

Distribution, abundance, and diversity of stream fishes under variable environmental conditions

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Abstract: The effects of stream size and flow regime on spatial and temporal variability of stream fish distribution, abundance, and diversity patterns were investigated. Assemblage variability and species richness were each significantly associated with a complex environmental gradient contrasting smaller, hydrologically variable stream localities with larger localities characterized by more stable flow regimes. Assemblages showing the least variability were the most species-rich and occurred in relatively large, stable environments. Theory suggests that species richness can be an important determinant of assemblage variability. Although this appears to be true in our system, we suggest that spatial and temporal heterogeneity in the environment largely determines both assemblage richness and variability, providing a more parsimonious explanation for the diversity–variability correlation. Changes in species richness of local assemblages across time were coordinated across the landscape, and assemblages formed spatially and temporally nested subset patterns. These results suggest an important link between local community dynamics and community-wide occurrence. At the species level, mean local persistence was significantly associated with regional occurrence. Thus, the more widespread a species was, the greater its local persistence. Our results illustrate how the integrity of local stream fish assemblages is dependent on local environmental conditions, regional patterns of species distribution, and landscape continuity.

Résumé : Nous avons étudié les effets de la taille du cours d'eau et du régime des eaux sur la variabilité spatiale et temporelle de la répartition, de l'abondance et des patrons de diversité des poissons dans ce cours d'eau. La variabilité du peuplement et la richesse en espèces sont toutes deux associées significativement à un gradient complexe du milieu, mais de façon différente dans les sites lotiques plus petits à hydrologie variable et les sites plus grands à régime hydrologique plus stable. Les peuplements qui subissent le moins de variabilité sont ceux qui ont la richesse en espèces la plus importante et qui se retrouvent sur les sites plus étendus et plus stables. La théorie écologique indique que la richesse en espèces peut être un important facteur déterminant de la variabilité des peuplements. Bien que cela semble être le cas dans le système que nous avons étudié, nous croyons que l'hétérogénéité spatiale et temporelle du milieu détermine en grande mesure tant la variabilité que la richesse des peuplements, ce qui explique de façon plus parcimonieuse la corrélation diversité–variabilité. Les changements de richesse en espèces des peuplements locaux au cours du temps sont synchronisés sur tout le paysage et les peuplements forment des patrons de sous-ensembles emboîtés spatialement et temporellement. Nos résultats indiquent un lien important entre la dynamique de la communauté locale et l'occurrence à l'échelle de la communauté. Au niveau spécifique, la persistance locale moyenne est associée significativement à l'occurrence régionale. Ainsi, plus une espèce est largement répartie, plus sa persistance locale est grande. Nos résultats montrent combien l'intégrité des peuplements locaux de poissons dépend des conditions locales de l'environnement, des patrons régionaux de répartition des espèces et de la continuité du paysage.

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Introduction

Two fundamental attributes of a community are the number of species present and their abundance structure. Both

attributes are dynamic, and it is logical to expect a relationship between them (Tokeshi and Schmid 2002). Indeed, one of the most hallowed tenets in ecology and conservation biology is the idea that diversity promotes the stability of

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communities and ecosystem processes. This idea can be traced to Elton (1958), who was concerned with the ecological impact of exotic animals and plants on native flora and fauna. It remains equivocal which aspect of diversity (number of species, functional groups, trophic groups, etc.) is the important causal factor, or whether the environment drives patterns of diversity and stability (Sankaran and McNaughton 1999). The stability–diversity question is obfuscated further by much disagreement over the meaning of the term “stability”. Grimm and Wissell (1997) identified 163 definitions and 70 different stability concepts.

In spite of these difficulties, the theoretical underpinnings of the stability–diversity hypothesis, as well as the attendant criticism and debate, allow tangible predictions to be made about the structure and function of ecological systems. We know that communities are affected by extrinsic factors (Brown and Lomolino 1998) ranging from historical processes (Cornell and Lawton 1992; Gorman 1992; Williams et al. 2003) to landscape- or regional-level processes (Turner 1989; Schlosser 1991; Pickett and Cadenasso 1995). Recent metapopulation- and macroecology-based studies have focused on identifying landscape-level processes and species-specific life history and ecological traits that may be important in determining various community properties. For example, regional processes, such as immigration and extinction dynamics, can have important effects on local community structure (Taylor and Warren 2001; Cottenie et al. 2003; Warren et al. 2003), and these dynamics may be associated with species-specific traits such as body size, mean local abundance, species–environment relationships, and regional occurrence (Gotelli and Taylor 1999).

In streams (and other ecosystems), interaction between the environment and population processes affects the distribution and abundance patterns of species and, thus, community structure (Brown 1984). Such interactions have been the focus of much research, including studies on species-specific habitat selection, intracommunity interactions, habitat size and complexity, isolation and fragmentation, and immigration and extinction dynamics. However, determining environmental influences on spatial and temporal assemblage patterns is difficult because different spatial and temporal scales yield different types of information (Wiens et al. 1986). Two complex environmental gradients appear to be very important in influencing stream fish assemblages and habitat structure: stream size and the flow regime (Gorman and Karr 1978; Horwitz 1978; Schlosser 1987). Longitudinal zonation or succession of fish assemblages is a well-known phenomenon (see Matthews 1998). A specific pattern embedded in this concept is the increase in the number of fish species from headwaters to higher-order streams (Sheldon 1968; Schlosser 1987; Rahel and Hubert 1991). This pattern often is attributed to a general increase in habitat size and heterogeneity, coupled with reduced variability in flow regime that occurs from upstream to downstream. These patterns are altered by habitat fragmentation at different scales. Locally, low flows may promote isolation of habitats that are connected during periods of ambient or high flows. At larger spatial scales, dams and channelization alter stream habitat and flow regime and reduce or curtail routes of dispersal. Thus, stream size and flow regime, as well as the disruption of these factors by fragmentation at multiple scales, may be

the most important drivers of observed patterns of assemblage stability and diversity of fishes in stream systems.

Taylor and Warren (2001) found that occupancy of local sites across time formed significant nested subset patterns at nine of the 12 localities from our study system. A nested subset pattern occurs when species-poor samples form subsets of species-rich samples, such that rare species (low incidence) occur only in the richest samples and common species (high incidence) occur in samples with a wide range of richness values. This highly structured temporal pattern indicated a gradient regarding local persistence of species. The strength of the nested pattern was strongly associated with local extinction rate, indicating a deterministic nature to the local extinction process. Additionally, there was spatial structure to immigration and extinction processes. Immigration rates were highest at large stream localities, and extinction rates were highest where variability in the flow regime was high (headwater localities).

