental variability measured across larger spatial scales. Most studies of stream fauna arc limited in their taxonomic scope, and spatial and temporal scales (Jackson & Harvey 1993). Our goal was to address variability at a much larger spatial scale in order to examine the influence of historical and ecological processes on regional fish and macroinvertebrate faunas. Jackson and Harvey (1993) found concordant patterns between fish and invertebrate assemblages in lakes across a large region in Ontario, although both groups seemed to respond differently to measured environmental variables. Based on their results, and because our system spans three different drainage basins, we hypothesized that fishes and macroinvertebrates would respond to the environment in different ways. Specifically, fishes are constrained to their historically defined drainage basins and we predicted that this historical constraint would strongly limit their response to environmental gradients at the geographic scale. In contrast, many macroinvertebrate taxa emerge from the aquatic environment as adults and choose future breeding sites based on environmental quality at a stream locality (Anderson & Wallace 1984). Many macroinvertebrates can also or are able to rapidly recolonize a site after a disturbance event (e.g., flood or drought; Stanley et al. 1994). Because of their recolonization potential and ability to cross basin barriers, macroinvertebrate response to environmental variability should differ from that of fishes (Plafkin et al. 1989, Lammert & Allan 1999); thus, regional macroinvertebrate faunas should be less constrained by historical effects. Finally, we were interested in how these patterns vary when faunas were classified by taxonomy versus trophic groups. We reasoned that trophic groups would be less constrained by phylogeny and biogeographic history than those organized by taxa. With taxonomic groupings, wc predicted endemic species would show a strong historical constraint; however, when placed in trophic categories these endemic species become less unique and should be associated more intimately with local environmental features. Thus, we predicted that trophic groups would show stronger associations with environmental variables than faunas defined by taxonomy.

Methods

Study area

The six streams in this study are located in forested watersheds of the Ouachita National Forest within the

basins of the Saline, Cossatot, and Petit Jean rivers in the Ouachita Mountains physiographic province (Table 1, Figure 1). The Ouachitas are a series of east-west oriented mountains located in southeastern Oklahoma and southwestern Arkansas. The mountains are composed of Paleozoic sedimentary rock, and streams are dominated by bedrock, boulder, and cobble substrata with some finer sediment interspersed (Robison 1986). The steep gradient of these streams produces high-velocity floods during periods of heavy rainfall. Most streams within the Ouachitas are maintained primarily by these rainfall events, and they may become intermittent during dry periods (Taylor & Warren 200 1).

Table 1. **Streams sampled by the USDA Forest Service in 1990-1992. All streams are located in the Ouachita National Forest. Arkansas, U.S.A.**

Stream	Drainage basin	Area (ha)
South Alum Creek	Saline River	1533
Bread Creek	Saline River	1517
Caney Creek	Cossatot River	2518
Brushy Creek	Cossatot River	3428
Dry Creek	Petit Jean	2170
Jacks Creek	Petit Jean	2938

Each pair of study streams is located in geographically disparate river systems, which in turn, support assemblages with distinctive characteristics. The Saline River is a tributary of the Ouachita R., which ultimately empties into the Red River in east-central Louisiana. The Cossatot River is part of the Little

