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DYNAMICS IN SPECIES COMPOSITION OF STREAM FISH ASSEMBLAGES: ENVIRONMENTAL VARIABILITY AND NESTED SUBSETS

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Abstract. Stream landscapes are highly variable in space and time and, like terrestrial landscapes, the resources they contain are patchily distributed. Organisms may disperse among patches to fulfill life-history requirements, but biotic and abiotic factors may limit patch or locality occupancy. Thus, the dynamics of immigration and extinction determine, in part, the local structure of assemblages. We sampled fishes and stream habitat at 12 localities for two years (96 samples) to examine the deterministic nature of immigration and extinction processes in stream fish assemblages. Mean immigration rates for assemblages were highest at large stream localities, where the pool of potential immigrants was largest. Mean extinction rates were highest where variability in the flow regime was high, though local refugia appeared to modify the extinction process at one locality. Significant nested subset patterns in species composition occurred over time for 7 of the 12 localities. The strength of the nesting was associated with mean immigration and extinction rates. Higher extinction rates corresponded to stronger nestedness, whereas higher immigration rates were associated with weaker nestedness. Across all species, both immigration and extinction rates were strongly associated with mean abundance. Species with high local abundances had higher immigration rates and lower extinction rates than did species with low local abundances. There were no significant associations between trophic guild or body size and immigration and extinction rate. This work supports the hypothesis that immigration and extinction rates for assemblages are predictable along environmental gradients, and that species are less prone to local extinction and more prone to colonize areas when they maintain high local abundances. The extinction process in local assemblages can be a highly ordered event leading to strong nested subset patterns, but immigration appears to be more stochastic.

Key words: environmental gradients: environmental variability; extinction; immigration: ***nestedness;*** *Ouachita Mountains, USA; species composition; stream jishes; stream size; upland streams.*

INTRODUCTION

Landscapes and the distribution of organisms that inhabit them are typically heterogeneous in space and time. Stream ecosystems are no exception (Matthews 1998, Ward 1998). As in terrestrial landscapes, spatial heterogeneity in streams is complex and evident across multiple spatial scales (Schlosser 1991). Streams are also dynamic ecosystems in that habitat size and connectivity can change rapidly due to flooding or drought. Stream materials are constantly moved downstream and organisms often must recolonize disturbed areas from refugia habitats (Osborne and Wiley 1992, Ward and Blaustein 1994). Because resources tend to be patchy and variable in quantity and quality at any given time (Townsend 1989), organisms may move among localities to fulfill their life-history requirements (Schlosser 1995). Successful immigration to a locality will augment local diversity, whereas within-locality biotic (e.g., predation, competition) and abiotic factors (e.g., floods, drought) may decrease local diversity. Thus, local immigration and extinction events may be very important in determining the structure of local assemblages.

Variation in flow regime, whether by flooding or drought, is the predominant natural disturbance that can alter community structure in streams (Resh et al. 1988, Poff and Ward 1990, Stanley et al. 1997). This variation is often spatially structured, e.g., large streams are often less temporally variable than small, headwater streams, especially where headwater streams are ephemeral (Larimore et al. 1959, Horwitz 1978, Schlosser 1987). Schlosser (1987) proposed a conceptual model that made general predictions about immigration and extinction processes for stream fishes along a gradient from headwaters to larger, downstream reaches. Headwaters were represented as "colonizing" habitats that contained temporally variable assemblages due to highly variable flow regimes and small, structurally simple

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habitats. In contrast, larger downstream habitats were viewed as environmentally stable with more stable and diverse fish assemblages that, on average, would be less prone to local extinction events. The general applicability of Schlosser's model across a wide range of geographic regions and stream types is largely untested. Our goal was to examine the generalizations of Schlosser's model regarding the importance of immigration and extinction events in structuring stream fish assemblages. We ask how immigration and extinction rates vary with the spatiotemporal interaction of stream size and flow regime, and whether the immigration and extinction processes produce general patterns in the composition of species assemblages. Our data set, which consists of 96 fish samples taken from 12 stream sites over a two-year period, provides a novel opportunity to examine these questions.