Based on the development of these concepts and the theory behind them, we had two major objectives in this study. For the first objective, we used an assemblage-based approach designed to identify important spatial and temporal trends in assemblage properties (structure, species richness, variability) and relate these to the underlying environmental template. To meet this objective, we examined relationships among assemblage structure, assemblage variability, species richness, and the spatial and temporal variability of the environment in our system. We predicted that assemblage properties would each show strong responses to gradients of stream size and flow variability and that environmental influence would render trivial any relationship that may occur between species richness and assemblage variability. Furthermore, given the temporally nested patterns of local persistence that Taylor and Warren (2001) found, we predicted that fluctuations in local species richness would be correlated across the landscape, suggesting a common response by assemblages to changing environmental conditions. Likewise, we also predicted that species-richness patterns across the landscape would form nested subset patterns and be strongly correlated through time. Such nonrandom, coordinated patterns in space and time would suggest an important link between local community assembly and community-wide occurrence patterns.

For our second objective, we used a species-based, macroecological approach to examine the relationships among species-specific properties, including regional occurrence, mean local abundance, and mean local persistence. Species vary with regard to their life history and ecological traits (Gotelli and Taylor 1999), and the structure of assemblages within a region is, in part, because of this inherent species-specific variation. If assemblages exhibit coordinated patterns in space and time, it is reasonable to presume a relationship between locally and regionally expressed attributes of species. For example, the positive association between regional occurrence and mean local abundance is a well-documented pattern for a wide variety of systems (Hanski et al. 1993; Gaston et al. 1997; Hughes 2000), and we predicted the same from our system. Further, if assemblages exhibit nested occurrence patterns in space (regional scale) as they have been shown to do in time (local scale), we hypothesize that species will show a positive association between

regional occurrence and local persistence. Delcourt et al. (1983), Wiens (1989), and Holling (1992) have all suggested that there is congruence between spatial and temporal scales in ecological processes. Such a pattern would have obvious and important conservation and management implications (Bissonette and Storch 2002), especially in highly fragmented systems where dispersal corridors are upset.

Materials and methods

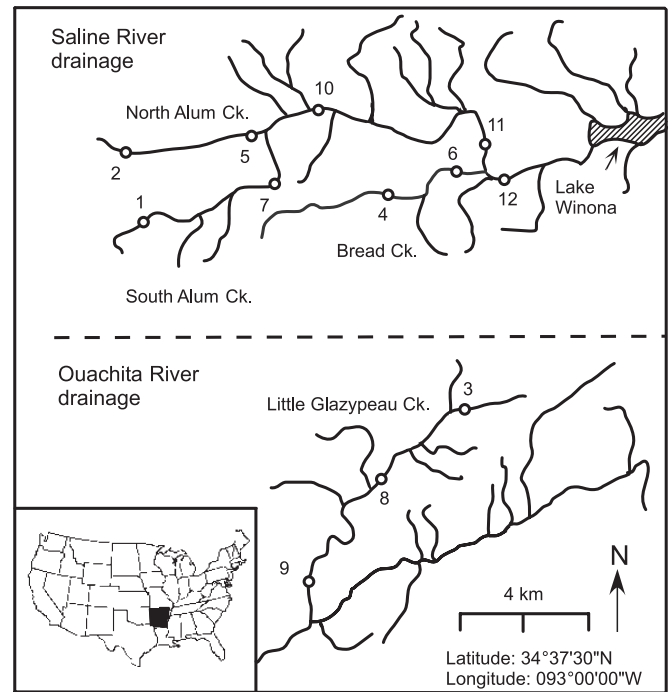
Study area

The Ouachita Mountains of Arkansas and Oklahoma are characterized by strongly folded, uplifted, sedimentary rock and pine–oak upland forest (Robison 1986). Our sample sites were located in two river systems within the Red River drainage on the eastern side of the uplift. Nine sites were located in the Alum Fork of the Saline River (hereafter Alum Fork) and three sites were in Little Glazypeau Creek of the Ouachita River system (Fig. 1). Both systems are high gradient with strong riffle–pool development. The water is generally clear except after extensive precipitation events (terrestrial runoff) and during drought (increased primary productivity in isolated pools). Pools ranged from a few metres to ≥ 50 m in length and, under ambient conditions, are separated by swift riffle habitats consisting of coarse substrate materials. These streams are characterized by high variability in the flow regime. Water levels can rise and fall rapidly with heavy precipitation events, and headwater reaches are intermittent, frequently drying to isolated pools during summer and autumn months. Thus, habitats and their corridors can grow, shrink, and change configuration rapidly (Taylor 1997; Taylor and Warren 2001; Williams et al. 2003). These small, hydrologically dynamic streams provide an ideal system to address questions concerning the effects of environmental variability on distribution and abundance patterns of fishes.

Data collection

From November 1995 through August 1998, we sampled fishes and measured environmental variables at 12 sites (144 total samples; Fig. 1). We sampled in November, February, May, and August in each year and always completed sampling within 3–4 days. At each site, we electrofished all habitat types within a 100 to 200 m stream reach (depending on stream size) that spanned at least two pool–riffle sequences. For stream fishes, the stream reach is a logical sample unit in a river system (Frissell et al. 1986), and the effects of disturbance on assemblage-level properties are measured most commonly at this scale (see Matthews 1998). The same individual (CMT) always operated the backpack electroshocker (model 12-A; Smith-Root Inc., Vancouver, Washington), and there were always two to three netters present to capture stunned fishes. Riffles were sampled from bottom to head, and runs and pools were sampled in a downstream direction. Because of the small size and clear water, we were able to sample stream reaches and all habitats therein efficiently. We opted for a representative reach approach (Frissell et al. 1986; Williams et al. 2004) and the increased spatial coverage rather than using intensive multipass procedures that would have required greater effort per habitat and a reduced reach length (see Taylor and Warren 2001). After sampling a

Fig. 1. Map showing the 12 study sites in south-central Arkansas, USA. Numbers represent rank in catchment area. The broken line indicates that geographic proximity of the two drainages is not as shown. Both drainages occur in the Red River system.



site, we identified and counted all fishes and returned them to the stream alive.