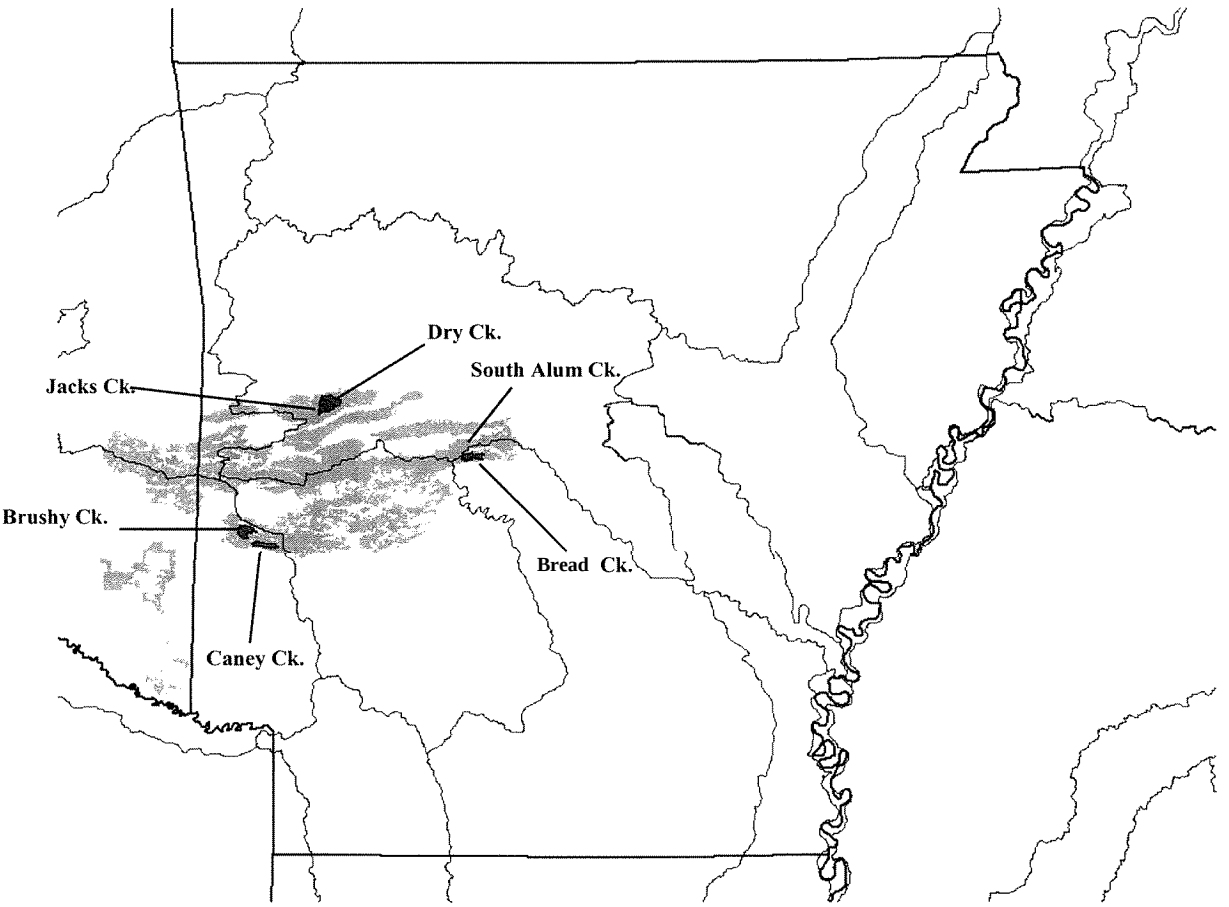

Figure 1. **Location of the six study streams within the Ouachita National Forest, Arkansas, U.S.A. Watersheds of each stream arc highlighted, and major drainage basins within the state are outlined. Jacks and Dry Creeks are tributaries of the Petit Jean/Arkansas Rivers. South Alum and Bread Creeks drain into the Saline/Ouachita/Red Rivers, and Brushy and Caney Creeks are tributaries of the Little/Red Rivers.**

River system, which also joins the Red River, but does so in southwestern Arkansas over 400-river km upstream of the mouth of the Ouachita River. The Petit Jean River is a tributary of the Arkansas River (Mississippi River basin) rather than the Red River. The aquatic fauna1 assemblages of the Ouachita, Little, and Petit Jean river systems differ in several characteristics, including species composition (Matthews & Robison 1988, Poulton & Stewart 1991, Moulton & Stewart 1996), species richness, species density, and endemicity (Mayden 1985, Crump & Warren 1999, Warren & Hlass 1999, Warren et al. 1999). As all six streams occurred in the headwaters with no reservoirs in close proximity, there was no evidence of species stockings or introductions in these systems (Nico & Fuller 1999). The Ouachita Mountains are bordered to the east and south by the Gulf Coastal Plain physiographic province and to the north by the wide, low-gradient floodplain of the Arkansas River (Robison 1986). These likely represent barriers to dispersal for many upland aquatic species, particularly endemics, effectively isolating assemblages in tributary systems, such as the Ouachita, Little, and Petit Jean rivers. Isolation in upland streams and headwater fauna1 exchange are hypothesized to explain patterns of genetic diversity, shared fauna, and endemism for many aquatic species in this endemic- and species-rich region (Echelle et al. 1975, 1999, Mayden 1985, Cross et al. 1986, Matthews & Robison 1988, Poulton & Stewart 1991, Moulton & Stewart 1996). Regardless of the mechanism, the streams in this study are geographically isolated and differ in their faunas so that consideration of historical constraint as a major component affecting observed assemblages is warranted.

Sampling methods

All streams were sampled in late May to early August from 1990 to 1992 by Forest Service inventory teams (led by JAC). As streams in the southern portion of the Ouachitas typically were more perennial, sampling proceeded from north to south. Streams within the same drainage were sampled in the same week. Jacks and Dry Creeks generally were sampled in June, followed by Bread and South Alum Creeks in July and Caney and Brushy Creeks in July/August. A mesohabitat classification system proposed by McCain et al. (1990) was used to divide each stream into habitat units from their headwaters to downstream reaches (Williams et al. *2002).*

Physical stream features were measured within each classified habitat unit. Stream width, mean depth, and thalweg depth were estimated along a transect at the midpoint of each habitat unit. Substrate composition was estimated visually as the percentage of six size-classes (i.e., bedrock, boulder, cobble, gravel, sand, and clay/fine sediments). Embeddedness was estimated as the average percent of cobble surrounded by fine sediments. Instream cover factors (i.e., undercut banks, large and small woody debris, whitewater, boulder ledges, terrestrial vegetation overhanging the stream, vegetation clinging to substrate, and rooted vegetation) were estimated visually as the percentage of area occupied within a habitat unit. A clinometer was used to estimate bank angle, and bank stability was estimated as the percentage of the bank that was not eroded. Canopy closure was determined from a spherical densiometer read at the center of each habitat unit.