To answer our questions, we sampled fish assemblages occupying stream reaches that varied in size, isolation, and flow regime. We hypothesized that immigration rates should be less at upstream sites, where stream size is smaller and isolation is greater. Thus, we anticipated that upstream localities would be "colonization limited" (e.g., Schlosser 1987). Downstream sites may provide refugia that upstream reaches are dependent upon for recolonization after disturbance events (floods and drought). We also hypothesized that extinction rates should increase with increasing environmental variability and decreasing stream size. Thus, we focused primarily on the flow regime, as it is the most dynamic and integrative attribute of stream environments (Poff et al. 1997, Merigoux et al. 1999).

We are also interested in the actual processes of immigration and extinction. Do species come and go randomly, or is there a structured pattern? The formation of nested species subsets is one type of structure that may be exhibited by communities that vary in species richness (Kodric-Brown and Brown 1993). A nested subset pattern occurs when species-poor assemblages form subsets of species-rich assemblages, such that rare species (low incidence) occur only in the richest assemblages and common species (high incidence) occur in assemblages with a wide range of richness values (Patterson and Atmar 1986). Nested patterns of species composition seem to commonly result from differential loss of species from assemblages via local extinctions in ecological time (Patterson and Atmar 1986, Wright et al. 1998). Differential immigration abilities among species can also potentially lead to nestedness (Cook and Quinn 1995), although there is ambiguity in the literature concerning the importance of this mechanism (Atmar and Patterson 1993).

Stream pool fish assemblages form spatially nested subset patterns that differ between isolated and connected pools (Taylor 1997), suggesting that differing immigration or extinction rates can lead to different patterns of community structure. Here, we have provided a new application of the nestedness methodology to examine more directly the effects of immigration and extinction on the formation of nested subset patterns. We used temporal (seasonal) matrices of species occurrences rather than traditional, "snapshot" spatial matrices assembled across sites. Our rationale is that we can observe the compositional dynamics of assemblages, thus making it possible to quantify the development of nested patterns through time at a given site, and then to relate this pattern to estimated immigration and extinction rates. We hypothesized that nestedness would be stronger in assemblages with high mean extinction rates and less evident for assemblages with high mean immigration rates. Finally, we examined immigration and extinction rates of individual species and asked if they were associated with patterns of abundance, body size, and trophic status.

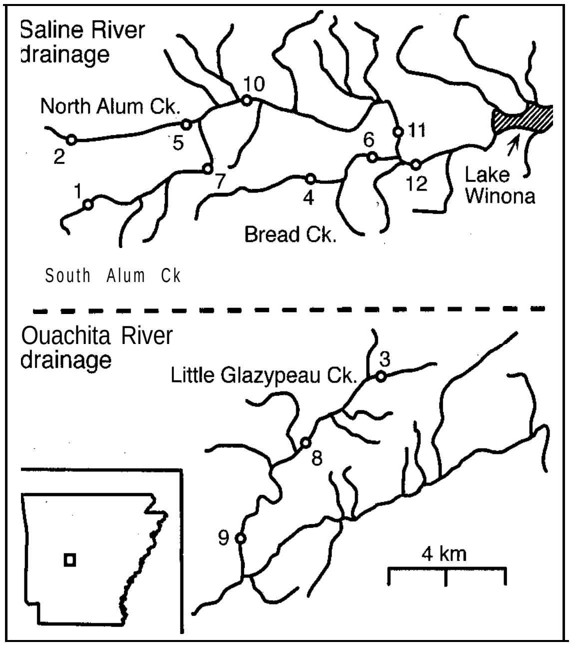

FIG. 1. Map showing the 12 sampled localities in south-central Arkansas. Stream locality numbers correspond to rank in catchment area. The dashed line indicates that the geographic proximity of the two creeks is not as shown. Both streams are tributaries to the Red River drainage system.

METHODS

Study area and species

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 (of the Red River drainage) that drain the eastern side of the uplift. Nine sites were located in the Alum Fork of the Saline River system and three sites were in Little Glazypeau Creek of the Ouachita River system (Fig. 1). These are clear-water streams except during high precipitation events, when dramatic increases in tur-

TABLE 1. Species, trophic groups, distributional information, mean immigration and extinction rates, and mean abundances (number of individuals) for fishes collected at 12 sites in Alum Fork and Little Glazypeau Creeks across two years (96 samples).