After fish sampling and processing, we measured habitat variables along transects (perpendicular to stream flow) spaced at 10 to 15 m intervals along the sampled stream reach. The number of transects varied (eight to 12) depending on the length of the sampled stream reach. We permanently marked transects and resurveyed them during each visit. At every other metre along transects, we measured current velocity, depth, and dominant substrate type. We categorized substrate following Taylor and Lienesch (1996a, 1996b) as bedrock, large boulder (>300 mm), small boulder (150–300 mm), cobble (50–149 mm), gravel (3–49 mm), or sand (<3 mm). We measured stream width at each transect and noted the presence or absence of aquatic macrophytes, algae, undercuts, and woody debris.

Data treatment and analyses

Stream size is a complex variable and many features of the environment often are used as its surrogate. For each site, we measured upstream catchment area, and for each sample (site–date), we determined means and maxima for stream width, stream depth, and current velocity. We then averaged these values to get site-specific measures of width, depth, and current speed across the three years. We log-transformed these environmental variables before analyses to improve normality and linearity. Because we also were interested in the temporal variation displayed by our measured environmental variables, we calculated coefficients of variation (CVs) for each site across sample dates for all width, depth, and current velocity variables.

To quantify spatial heterogeneity in our measured variables at each site, we chose one sample period in the spring (May 1997) and used the point substrate, depth, and current speed measurements to estimate variation within each site. For substrates, we used the Shannon–Weiner diversity index to calculate a measure of substrate heterogeneity for each site. For current speed and depth, we calculated CVs based on all point estimates.

Unless otherwise noted, we calculated local species richness as the total number of species collected across the entire study period at a site. This cumulative measure of species richness estimates the “realized species pool” for individual sites (Taylor and Warren 2001). For the macroecological analyses of species-specific traits, we limited our data to the nine sites in the Alum Fork drainage. We determined the regional occurrence of each species by totaling the number of occupied sites in the study area, regardless of the number of occupied samples at a site. For each species, we also counted the number of occupied samples for each site and averaged these numbers to obtain a mean local persistence. To calculate mean local abundance, we summed abundances across samples for each species and averaged these across all occupied sites.

To summarize the fish assemblage data and quantify the effects of stream size and habitat variability on fish assemblages, we used univariate and multivariate statistical methods. We conducted ordinations with PC-ORD software (B. McCune and M.J. Mefford 1995). We performed all other data analyses with SYSTAT (SPSS Inc. 2000), EcoSim (Gotelli and Entsminger 2001), and the Nestedness Temperature Calculator (Atmar and Patterson 1995).

We used nonmetric multidimensional scaling (NMS) to provide a convenient and interpretable picture of fish assemblage change across spatial and temporal gradients. NMS is an indirect ordination technique designed to summarize complex community data (Gauch 1982). Because it is not based on any distributional assumptions (McCune and Grace 2002), NMS is well suited for use with ecological data and is not plagued with problems of other ordination methods such as correspondence analysis and detrended correspondence analysis (Wartenburg et al. 1987; Jackson and Somers 1991; Legendre and Legendre 1998). The technique is based on an iterative search algorithm that minimizes departure from monotonicity in the relationship between dissimilarity in the original data matrix and distances in the reduced ordination space (McCune and Grace 2002).

We used NMS on two data sets: in the first, we ordinated all samples to assess temporal variation in assemblages at each site, and in the second, we summed abundances at each site to examine among-site differences in overall assemblage structure. Before running the NMS procedure, we square-root-transformed fish abundance data and computed Bray–Curtis distances among all sample units. We followed the general NMS procedure outlined by McCune and Grace (2002, pp. 135–136).

To quantify assemblage variability at sites, we calculated all pairwise Bray–Curtis distances across all samples for each site and then used the average distance as an overall site-specific measure of variability. The Bray–Curtis distance is sensitive to changes in species abundance (Wolda 1981), a desirable trait for our purposes. Absolute and relative changes

in abundance are both sources of assemblage variability that we wanted to quantify among samples for a given site. Beals (1984) highly recommended the Bray–Curtis distance based on its success over a wide range of ecological systems (Ludwig and Reynolds 1988). We then used linear regression to assess the relationship between assemblage variability and species richness.

Principal components analysis (PCA) was used on all stream size variables and associated CVs to identify the primary environmental gradients in the system. These gradients were then used in regression analyses to test our hypothesis that assemblage structure, diversity, and variability patterns would be strongly associated with local environmental conditions.

Because our regression analyses assume independence of data points (sites), we first examined our variables for spatial patterning using the Mantel test. First, pairwise stream distances (km) were measured among sites (Alum Fork drainage). Difference matrices were then constructed for all variables and matrix correlations were computed with the geographic matrix. Significance was assessed with a Monte Carlo procedure (Fortin and Gurevitch 1993) based on 5000 permutations.

We used Atmar and Patterson’s (1993) T (temperature) to assess the degree of nestedness across the landscape for each sampling period in the Alum Fork system. Their T is well correlated with other measures of nestedness that have been proposed in recent years (see review by Wright et al. 1998). The T is derived from entropy and information theory and describes the unexpected presences and absences of species in a matrix that has been packed into a state of maximum nestedness. A T of 0° defines complete order and perfect nestedness, whereas a T of 100° would result from a completely random matrix. We used a Monte Carlo procedure (5000 randomizations) to assess the probability that such a distribution pattern could occur by chance. Fischer and Lindenmayer (2002) found that T was prone to Type I errors but cautioned that other methods may be prone to Type II errors. Thus, we conservatively set α at 0.01 for our nestedness analyses. In a review of null models, Gotelli (2000) discussed different types of errors that may affect the significance of various null models.

Finally, we assessed site-specific change in the species richness of samples in the Alum Fork system (nine sites) across all time periods and compared these patterns across the landscape with Kendall’s coefficient of correlation. Likewise, we use the coefficient to assess changes in landscape patterns of species richness across time.

Results

We collected a total of 30 fish species (and numerous individuals of a hybrid sunfish, *Lepomis megalotis* × *cyanellus*) from the 12 sites. Species varied greatly in their overall relative abundances and distribution across sites (Table 1). At the coarsest level, five species were collected only from the Little Glazypeau system, and six species were collected only in the Alum Fork system. Large-scale historic differences in geomorphology, speciation, extinction, and dispersal account for the nonshared components between the regional assemblages (Cross et al. 1986). The two systems

Table 1. Species, occurrences in the two drainage systems, relative abundances, and Pearson correlations of species with the first two axes from a nonmetric multidimensional scaling (NMS) analysis on the species-by-site summed abundance matrix.