Water samples were collected in 10% of each type of habitat unit (e.g., if 300 mid-channel pools were present in a stream, 30 were sampled). These collections were stratified along the length of streams (Clingenpeel & Cochran 1992). Water samples from each site were analyzed for conductivity, pH, bromide, nitrate, phosphorus, manganese, magnesium, sodium, cobalt, calcium, and sulfate. Analyses were conducted at Berea, Kentucky, U.S.A. with 1983 EPA Methods for Chemical Analysis of Water and Wastes. Dissolved oxygen and temperature were measured in the held with a digital meter when water samples were collected.

Fishes and macroinvertebrates were also collected in 10% of habitat units arranged longitudinally in each stream. Fishes were collected with multiple-pass electrofishing and block nets (Van Deventor & Platts 1985, Clingenpeel & Cochran 1992) and preserved for identification. Macroinvertebrates were collected at each site with a kick-net and substrate washing (5 min each). These samples were pooled and preserved for later identification (Clingenpeel & Cochran 1992). Macroinvertebrates (predominantly insect larvae) were identified to genus in most cases.

Data analysis

We summarized stream habitat and water chemistry characteristics for each stream by year and computed means for all measured variables. We calculated an overall mean and coefficient of variation for depth measurements (transect and thalweg). We used 39 physico-chemical variables in a principal components

analysis (PCA) to reduce the dimensionality of these data and applied the broken-stick model (Jackson 1993) to evaluate axis strength. Eigenvalues exceeded those of the broken-stick model for the first five axes, which accounted for 72% of the total variance. We did not attempt to interpret PCA axes; rather, we used PCA to objectively select a small subset of the original data that represented 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 because they had the highest respective component loadings for the first five axes. Conductivity and canopy cover had equally high loadings on the first axis, so we retained both variables.

We also summarized fish and macroinvertebrate data for each stream by year. For taxonomic analyses, we used fish species and macroinvertebrate genera (or order/family when the genus was not determined). We did not distinguish between juveniles and adults for fishes, but most individuals observed were adults. We classified fishes and macroinvertebrates into trophic groups according to Horwitz (I 978) and Merritt & Cummins (1984), after Allan (1995).

We used canonical correspondence analysis (CCA; ter Braak 1986, ter Braak & Smilauer 1998) to describe the relationships between regional fish and macroinvertebrate faunas (taxonomic and trophic) and the reduced set of environmental variables. We then used partial CCA to partition faunal variability (Borcard et al. 1992, Magnan et al. 1994, Aude & Lawesson 1998) into three variance components: ecological effects of the six environmental variables, effects related to the historically defined drainage basins, and their shared variation that could not be partitioned into pure effects (i.e., environmental variation unique to the drainage basins). We used Monte Carlo tests (1000 permutations) to estimate the significance of each model derived from CCA.

We used Mantel tests (Mantel 1967, Fortin & Gurevitch 1993) to examine the association between regional faunas and measured environmental variables. We were specifically interested in the amount of variation in taxonomic and trophic matrices that could be accounted for by the environmental matrix, and how dependent trophic matrices were on the taxonomic makeup of the regional faunas. For the Mantel test, we used rectangular n x n matrices (e.g., fish taxa by region) to construct triangular correlation matrices across all pairwise regional comparisons. The Mantel test determines the association between two of these triangular correlation matrices at a time, testing the null hypothesis that there is no association within elements of the matrices. Wc tested the ability of the environmental matrices to explain variation in the taxonomic and trophic matrices. We also examined the strength of the correlation between trophic and taxonomic matrices. We expected some correlation because the trophic matrices were built from taxonomic matrices. Because the trophic matrices were constructed from taxonomic matrices and are not independent, we focused only on the strengths of matrix correlations (r) and not associated p-values. We also performed partial Mantel tests, which are comparable in function and interpretation to partial correlation analyses (Zar 1996, Manly 1997). We conducted all Mantel tests separately for fishes and macroinvertebrates.

Results

A total of 30 species (9 families) of fishes (Appendix A) and I.52 genera (65 families, 20 orders) of macroinvertebrates (Appendix B) were collected over the 3-year study period. Examples of all major trophic groups (Horwitz 1978, Merritt and Cummins 1984, Allan 1995) were represented in these data.