Species	Trophic groups	Alum Fork	Little Glazypeau	Immigration rate	Extinction rate	Mean abundance
Campostoma anomalum	benthic herbivore	X	X	0.318	0.145	18.7
Erimyzon oblongus	benthic insectivore	X	x	0.378	0.277	4.8
Etheostoma blennioides	benthic insectivore	X	X	0.069	0.417	1.5
Etheostoma collettei	benthic insectivore	X		0.192	0.135	12.0
Etheostoma radiosum	benthic insectivore		X	0.500	0.118	19.1
Etheostoma whipplei	benthic insectivore	X		1.000	0.085	9.8
Hypentelium nigricans	benthic insectivore		X	0.273	0.500	2.2
Noturus nocturnus	benthic insectivore		X	0.050	1.000	1.0
Noturus lachneri	benthic insectivore	X		0.182	0.024	7.8
Percina caprodes	benthic insectivore	X	X	0.110	0.455	2.9
Aphredoderus sayanus	generalized insectivore	x	X	0.259	0.538	2.5
Chaenobryttus gulosus	generalized insectivore	X		0.033	1.000	1.0
Lepomis cyanellus	generalized insectivore	X	X	0.889	0.105	6.1
Lepomis macrochirus	generalized insectivore	X	X	0.181	0.833	2.5
Lepomis megalotis	generalized insectivore	X	X	0.350	0.094	18.4
Luxilus chrysocephalus	generalized insectivore		X	0.286	0.143	3.1
Lythrurus umbratilis	generalized insectivore	X	X	0.315	0.367	13.9
Notropis boops	generalized insectivore	X	X	0.090	0.429	6.0
Notropis ortenburgeri	generalized insectivore	X		0.115	0.194	6.9
Semotilus atromaculatus	generalized insectivore	X	X	0.267	0.256	5.7
Ameiurus natalis	omnivore	X	X	0.194	0.563	1.5
Pimephales notatus	omnivore	X	x	0.081	0.227	4.6
Esox americanus	piscivore	X	X	0.296	0.533	1.6
Micropterus dolomieu	piscivore		X		0.000	3.3
Micropterus punctulatus	piscivore	X	X	0.139	0.500	1.4
Micropterus salmoides	piscivore	X	X	0.090	0.500	1.8
Fundulus catenatus	surface feeder		X		0.000	5.3
Fundulus olivaceus	surface feeder	X	X	0.241	0.127	5.3
Labidesthes sicculus	surface feeder	X	X	0.188	0.600	2.4
Zchthyomyzon gagei	N/A†	X		0.051	1.000	1.3

† A nonparasitic lamprey (i.e., adults do not feed).

bidity are evident. Because of the high gradient of these streams, riffle-pool development is strong. Pools ranged from a few meters to 50 m or more in length, and were usually 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 very 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.

We collected a total of 30 species of fishes from the 12 sites. Species were taxonomically distributed across six families and functionally distributed across six trophic groups (according to Allan 1995, and Poff and Allan 1995). Species, trophic groups, and distributional information are in Table 1. Life history information for most of these species is poorly known, especially regarding short and/or long-term movement patterns. Smithson and Johnston (1999) documented random or exploratory movement for many of these species and stream fishes generally will move to exploit "new" habitats (Meffe and Sheldon 1990, Peterson and Bayley 1993, Lonzarich et al. 1998).

Data collection

From November 1995 through August 1997, we sampled fishes and measured environmental variables at the 12 sites for a total of 96 samples. Samples for both years were taken in November, February, May, and August and were always completed within 3-4 d. 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 (Frissell et al. 1986), and the effects of disturbance on assemblage level properties are measured most commonly at this scale (see Matthews 1998). All sampling methods are biased and electrofishing is no exception (Reynolds 1983). However, our system consisted of small, clear streams (first to third order) that were wadeable and could be sampled in a consistent manner each time. The same individual (CMT) always operated the backpack electroshocker and there were always two or three netters present to pick up stunned fishes. Thus, we are confident that we adequately assessed the composition of fish assemblages at a given site for each sample date. After sampling a site, all fishes were identified, counted, and returned to the stream alive.

After fish sampling, we measured habitat variables along transects (perpendicular to stream flow) spaced at 10-15-m intervals along the sampled stream reach. The number of transects varied (8-12) depending on the length of the sampled stream reach. Transects were permanently marked and resurveyed during each visit. We measured stream width at each transect, and current velocity, depth, and dominant substrate type at every other meter along transects., We categorized substrate following Taylor and Lienesch (1996*a*, b) as bedrock, large boulder (>300 mm), small boulder (150–300 mm), cobble (50-149 mm), gravel (3-49 mm), or sand (<3 mm).