Species	Alum Fork	Little Glazypeau	Percent abundance	NMS 1 (0.50)	NMS 2 (0.47)
<i>Ameiurus natalis</i>	5	2	<0.01	-0.73	0.60
<i>Aphredoderus sayanus</i>	8	1	0.01	-0.39	-0.57
<i>Campostoma anomalum</i>	8	3	0.18	-0.86	0.61
<i>Chaenobryttus gulosus</i>	1	0	<0.01	-0.33	0.03
<i>Erinomyzon oblongus</i>	9	3	0.04	.01	-0.75
<i>Esox americanus</i>	8	2	0.01	-0.16	-0.68
<i>Etheostoma blennioides</i>	2	1	<0.01	-0.57	0.31
<i>Etheostoma collettei</i>	6	0	0.07	-0.68	-0.14
<i>Etheostoma radiosum</i>	0	3	0.05	-0.04	0.81
<i>Etheostoma whipplei</i>	9	0	0.09	0.21	-0.86
<i>Fundulus catenatus</i>	0	2	0.01	-0.24	0.73
<i>Fundulus olivaceus</i>	7	3	0.05	-0.89	0.18
<i>Hypentelium nigricans</i>	0	2	<0.01	-0.25	0.73
<i>Ichthyomyzon gagei</i>	3	0	<0.01	-0.56	-0.02
<i>Labidesthes sicculus</i>	6	0	0.01	-0.67	-0.08
<i>Lepomis cyanellus</i>	9	3	0.07	0.29	0.35
<i>Lepomis hybrid</i>	5	0	<0.01	-0.06	-0.57
<i>Lepomis macrochirus</i>	5	3	0.01	-0.43	0.47
<i>Lepomis megalotis</i>	8	3	0.19	-0.93	0.34
<i>Lythrurus umbratilis</i>	7	3	0.07	-0.55	-0.01
<i>Luxilus chrysocephalus</i>	0	3	0.01	-0.15	0.81
<i>Micropterus dolomieu</i>	0	1	<0.01	-0.25	0.49
<i>Micropterus punctulatus</i>	4	2	<0.01	-0.72	0.43
<i>Micropterus salmoides</i>	3	2	<0.01	-0.35	0.24
<i>Notropis boops</i>	6	1	0.02	-0.51	-0.01
<i>Notropis ortenburgeri</i>	3	0	0.01	-0.23	-0.33
<i>Noturus nocturnus</i>	0	1	<0.01	-0.25	0.49
<i>Noturus lachneri</i>	7	0	0.05	-0.66	-0.29
<i>Percina caprodes</i>	4	1	0.01	-0.64	0.41
<i>Pimephales notatus</i>	4	1	0.02	-0.60	0.19
<i>Semotilus atromaculatus</i>	7	2	0.04	0.72	-0.10

Note: Parentheses indicate coefficient of determination for the correlations between ordination distances and dissimilarity in the original distance matrix.

are adjacent, separated by an east–west trending ridge, and both drain into the Red River but are isolated by long distances of lowland, big-river habitat. The effectiveness of this isolation is demonstrated by the evolution of one endemic species (*Noturus lachneri*, Alum Fork system). Within both drainages, abundances and occurrences were highly variable across space and time, reflecting the different ecological conditions along the stream continuum (Table 2).

Two gradients of stream size and flow variables accounted for 50% (PC1) and 20% (PC2) of the variation in the PCA of the environmental variable-by-site data matrix. The first gradient (PC1) contrasted small, intermittent, headwater streams with larger, more heterogeneous, and less hydrologically variable streams (Table 3). The second gradient (PC2) was associated primarily with temporal variability in stream width and depth.

The structure of site-specific assemblages across time showed considerable variability (Fig. 2), but between basin assemblages were distinctive (Fig. 3). The overall large spread of points in the two-dimensional NMS space was in-

dicative of high variability among the sites (Gauch 1982). This was especially evident when comparing sites from the Little Glazypeau system (sites 3, 8, and 9) with sites from the Alum Fork system. By summing abundance for each site, thus collapsing the variation across time, the two drainage basins were clearly separated (Fig. 3). For a given locality, the variability (represented by the spread of sample points in the two dimensional space) was considerably less across time at larger, downstream sites compared with smaller, upstream sites (Figs. 1 and 2). Despite variability in assemblage structure for each site across time, each locality was confined to a relatively small proportion of the overall two-dimensional ordination plot (Fig. 2).

Species correlations with both NMS axes indicate their relative importance across the 12 localities (Table 1). For example, *Campostoma anomalum*, *Fundulus olivaceus*, and *Lepomis megalotis* were all relatively common species that had strong negative correlations with the first axis, thus indicating their importance at sites on the left side of the ordination plot in Fig. 3. *Etheostoma radiosum* and *Luxilus*

Table 2. Substrate characteristics (percent composition of point estimates), mean stream width, mean stream depth, and mean stream current speed for the 12 sampled localities.

Sites	Substrate						Mean width (m)	Mean depth (cm)	Mean velocity (m·s ⁻¹)
	Sand	Gravel	Cobble	Small boulder	Large boulder	Bedrock			
1	0	10	23	45	23	0	3.7	30.0	0.02
2	0	30	25	15	10	20	2.6	16.7	0.07
3	0	62	31	4	0	4	2.8	22.1	0.05
4	0	3	53	29	15	0	4.0	29.1	0.13
5	0	0	43	36	14	7	3.7	21.9	0.15
6	0	3	21	21	9	47	6.0	30.0	0.07
7	0	16	16	42	26	0	6.7	40.0	0.09
8	3	26	43	23	3	0	4.9	28.6	0.13
9	0	34	6	23	37	0	11.3	34.7	0.13
10	8	11	70	11	0	0	4.9	34.0	0.14
11	0	0	21	38	41	0	7.9	36.1	0.19
12	0	18	33	24	6	18	10.8	39.4	0.15

Note: Substrate composition is reported for November 1996 samples under ambient flow conditions. Means for other variables are calculated across the entire study period. Stream locality numbers correspond to rank in upstream catchment area and Fig. 1.

Table 3. Loadings for first two principal components.