For fishes (grouped by taxonomy and trophic affiliation), streams within individual drainage basins were associated closely and separated from other basins in multivariate space (Figure 2a and b). The six environmental variables we used in the analyses successfully separated both fish species and trophic groups into their respective streams according to drainage basins. In general, streams in the Saline basin had greater aerial canopy cover and more rooted vegetation. Streams in the Arkansas basin were characterized by more boulder substrate and greater bank stability, and streams in the Cossatot system had higher conductivity and greater variability in stream depth. Monte Carlo tests were significant for CCA axes 1 and 2 (Figure 2a, p = 0.01 and 0.02; Figure 2b, p = 0.01 and 0.05, for axis 1 and 2, respectively). Species with negative association along axis 1 included: *Lepomis* hybrids, *Noturus lachneri* (endemic to the Saline and Ouachita River systems), *Etheostoma collettei*, *Micropterus salmoides*, and *Aphredoderus sayanus*. These species were more common in tributaries of the Saline River, except *M. salmoides*, which was most common in tributaries of the Arkansas River. Species with high positive relationship with axis 2, indicating strong association with tributaries of the Arkansas River, included: *E. spectabile*, N. *exilis*, *M. salmoides*, and *Pimephales*

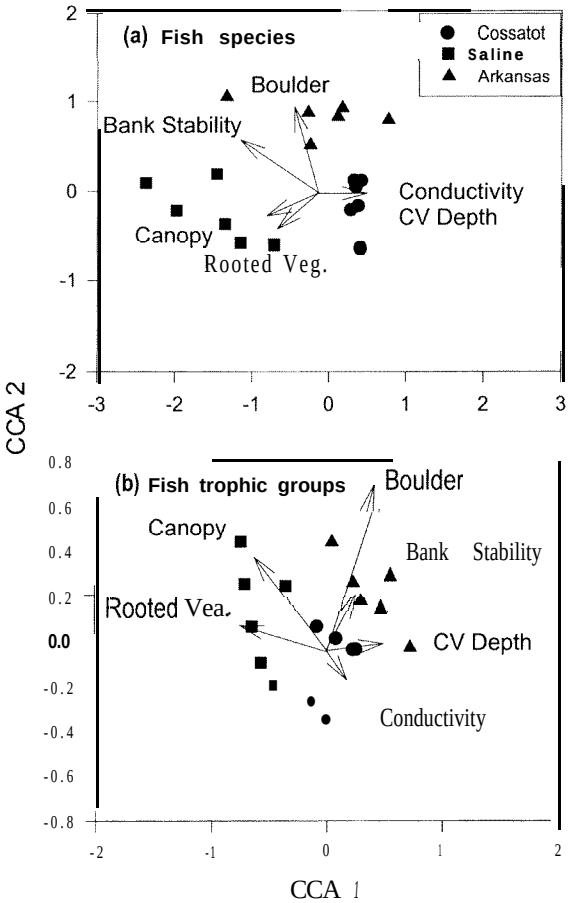

Figure 2. The relationship between environmental gradients (vectors), streams by year, and fish taxa (a) and trophic groups (b) for six streams located in the Ouachita Mountains. Shown are the first (x) and second (y) ordinalion axes derived from CCA. Axes I and 2 were significant (Monte Carlo randomization test) for both fish taxa (p = 0.01 and 0.02) and trophic groups (p = 0.01 and 0.05).

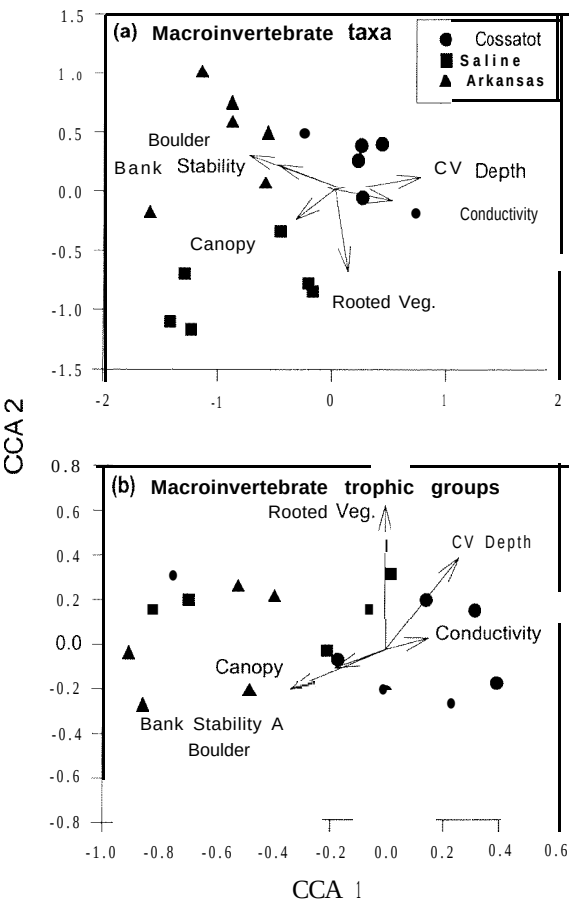

Figure 3. The relationship between environmental gradients (vectors), streams by year, and macroinvertebrate taxa (a) and trophic groups (b) for six Ouachita Mountain streams. Shown are the first (x) and second (y) ordination axes derived from CCA. Both nxes I and 2 were significant (Monte Carlo randomization test) for taxa (p = 0.01), and the first axis was significant for trophic groups (p = 0.0 1).