Data treatment and analyses

To quantify stream size and flow variability, we performed two principal components analyses (PCAs). Rather than combine all variables into one PCA, we chose separate analyses to quantify size vs. variability. We anticipated some level of correlation between these two groups, but chose to separate them a priori because they represent different concepts, each with its own potential effect as well as the possibility for interactive effects.

For the stream-size PCA we first calculated the mean and maximum width, mean and maximum depth, and mean and maximum current velocity for each site/date. We then calculated the mean of these values across sample dates for each site, calculated the upstream catchment area of each site, and log-transformed all values before analysis. Our goal was to collapse this multivariate data set into a single principal component (PC) that would best reflect stream size.

For the flow-variability PCA we used variables that reflect variation through time in stream width, depth, and flow. We included coefficients of variation (cvs), calculated for each site across sample dates, for mean and maximum width, mean and maximum depth, and mean and maximum current velocity. We also included a binary variable (permanence) that indicated whether flow ceased at the site some time during the study period.

We counted the number of species collected at each site across the entire study period and used this as a cumulative measure of species richness for the site. This measure estimates the "realized species pool," i.e., that part of the total species pool that we considered to be available for potential immigration into a given locality over the sampling period. The total species pool was the combined number of species collected from the entire system.

We used the time series of presence and absence for each species to estimate extinction and immigration rates. In patchy systems where individuals may inhabit more than one patch during their lifetime, local turnover is the product of mortality and the movements of individuals (Harrison 1991). Thus, we use the term extinction to indicate the absence of a species that was present in the previous census, whether due to extirpation or emigration. The term colonization is also problematic and can be dissected into several processes, including dispersal, survival, and reproduction in the new habitat patch (Ebenhard 1991). We use the term immigration to indicate simply the presence of a species that was absent in the previous census. We estimated species-specific extinction rates at each site according to Gotelli and Taylor (1999*a*, b). The method is based on simple probability and is calculated as follows:

$$\begin{aligned} P_e = {} & \text{number of times a site was occupied at time } (t) \\ & \text{but was unoccupied at time } (t + 1) \\ & \div \text{ number of times the site was occupied at time } (t). \end{aligned}$$

Similarly, immigration rates were calculated as

$$\begin{aligned} P_i = {} & \text{number of times a site was unoccupied at} \\ & \text{time } (t) \text{ but was occupied at time } (t + 1) \\ & \div \text{ number of times the site was unoccupied at } (t). \end{aligned}$$

These rates were then averaged across species for each site to give mean extinction and immigration rates. Alternative formulae, based on a Markovian model, may be used when censuses are sporadic and rates of immigration and extinction are constant (Clark and Rosenzweig 1994). The assumption of rate constancy is not realistic for our system, where stream flows vary seasonally and intermittency is common in headwaters during summer and early autumn.

For species-level analyses, rates were estimated for each species across all sites. The only exception was for species that occurred in only one of the two systems (see Table 1). For these species, we restricted the calculations to sites only within the system in which they occurred. We placed species into trophic groups based on known trophic affiliations (adapted from Allan 1995, and Poff and Allan 1995; see Taylor 1997). Body size data were obtained from Lee et al. (1980) and represent the maximum recorded body size for each species (see Taylor and Gotelli 1994). Mean abundances were calculated for each species based on all occupied site/times (according to Gotelli and Taylor 1999b).

An important consideration to any investigation of immigration and extinction dynamics is the sampling interval relative to the system's actual dynamics (see Diamond and May 1977, Clark and Rosenzweig 1994). Consider a system where the dynamics are slower than the sampling interval. At worse, the patterns will suggest no dynamics because the samples were unable to capture any variability. If the dynamics were faster than the sampling interval, such that multiple immigration and extinction events occurred between intervals, we might expect no detectable pattern to occur (i.e., noise). Therefore, the goal is to strive for something in between that is logical and logistically feasible.

TABLE 2. Localities (see Fig. 1), realized species pool (RSP), percentage fill of matrix, nestedness *T* values (probabilities in parentheses), number of standard deviation units. (a) of observed *T* values from the mean of 5000 randomly generated *T* values, mean immigration and extinction rates, and scores for each site from two principal component (PC) analyses.