Variables	Component loadings	
	PC1 (49.7) ^a	PC2 (19.6) ^a
Upstream watershed area	0.93	-0.5
Maximum depth	0.90	0.28
Maximum current speed variability ^b	-0.90	-0.01
Width	0.88	0.30
Maximum current speed	0.86	-0.12
Maximum width	0.83	0.49
Depth	0.80	0.46
Permanence	-0.77	0.17
Current speed	0.75	-0.53
Current speed heterogeneity	0.75	-0.37
Depth heterogeneity	0.64	0.62
Maximum depth variability	-0.36	0.75
Depth variability	-0.40	0.72
Maximum width variability	-0.47	0.61
Current speed variability	-0.49	-0.12
Width variability	-0.21	0.35
Substrate heterogeneity	0.45	0.28

^aPercent variance accounted for is given in parentheses.

^bVariability expressed as the coefficient of variation.

chrysocephalus had strong positive correlations with the second axis and occurred only at Little Glazypeau sites (top of the ordination plot), but *E. whipplei* was correlated negatively with this axis and only occurred at Alum Fork sites.

Results from the Mantel tests to evaluate spatial structure were all insignificant. The strongest relationship occurred for assemblage variability (matrix $r = 0.28$, $P = 0.07$). Thus, we assumed independence of sampling localities for regression and correlation analyses.

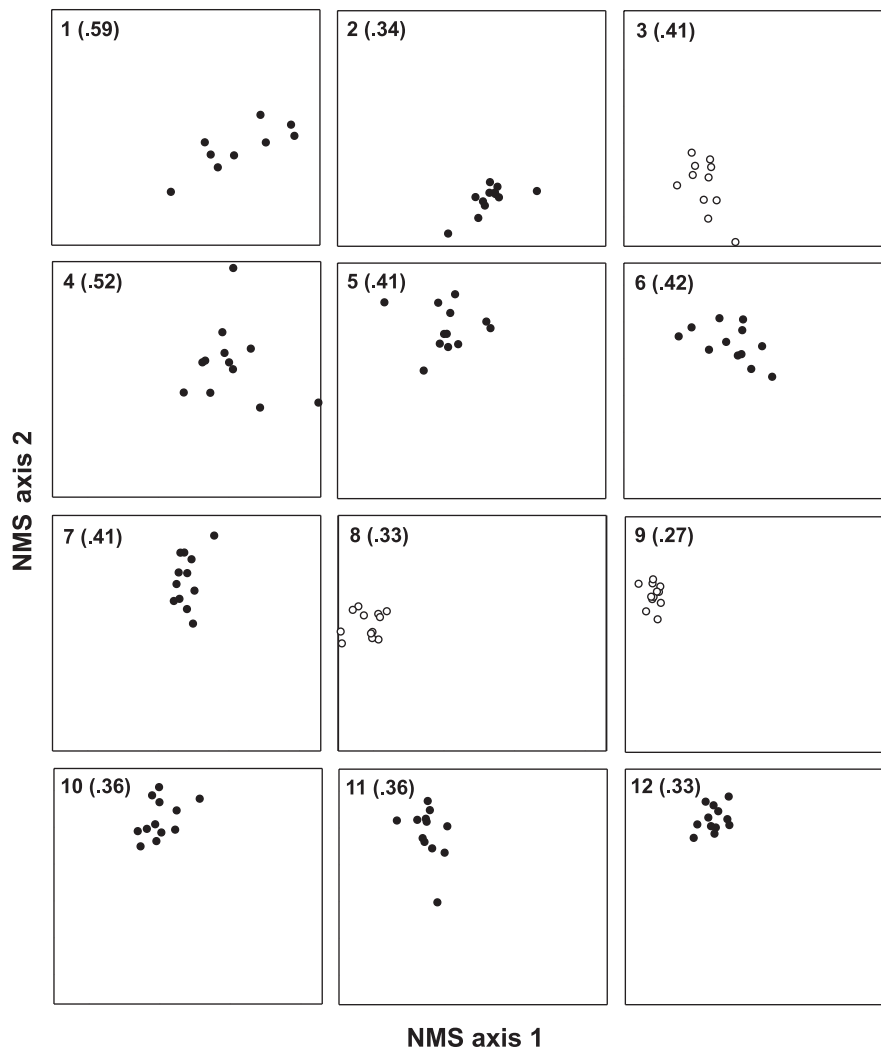
As predicted by the stability–diversity hypothesis, assemblage variability and species richness were associated significantly with each other ($r = -0.76$, $P = 0.006$; Fig. 4), but only after removal of an outlier site. This site was the smallest and most variable with respect to flow, but it had a per-

manent refuge pool that held water throughout the study period. The refuge moderated the local extinction process (Taylor and Warren 2001) and provided a relatively high level of assemblage stability, even under conditions of high environmental variability.

However, as we predicted, the primary environmental gradient (PC1) significantly explained species richness ($r = 0.86$, $P < 0.001$; Fig. 5a) and assemblage variability ($r = -0.54$, $P = 0.07$; Fig. 5b). Removal of the same outlier site improved the relationship between the environmental gradient and the assemblage variability ($r = -0.72$, $P = 0.012$). Thus, larger, less variable (e.g., flow regime) stream localities had greater species richness and generally exhibited less assemblage variability through time. Assemblages were structured strongly along this environmental gradient as well. The first PC was associated strongly with the first NMS axis ($r = -0.92$, $P < 0.0001$; Fig. 5c). The second PC was not associated significantly with species richness, assemblage variability, or assemblage structure. With all assemblage properties responding strongly to the environmental gradient, it was not surprising that temporal (mean Bray–Curtis distances) and spatial (NMS axis 1) assemblage properties were strongly associated ($r = 0.74$, $P = 0.010$).

Sites in the Alum Fork watershed showed strong and significant ($P < 0.01$) nested subset patterns for 11 of the 12 sample periods (mean $T = 21.3^\circ$, range = 14.5° – 29.0°). Only the summer 1998 samples produced a relatively weak pattern of nestedness ($T = 30.8^\circ$, $P = 0.015$). When all samples at a site were summed to include the realized species pool, the T value remained low and highly significant ($T = 22.04^\circ$, $P < 0.0001$), with sites furthest downstream containing the rarest species. There was no significant difference among seasons for T values or standard deviation units (δ) of observed T values from the mean of the randomized values (T , $F = 0.479$, $P = 0.706$; δ , $F = 0.615$, $P = 0.624$). Local species richness values across the landscape were correlated through time (Kendall Coefficient of Concordance = 0.34, $P = 0.0004$), and fluctuations in local species richness were correlated across the landscape (Kendall Coefficient of Concordance = 0.80, $P < 0.00001$).