notatus. Species located near the center of the plot were more common in tributaries of the Cossatot River, and included: *Campostoma anomalum*, *E. radiosum*, *Fundulus catenatus*, *Ameiurus nebulosus*, *Notropis boops*, and *Lythrurus snelsoni* (endemic to the Little River system).

Macroinvertebrate taxa showed a similar pattern to fish species, but the separation of streams into their respective basins was not as evident for macroinvertebrate trophic groups (Figure 3a and b). The same environmental gradients that separated basins for fishes also differentiated macroinvertebrate taxa among basins, and Monte Carlo tests were significant for both axes (p = 0.01 for both). Several taxa were associated with only one drainage basin. Gastropods and bivalves were only found in tributaries of the Saline River, as were the families Saldidae, Curculionidae, Culicidae and Phoridae. Tributaries of the Cossatot River had the most unique taxa, including: Nematomorpha, Astacidae, Ephemeridae, Isonychiidae, Calopterygidae, Capniidac, Mesoveliidae, Helicopsychidae and Psychomyiidae. The families Ephemerellidae, Nemouridae, Glossosomatidae, Tortricidae and Muscidae were unique to tributaries of' the Arkansas River. For macroinvertebrate trophic groups, streams were not clearly separated by drainage

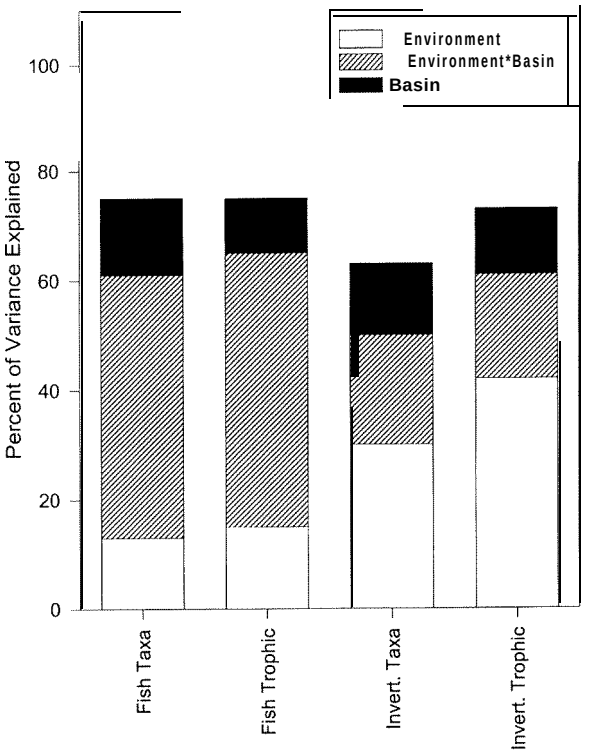

Figure 4. **Amount of variation in** fish **and macroinvertebrate** taxa **and trophic groups explained by drainage basins (basin), environmental** gradients **independent** of **drainage basins (environment), and** their **shared variance components (i.e., spatially structured environmental features;** environment∗basin).

basin (Figure 3b), and Monte Carlo tests were significant only for the first axis (p = 0.01).

Variance partitioning with partial CCA indicated that fishes and macroinvertebrates responded differently to historical and environmental variance components. Most of the variation for fishes was explained by basin-level differences in the environmental variables (environmentcbasin; Figure 4). In contrast, environmental variation that was independent of drainage basins explained most of the variation for macroinvertebrates (environment; Figure 4). This was particularly true for macroinvertebrate trophic groups, with more than 40% of their variation being explained by environmental variability independent of historical, basin-level constraint. Drainage basins alone explained only a minor portion (basin; Figure 4) of the variability for either fishes or macroinvertebrates. This factor represents a purely historical component (i.e., drainage basin isolation effects) of the analyses.