Localities	RSP	Fill (%)	T° (P)	σ	Mean immigration rate	Mean extinction rate	Stream size (PC1)	Size variability (PC1)	Flow variability (PC2)
1	9	56.2	5.31 (0.008)	-2.41	0.160	0.552	-2.34	5.17	-0.06
2	4	66.6	0.00 (0.110)	-1.23	0.052	0.170	-3.92	0.33	1.41
3	12	51.7	9.9 (0.017)	-2.95	0.169	0.580	-3.30	-1.10	2.81
4	11	53.4	18.39 (0.004)	-2.66	0.198	0.435	-0.46	-0.89	1.50
5	17	55.7	28.09 (0.032)	-1.86	0.357	0.406	-1.48	0.57	-0.44
6	19	50.0	26.42 (0.001)	-3.01	0.420	0.475	0.08	1.64	0.03
7	18	58.9	22.82 (0.009)	-2.38	0.438	0.441	1.69	-0.98	0.75
8	18	53.8	29.45 (0.024)	-1.99	0.384	0.394	1.35	-0.83	-2.10
9	18	56.0	36.98 (0.174)	-0.94	0.378	0.357	1.87	-2.08	-0.84
10	23	54.4	32.96 (0.032)	-1.86	0.537	0.449	0.90	-1.56	-0.81
11	21	36.3	28.46 (0.029)	-1.97	0.255	0.457	2.21	-0.03	-0.48
12	22	52.9	46.52 (0.393)	-0.28	0.471	0.430	3.40	-0.25	-1.79

Notes: The first analysis provided a PC termed “stream size,” and the second provided two PCs termed “size variability” and “flow variability.” Loadings for these PCs are given in Table 3. Stream locality numbers correspond to rank in catchment area.

To assess our seasonal sampling interval in relation to potential dynamics associated with immigration and extinction, we examined daily stream-stage records that were available for a headwater site (site 2; Fig. 1, Table 2) for August 1996 to August 1997 (J. Nettles and D. Marion, *personal communication).* Since reduced depths and flows have been shown to hinder movement of stream fishes in the Ouachita Mountains (Lonzarich et al. 1998, Warren and Pardew 1998), we assumed that >4 continuous days of low stages (≤5 cm) would reduce migration by most fishes in our system and >4 continuous days of stages >6 cm would facilitate migration. During the 12-mo period having appropriated records, site 2 had ≤2 interruptions (of >4 d) of either low or high stage occurrences (lasting from 8 to 46 d) in all sampling intervals. Hence, the hydrological dynamics of this site appear to equal or are only slightly faster than our sampling interval and should, if anything, decrease our ability to detect pattern in immigration and extinction events.

We used regression analyses to describe the relationships, between the three multivariate environmental gradients (stream size, and size and flow variability), and immigration and extinction rates. For the species-level analyses, we used linear regression to determine the relationships between immigration and extinction rates, and mean abundance and body size. For all regression analyses we used a randomization procedure to determine probabilities. The dependent variable was shuffled 5000 times, and the observed regression coefficient was compared to the distribution of coefficients obtained from the randomizations. We used one-tailed tests because we hypothesized directionality for each relationship. We used a Kruskal-Wallis test to test for differences among trophic groups for immigration and extinction rates, before and after statistically controlling for abundance. Friedman’s method for randomized ‘blocks (Sokal and Rohlf 1981) was used to determine if there were any overall differences in immigration and extinction rates among species.

We used Atmar and Patterson’s (1993) *T* (temperature) to determine the degree of nestedness for each locality over time. This metric measures the unexpected presences and absences of species in samples that have been “packed” into a state of maximum nestedness. At 0°, complete order exists, while at 100” there is no order. A Monte Carlo procedure was used to assess the probability (based on 5000 permutations) that such a distribution pattern could occur by chance (Atmar and Patterson 1995). The procedure generates null matrices without any row or column constraints; only the total number of presences is fixed at the observed value. We then used linear regression to examine the association of *T* with immigration and extinction rates, and the environmental gradients. The characteristic temperature, T_0, of randomized matrices tends to increase (less order) as a matrix increases in size, becomes more square, and approaches 50% fill (Atmar and Patterson 1995). Furthermore, Wright et al. (1998) found a positive correlation between T and matrix size. Thus, the possibility of finding a very high T that is insignificant is increased for very small, asymmetrical matrices. Because our matrices differed in size, shape, and fill (Table 2), we also examined the significance level of the nested patterns along gradients of immigration and extinction. These relationships were assessed by plotting the number of standard deviation units (a) each observed T was from the mean of its randomly generated populations against immigration and extinction rates.