Fig. 2. Nonmetric multidimensional scaling (NMS) ordination of all sites and samples across the 3-year period. Sample scores are plotted in multivariate space defined by NMS axes 1 and 2. Numbers correspond to Fig. 1 and represent rank in catchment area and average Bray–Curtis distance among all samples at a site (parentheses). ●, Alum Fork sites; ○, Little Glaypeau sites. Scaling is equivalent among plots.



Mean local abundance across species was associated positively with regional occurrence ($r = 0.535$, $P = 0.006$), and the observed shape of the points was triangular with a significant boundary (observed points within space = 22, mean of 5000 simulated runs = 19.65, variance of simulated points = 1.22, $P = 0.037$; Fig. 6). Mean local abundance also was associated strongly with mean local persistence rates ($r = 0.80$, $P < 0.0001$) such that the more locally abundant a species was, the greater its chance of persisting at localities (Fig. 7). Finally, regional occurrence was associated positively with mean local persistence ($r = 0.67$, $P = 0.0003$), and this relationship was retained after factoring out the influence of local abundance on local persistence (partial $r = 0.47$, $P = 0.020$; Fig. 8).

Discussion

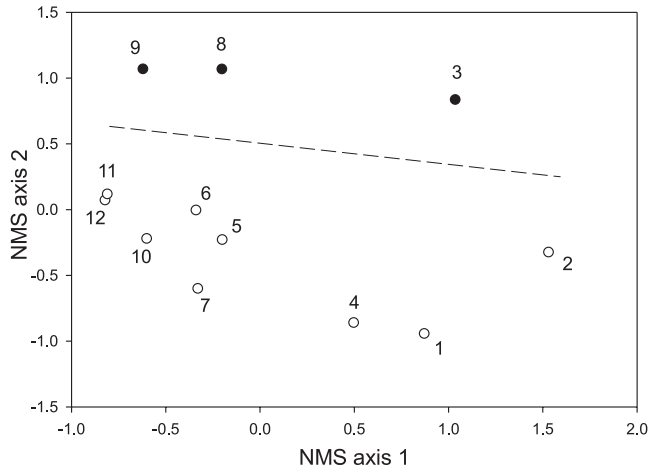
Assemblage structure, variability, and diversity

Ecological communities are assembled and maintained by a variety of factors and processes, including historical contingency, spatial and temporal aspects of the environment,

and species interactions (Pianka 1994). For many systems, complex habitats generally support more species than homogeneous habitats. Increased habitat heterogeneity provides a greater variety of resources for species, possibly reducing competition through resource partitioning (Schoener 1988). For stream fishes in headwater streams, habitat heterogeneity is associated positively with species diversity, and both factors tend to increase along the downstream gradient (Sheldon 1968; Gorman and Karr 1978; Schlosser 1987). In our system, three groups of variables showed significant changes from upstream to downstream. Habitat size and heterogeneity were associated positively with the upstream to downstream gradient, but flow variability decreased at downstream localities. Assemblages were strongly structured along this gradient and were more species-rich and less variable in relatively stable, heterogeneous, downstream habitats.

Ecologists have developed a large body of theory to understand and explain patterns of community organization and gradients in species diversity. Levins (1968) and MacArthur (1972) formulated a model based on the concept that

Fig. 3. Nonmetric multidimensional scaling (NMS) ordination of all sites. Abundance data are summed across samples for each site. Sample scores are plotted in multivariate space defined by NMS axes 1 and 2. Labels corresponds to Fig. 1. ●, Alum Fork sites; ○, Little Glazypeau sites. The broken line indicates separation of the two drainages along NMS axis 2.

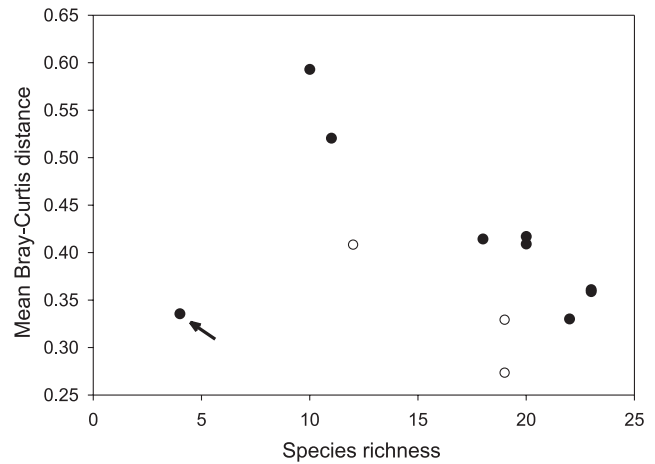


persistence in a community is tied to resource specialization and environmental stability (Leigh 1990). Generally, a benign environment should promote specialization and increased "species packing" (after MacArthur 1972) and should support more stable assemblage dynamics. This suggests a positive relationship between environmental stability and species diversity and predicts that more stable environments support more species-rich assemblages. The model of MacArthur and Levins has been highly criticized (Leigh 1990), in large part because of its foundation in competition theory and the assumption that communities exist in a competitive equilibrium. Further, measuring or even defining ecological specialization is very difficult. These criticisms, along with observations that disturbance can reduce or maintain diversity, depending upon its frequency or intensity (Connell 1978), diminished interest in competition as an organizing force in communities (Leigh 1990).

Huston (1979) developed a nonequilibrium hypothesis to explain community diversity that incorporates two important and interacting gradients: disturbance and competitive ability. His model predicts diversity to be highest where competitive displacement and disturbance frequency or intensity are low. The model provides a basis for understanding how disturbance allows coexistence of species but was criticized for not addressing traits or features of species that allow for coexistence (Leigh 1990).

Though conceptually straightforward, competitive ability and ecological specialization are operationally difficult. How does one quantify these concepts? If we assume that habitat heterogeneity (a measurable concept) reduces competitive displacement and promotes ecological specialization, both of the above models become more tractable. Another difficulty pertains to the time scale on which competition and environmental variability may interact to cause divergence and specialization. The theoretical basis of the Levins and MacArthur model assumes an evolutionary time frame, but plasticity in resource use and (or) species-specific traits in response to

Fig. 4. Relationship between assemblage variability (Bray–Curtis distance) and species richness. ○, sites from the Little Glazypeau system; ●, sites from the Alum Fork system. The arrow indicates an outlier locality (site 2).