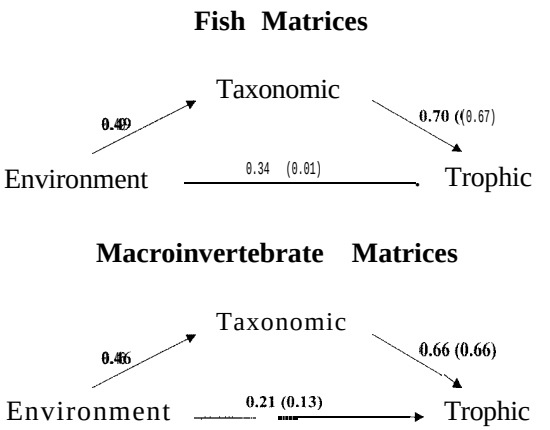

Figure 5. **Results from Mantel tests showing the relationships(r) between taxonomic and trophic matrices** and **large-scale environmental variability. Results from partial Mantel tests are indicated in parentheses.**

Mantel tests indicated that fish and macroinvertebrate trophic groups were associated with environmental variables and taxonomic matrices but were associated most strongly with taxonomic groups. The strongest correlations were between trophic and taxonomic matrices for both fishes and macroinvertebrates (Figure 5). Correlations between trophic groups and environmental variability were not as strong, and when the effect of taxonomy was removed (partial Mantel; For-tin & Gurevitch 1993), there was little correlation left between trophic **groups** and environmental variables (Figure 5). Thus, the correlations between trophic and environmental matrices were confounded by the strong relationships between trophic and taxonomic matrices. For fishes particularly, these results are congruent with the similar patterns observed for taxonomic and trophic **groups** when variance was partitioned among effects (Figure 4). Perhaps the most interesting pattern to emerge from these analyses was that fish and macroinvertebrate taxa were associated more strongly with environmental variables than were trophic groups (Figure 5). This pattern was the opposite of our original prediction that trophic groups would be associated more strongly with environmental variability than taxa.

Discussion

Streams can be extremely complex and variable environments, and this variability contributes to the dynamic nature of their faunal assemblages (Lancaster et al. 1990). At the stream reach scale,

environmental variability is important in structuring fish and macroinvertebrate assemblages (Gorman & Karr 1978, Matthews et al. 1988, Lancaster et al. 1990, Richards & Host 1994, Clenaghan et al. 1998, Lonzarich et al. 1998, Taylor & Warren 2001). However, species assembly at smaller spatial scales is also influenced by regional and historical processes (Hugueny 1997, Ricklefs et al. 1999), and knowledge of these regional and historical influences are critical for refining hypotheses of community assembly and organization for stream biota (Brooks & McLennan 1993, Caley & Schluter 1997, Angermeier & Winston 1998). Large-scale influences provide a physical and biogeographic framework for stream systems within which local processes must operate (Tabacchi et al. 1998). Thus, it is important to understand the role of history and large-scale environmental effects on the abundance and distribution of regional faunas.

Because most fish species are constrained to their historically defined drainage basins and many insect taxa (after emergence) are free to cross basin barriers, we anticipated that each taxonomic group would respond differently to the environmental variables that were examined. Fish species were influenced more by spatially structured environmental features (i.e., environmental variability associated with an individual drainage basin) than variability that was independent of the drainage basins. Environmental variability associated with drainage basins likely reflects historical differences in geology and climate, and the resulting differences in hydrology and other physical stream features. This type of variability could also represent differences in land use among basins, but Williams et al. (2002) used these same data to address land use impacts and found no significant impacts of silvicultural activities on regional fish or macroinvertebrate faunas in these systems. Thus, as we predicted, historical constraint was an important limitation on regional fish faunas. History, in this case, was operating as a constraint on local habitat conditions, which, in turn, affected the types of assemblages that would occupy those streams.

In contrast, macroinvertebratc taxa were influenced more strongly by environmental variability that was independent of drainage basins, indicating less historical constraint than for fishes. In short, macroinvertebrates were associated with large-scale environmental gradients regardless of basin. Insects associated with both terrestrial and aquatic systems at different life-history stages can choose breeding sites based on environmental conditions at a stream locality (Anderson & Wallace 1984) and have the potential to cross drainage basin boundaries. These same basin boundaries represent historical barriers to fish dispersal. In general, macroinvertebrates seem to respond more to local environmental conditions that vary across a larger geographic region than do fishes, which are more affected by environmental factors unique to the drainage basins that contain them (Lammert & Allan 1999).

Fish taxa and trophic groups showed a similar response to the measured environmental variables and also similar degrees of historical constraint. For macroinvertebrates, trophic and taxonomic groups also seemed to show similar patterns, although the trophic groups were less constrained by basin-level properties. These results were surprising, particularly for macroinvertebrates, considering that the trophic groupings we used reflect their functional feeding role in streams (Merritt & Cummins 1984, Allan 1995). We did not expect such a similar pattern between the taxonomic and trophic groups for fishes or macroinvertebrates. We predicted that trophic groups would be strongly associated with measured environmental variables (independent of drainage basins) and less influenced by historical, basin-level processes than taxonomic groupings. This was generally the case for macroinvertebrates, but for fishes, both trophic and taxonomic groups separated along the same multivariate gradients.