RESULTS

The stream-size PCA resulted in only one meaningful axis, which we refer to as stream size. All seven variables loaded highly on the axis, and it accounted

Table 3. Loadings (correlations) of environmental variables from two principal components analyses.

Environmental variable	Stream size (77%)	Variability Size (52%)	Variability Flow (29%)
Width	0.95	0.93	-0.17
Maximum width	0.87	0.93	0.04
Depth	0.90	0.82	0.21
Maximum depth	0.92	0.88	0.22
Current velocity	0.70	-0.52	0.73
Maximum current velocity	0.88	-0.21	0.89
Upstream catchment area	0.92	...	...
Permanence		0.44	0.75

The first analysis produced one meaningful component (stream size), and the second produced two (size variability and flow variability). The stream-size PC analysis was based on variable means for each site calculated across time (except for upstream catchment area). The second PC analysis was based on coefficients of variation for given variables calculated across time, except for permanence which was a binary variable. Values in parentheses indicate variance accounted for by each axis.

for 77% of the variation in the original data matrix (Table 3). The flow-variability PCA produced two interpretable axes that represented site-specific variation in stream size and stream flow over time. Width and depth cvs loaded highly on the first PC, which we refer to as stream-size variability, and all flow related variables loaded highly on the second PC, which we call flow variability (Table 3). As we anticipated, environmental variability was associated with stream size. Stream size was negatively associated with flow variability (r = -0.71, P = 0.014), but the negative association was not significant for size variability (r = -0.39, P = 0.113).

Mean immigration rate was positively associated with stream size (r = 0.76; Fig. 2A) and negatively associated with stream-size variability ($r = -0.36$; Fig. 2B) and flow variability (r = -0.65; Fig. 2C). A backwards elimination stepwise multiple regression procedure ($P > 0.05$ to remove) retained only stream size as a predictor of immigration (P = 0.004). Realized species pool was also positively related to stream size (r = 0.85, $P < 0.001$) and immigration rates ($r = 0.90$, $P < 0.001$). Thus, immigration rates were higher downstream where there were a greater number of potential species to immigrate into a given locality.

Extinction rates were also associated with the environmental gradients. However, it was first necessary to remove a single strong outlier that obscured underlying linear relationships (Fig. 2D–F). After removal of this outlier (*see Discussion* for rationale), extinction rate was negatively associated with stream size (r = -0.68; Fig. 2D), and positively associated with stream size variability (r = 0.51; Fig. 2E) and flow variability (r = 0.63; Fig. 2F). A backwards elimination stepwise procedure ($P > 0.05$ to remove) retained only flow