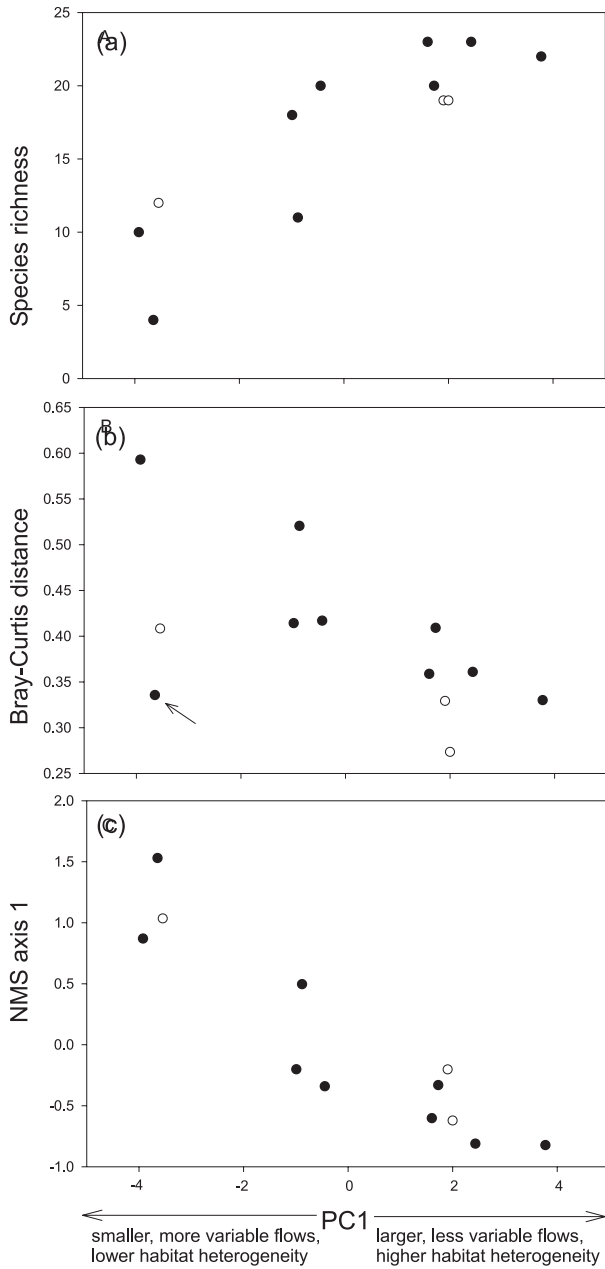
disturbance or biotic interactions is well known (Werner and Hall 1976; Komer 1997; Werner and Peacor 2003), making the theory applicable at ecological time scales. Mechanisms involving resource specialization were not investigated in this study, but there is support for the idea that resource specialization may increase along the downstream gradient. Taylor (2000) found that riffle and pool assemblages diverged in structure along the stream gradient in several Ouachita Mountain streams. Larger stream localities had more distinct riffle and pool assemblages, whereas in smaller, headwater streams, riffle and pool assemblages converged in structure and riffle habitats were ephemeral.

Nested assemblages, regional occurrence, local abundance, and persistence

The primary gradient in community structure (NMS axis 1) within the Alum Fork watershed was strongly associated with species richness ($r = 0.97$), and assemblages across the watershed were strongly nested, such that the rarest species occurred at the largest, downstream-most sites. These combined results provide strong evidence for a nested community structure, notwithstanding the potential limitations of the various measures of nestedness (Leibold and Mikkelsen 2002).

Rare has two meanings in the context of this study: one is based on regional occurrence and the other is based on local abundance. Species can have low or high local abundances if widely distributed, though species rare in occurrence tended to have low local abundances. For example, *Ameiurus natalis* and *Aphredoderus sayanus* were found at most sites but accounted for very little of the total catch with average local abundances of 3 and 9.5, respectively. However, *Lepomis megalotis*, also very widespread, accounted for about 20% of the total catch and had an average local abundance of 133.5. This distribution and abundance pattern produced a triangular dispersion of species in a bivariate plot of regional occurrence as a function of mean local abundance. A positive association between occurrence and abundance is well documented from a number of different systems (Hanski et al.

Fig. 5. Relationship between the environmental gradient (PC1) and three assemblage properties: (a) species richness, (b) assemblage variability (Bray–Curtis distance), and (c) assemblage structure (NMS axis 1). ○, sites from the Little Glazypeau system; ●, sites from the Alum Fork system.



1993; Gaston et al. 1997; Hughes 2000), and at least eight hypotheses have been put forth to explain this relationship (Gotelli and Taylor 1999). Recently, it has been shown how this pattern can result from the density and spatial distribution of species that are structured as metapopulations (He et al. 2002). The triangular dispersion we show with our data is novel and indicates that with thorough and repeated sampling, widespread and rare species are eventually sampled and fill out the upper left corner of the bivariate space. Notably, the dispersion pattern implies that unmeasured variables are constraining widespread but locally rare species from ap-

Fig. 6. Relationship between mean local abundance and regional occurrence for all species in the Alum Fork system (nine sites). The broken line indicates a boundary set by the limits of the data (min x , min y), (max x , max y).

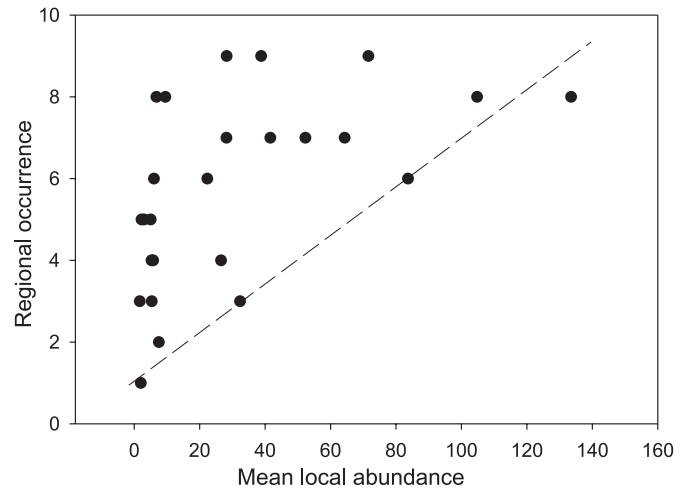
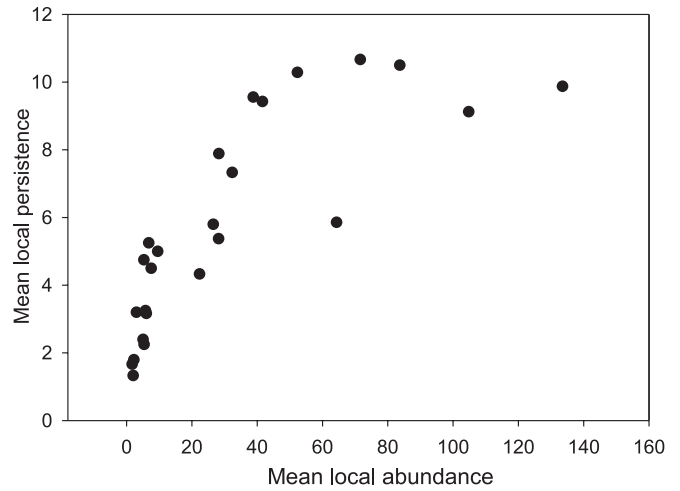