Trophic groupings for fishes and macroinvertebrates were associated with both environmental variables and taxa, with the strongest correlations between trophic and taxonomic matrices. In contrast to our original prediction, we found that taxa were associated more closely with the environmental variables than trophic groups, at least at the drainage basin scale. Originally, we predicted that the trophic groups would have a stronger association with large-scale environmental variability because of their relative freedom from phylogenetic and historical constraints, but this was not the case. Although the causal mechanisms responsible for this pattern are beyond the scope of our analyses, we propose two potential explanations. The first is an issue of scale, in that these patterns may be affected by the basin-level sampling design. We were essentially comparing the 'entire' species pool of one stream with the 'entire' species pool of other streams, rather than comparing discrete samples from discrete habitat types. At this broad spatial scale, trophic groups may be too coarse of a classification system to elucidate meaningful relationships with environmental variability. The second explanation is related to the trophic categories themselves. Our results are highly dependent on the

trophic classification system we used (see Horwitz 1978, Merritt & Cummins 1984, Allan 1995). The patterns we found may differ with more detailed trophic groupings. If trophic groups are to be used as an ecological measure in basin-level studies, a more thorough analysis of the relationships between different trophic classification schemes and their taxonomic make-up should be attempted. Perhaps better trophic classification systems are needed for stream organisms, particularly for fishes where most schemes are based on diets rather than functional feeding roles (Matthews 1998). Because many government agencies are recommending and adopting these types of basin-level studies to manage aquatic systems (Ponce et al. 1982, Hankin 1984, Hankin & Reeves 1988, Clingenpeel & Cochran 1992, Williams et al. 2002), the limitations of some measures (i.e., trophic groupings) in elucidating ecological relationships need to be addressed. As modeled, trophic groups had a comparatively weak relationship with environmental variability at the regional scale.

One of the primary goals of ecology is to quantify the relationship between species and their environment (Krebs 2001), but understanding these relationships is complicated by their strong dependence on spatial and temporal scale (Wiens et al. 1986, Lohr & Fausch 1997). In stream systems, factors like history, climate, and hydrology are important in determining the structure of assemblages at larger scales. As the spatial scale is reduced, local habitat variability becomes more important (Poff & Ward 1989, Wiley et al. 1997, Cooper et al. 1998, Pusey et al. 1998). As shown here, the structure of regional fish (and to a lesser degree macroinvertebrate) faunas was dependent in large part on biogeographical history and the degree of spatial constraint operating on environmental gradients. Although most studies of streams are conducted at smaller scales, large-scale and historical factors must be considered to fully understand the structure and function of local assemblages (Brooks & McLennan 1993, Angermeier & Winston 1998, Caley & Schluter 1997). If limitations (e.g., interpretation of causal relationships) are understood, multivariate analyses can be a useful tool to assess these relationships at different scales and contribute to our ability to understand, predict, and effectively manage aquatic systems (Tonn et al. 1983, Williams et al. 2002).

Acknowledgements

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Appendix A. Fish species collected by U.S. Forest Service inventory teams in the six study streams (grouped by basin) and their assigned trophic groups.* Presence in a drainage basin indicated by 'I'.

Family/species	Trophic group	Saline	Cossatot	Arkansas
Cyprinidae				
Campostoma anomalum	ALG	I	I	I
Luxilus chrysocephalus	GI	0	I	0
Lythrurus snelsoni	WCI	0	I	0
Lythrurus umbratilis	WCI	I	I	I

Appendix A. (Continued)

Family/species	Trophic group	Saline	Cossatot	Arkansas
Notropis boops	WCI		1	
Pimephales notatus	OMN		0	
Semotilus atromaculatus	GI		1	1
Catostomidae				
Erimyzon oblongus	OMN			
Ictaluridae				
Ameiurus natalis	OMN		1	
Ameiurus nebulosus	OMN	0	1	0
Noturus exilis	BI	0	0	
Noturus lachneri	BI		0	0
Esocidae				
Esox americanus	PIS			0
Aphredoderidae				
Aphredoderus sayanus	OMN	1		0
Fundulidae				
Fundulus catenatus	SI	1		0
Fundulus olivaceus	SI	1		0
Atherinidae				
Labidesthes sicculus	WCI	1	0	0
Centrarchidae				
Lepomis cyanellus	GI			1
Lepomis macrochirus	CI			0
Lepomis megalotis	GI	1		1
Lepomis punctatus	GI	1	0	0
Lepomis hybrid	GI	1	0	0
Micropterus dolomieui	PIS	0		0
Micropterus punctulatus	PIS		0	0
Micropterus salmoides	PIS		0	0
Percidae				
Etheostoma collettei	BI	1	0	0
Etheostoma radiosum	BI	0		1
Etheostoma spectabile	BI	0		1
Etheostoma whipplei	BI			
Percina caprodes	BI	1	0	0

*Assigned trophic groups are as follows: ALG = algivore, BI = benthic insectivore, GI = general insectivore, OMN = omnivore, PIS = piscivore, SI = surface insectivore, and WCI = water-column insectivore.

Appendix B. Macroinvertebrate taxa collected by U.S. Forest Service inventory teams in the six study streams (grouped by basin) and their assigned trophic groups*. Presence in a drainage basin indicated by '1'.

Order/family (no. genera)	Trophic group	Saline	Cossatot	Arkansas
Gastropoda				
Ancylidae (1)	SH	1	0	0
Planorbidae (1)	SH	1	0	0
Bivalvia				
Sphacriidae	CF	1	0	0
Nematomorpha	NF	0	1	0
Oligochaeta	CG	1	1	1
Branchiohdellida	co	1	1	1
Hirudinen	PA	1	1	0

Appendix B. (Continued)

Order/family (no. genera)	Trophic group	Saline	Cossatot	Arkansas
Amphipoda				
Crangonyctidae (2)	CG	1	0	1
Talitridae (1)	CG	1	1	1
Isopoda				
Asellidae (2)	CG	1	1	1
Decapoda				
Astacidae	CG	0	1	0
Cambaridae (2)	CG	1	1	1
Hydrachnida				
Hydrachnidae	PR	1	1	1
Collembola	CG	1	1	0
Ephemeroptera				
Raetidae (3)	CG	1	1	1
Caenidae (1)	CG	1	1	1
Ephemerellidae (2)	CG	0	0	1
Ephemeridae (2)	CG	0	1	0
Heptageniidae (4)	SC	1	1	1
Leptophlcbiidac (3)	CG	1	1	1
Isonychiidae (1)	CF	0	1	0
Lcptohyphidae (I)	CG	1	1	0
Odonata				
Aeshnidae (1)	PR	1	1	1
Calopterygidae (2)	PR	0	1	0
Coenagrionidae (2)	PR	1	1	1
Corduliidae (3)	PR	1	1	0
Gomphidae (3)	PR	1	1	1
Libellulidae (1)	PR	1	1	0
Plecoptera				
Capniidae (1)	SH	0	1	0
Leuctridae	SW	1	1	1
Nemouridae (I)	SH	0	0	1
Perlidae (5)	PR	1	1	1
Hemiptera				
Corixidae (2)	PI	1	0	1
Gerridae (4)	PI	1	1	1
Mesoveliidae (1)	PI	0	1	0
Notonectidae (1)	PI	1	1	1
Saldidae (1)	PI	1	0	0
Veliidae (2)	PI	1	1	1
Megaloptera				
Corydalidae (2)	PR	1	1	1
Sialidae (1)	PR	1	1	1
Trichoptera				
Glossosomatidae (1)	SC	0	0	1
Helicopsychidae (1)	SC	0	1	0
Hydropsychidae (4)	CF	1	1	1
Lepidostomatidae (1)	SH	1	1	1
Leptoccridae (2)	CG. PR	1	1	0
Limnephilidae (2)	SC, SH	1	0	1
Philopotamidae (2)	CF	1	1	1
Polycentropodidae (1)	PR	1	1	1
Psychomyiidae (1)	SC	0	1	0
Rhyucophilidae (1)	PR	1	1	1

Appendix B. (Continued)

Order/family (no. genera)	Trophic group	Saline	Cossatot	Arkansas
Lepidoptera				
Pyralidac (1)	SH	1	1	0
Tortricidae (1)	SH	0	0	
Coleoptera				
Curculionidae (1)	SH	1	0	0
Dryopidac (1)	SH	1	1	1
Dytiscidae (7)	PI, PR	1	1	1
Elmidae (5)	CG	1		1
Gyrinidae (I)	PR			1
Hydrophilidae (4)	PI, PR	1	1	1
Psephenidae (2)	SC	1	1	1
Staphylinidae (1)	PR	0		1
Diptera				
Ceratopogonidae (2)	PR		1	1
Chironomidae (35)	CG, PR, SH, CF, SC	1		1
Culicidae (1)	CF	1	0	0
Dixidae (2)	CC	0	1	1
Empididae (1)	PR			1
Muscidae (1)	PI	0	0	
Phoridae	PR		0	0
Simuliidae (2)	CF	1		1
Tabanidae (4)	CG, PI		1	1
Tipulidae (5)	PR, SH, CG			

'Assigned trophic groups are as follows: CF = collector-filterer, CG = collector-gatherer, CO = commensal, NF = non-feeding, PI = predator-piercer, PR = predator-engulf&, SC = scraper, and SH = shredder.