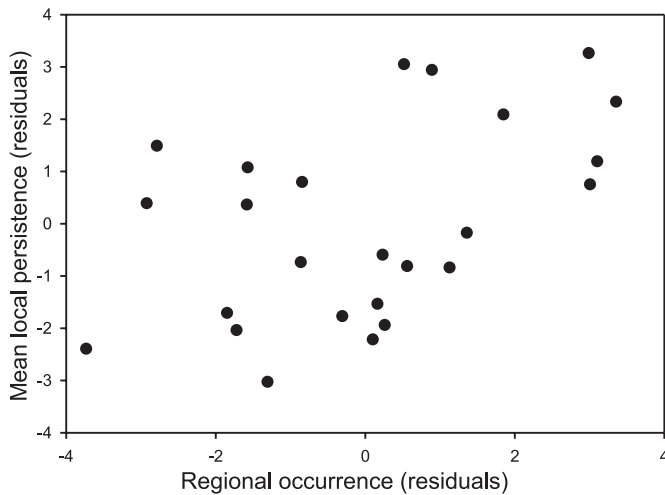
Fig. 7. Relationship between mean local persistence and mean local abundance for all species in the Alum Fork system (nine sites).



proaching the boundary. Given our data, we are unable to identify the nature of these species-specific constraints but suggest they may be related to habitat limitation, biotic interactions, or both.

Taylor and Warren (2001) showed that local abundance was associated strongly with immigration and extinction rates in this system. Thus, we correctly anticipated a strong positive relationship between mean abundance and mean persistence rates, such that species with high local abundances tended to be the most persistent at localities. Local persistence of species manifested as a temporally nested subset pattern at seven of nine sites in the Alum Fork system (Taylor and Warren 2001). The strength of the nested pattern was associated positively with local extinction rates, which were determined by stream size and flow variability. In this study, we also show the converse pattern: significant nested subsets occurred across space for each sample date and for summed

Fig. 8. Relationship between mean local persistence and regional occurrence for all species in the Alum Fork system (nine sites) after statistically removing the effects of mean abundance from both variables.



samples at each site. Furthermore, all quantified community properties were associated strongly with the stream size and flow variability gradient.

We find it intriguing that nested subset patterns in this system occur across space at the landscape scale (this study) and through time at the local scale (Taylor and Warren 2001) and that both were strongly associated with the environmental template. Further, loss and gain of species at the local scale occurred similarly across the landscape, presumably in response to large-scale seasonal changes in the hydrologic cycle. This consistency in pattern for both space and time scales suggests an important link between local community assembly and community-wide spatial structure. Such a relationship would imply that patterns of occurrence across space and time are fundamentally related to each other. Indeed there was a strong positive relationship such that species with a high frequency of occurrence across the landscape also tended to have high average rates of local persistence. Because mean local abundance accounted for about 64% of the variability in mean local persistence and also was correlated strongly with occurrence, it is possible that the relationship between local persistence and regional occurrence was spurious. However, the relationship remained significant after statistically accounting for the effect of abundance on persistence. These results are consistent with theoretical models implicating the importance of interaction between space and time scales in determining the evolution of dispersal rates in fragmented habitats (Paradis 1998) and with empirical studies that attempt to explain local diversity based on regional processes (Kiflawi et al. 2003).

In conclusion, hydrologic variability and habitat heterogeneity were structured spatially in these low-order Ouachita Mountain stream systems such that smaller headwater stream localities were more variable with respect to flow than larger, more heterogeneous downstream localities. We suggest that this complex environmental gradient is the primary determinant of assemblage diversity and variability in our system. We do not imply that species diversity has no impact on as-

semblage stability in our system but reiterate the importance of explicitly defining what kind of “stability” is in question. A major goal for ecologists is to identify repeated and general patterns in nature (MacArthur 1972), which is difficult to do if researchers are not on the same page. Future studies examining variability in stream assemblage properties should focus on how these properties change along stream size, hydrologic, and habitat diversity gradients according to various theoretical frameworks. We suggest that revisiting the original ideas put forth by Levins and MacArthur might prove useful, especially in conjunction with Huston’s nonequilibrium disturbance-based model. This would involve scrutinizing the biological processes and mechanisms of resource specialization that operate and vary across the environmental template.

In addition, our results suggest that community-wide occurrence may interact with patterns of local persistence for fish species in this fragmented stream system. This spatio-temporal coupling has strong implications for the conservation and management of fragmented river systems. Dams in river and stream systems disconnect entire catchments or watersheds from the remainder of the system. Such isolation from downstream populations may cause the system to eventually “relax” to a lesser regional diversity. Anthropogenic disturbances such as poor watershed management practices (Ross et al. 2001) and natural disturbances such as drought can render entire stream reaches uninhabitable for a given species. Hydrological connectivity controls the transfer of materials and products of ecological processes (Jenkins and Boulton 2003), and rare and (or) sensitive species are at risk to such disturbances. Without opportunity of rescue (Brown and Kodric-Brown 1977) from the contiguous stream landscape, they are possibly doomed to regional extinction. Thus, we emphasize the importance of maintaining landscape linkages at multiple spatial scales. The highly variable flow regime in our system causes seasonal fragmentation within the catchment and impacts immigration and extinction dynamics, whereas a dam on the mainstem represents fragmentation at a more extreme level, disconnecting the catchment from the rest of the system. Given the extreme fragmentation of watersheds throughout the world (Zwick 1992; Dynesius and Nilsson 1994) and the growing evidence suggesting that anthropogenic disturbances can have strong effects at long distances from their source (Winston et al. 1991; Pringle 1997; Fausch et al. 2002), we suggest that our results may represent general phenomena in riverine systems, important for stream fishes and perhaps other aquatic species.

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