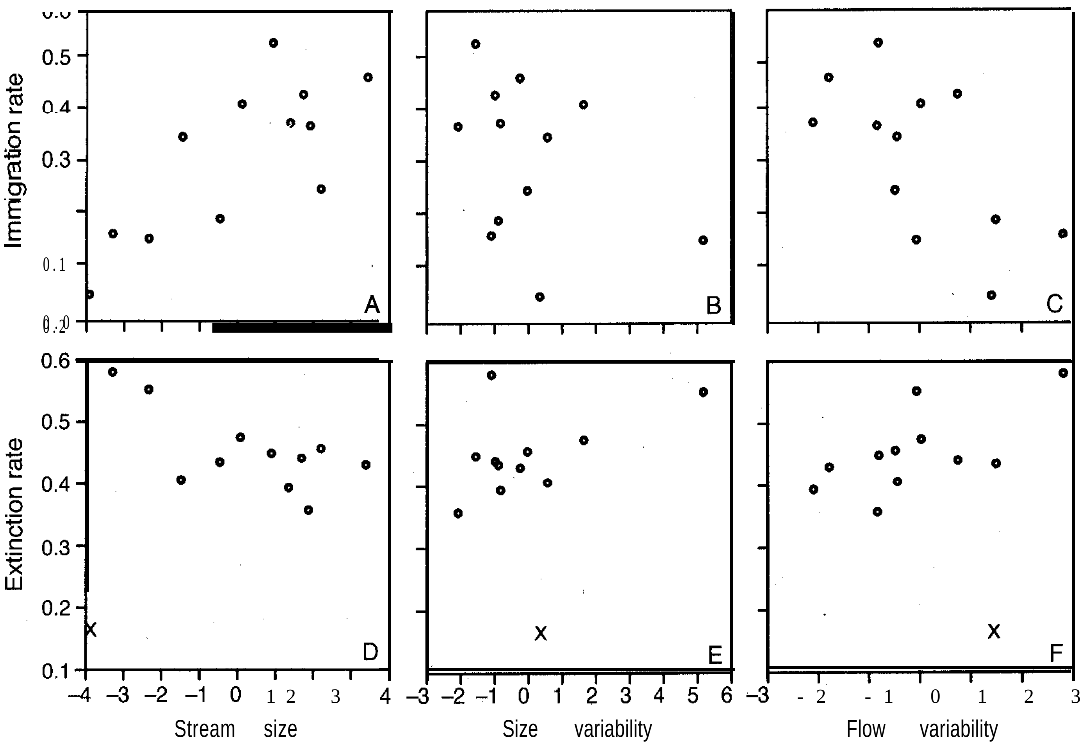

Fig. 2. Mean immigration and extinction rates of the 12 sampling localities plotted as functions of stream size (A, D), size variability (B, E), and flow variability (C, F). The "X" symbols indicate an outlier locality (site 2; see Fig. 1 and Table 2). Each independent variable represents a principal component further defined in Table 3; units are standard deviations.

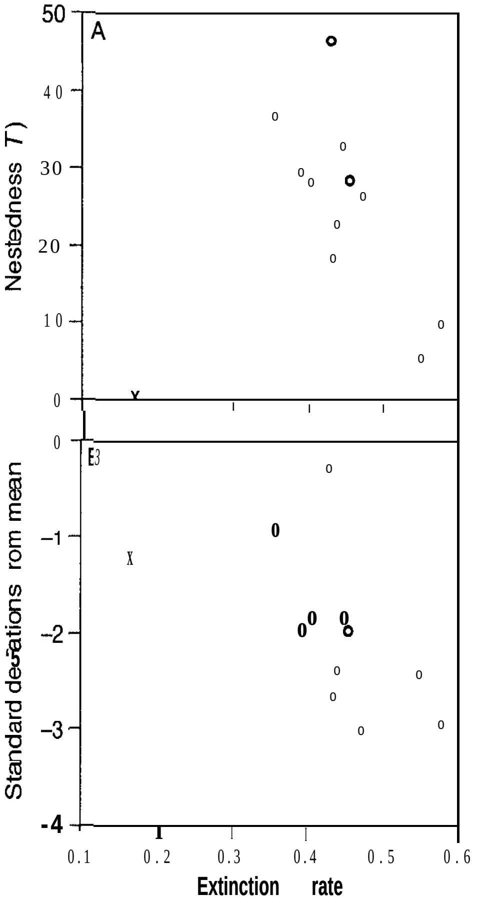

FIG. 3. Relationships of (A) nestedness (*T*) and (B) sigma (a) with extinction rate. Sigma (a) is the number of standard deviation units the observed *T* lies from the mean of 5000 randomly generated *T* values.

variability (P = 0.029) as a predictor of extinction rates. Mean immigration and extinction rates were negatively correlated with each other (r = -0.57, P = 0.041), as expected, since both rates were associated with measured environmental gradients in opposite directions.

Nine of 12 localities contained assemblages that were significantly nested over time (Table 2). Both extinction and immigration rates were associated with T. As predicted, the association was negative for extinction (r = -0.76, P = 0.006; Fig. 3A), indicating more ordered matrices at higher extinction rates. The association was positive for immigration (r = 0.85, $P <$ 0.001; Fig. 4A), indicating less ordered matrices at higher immigration rates. Extinction rate was also associated negatively with σ (I = -0.59, P = 0.017; Fig. 3B), such that the higher the extinction rate, the less likely the observed T would occur by chance. Immigration rate was not associated with σ (r = 0.22, P = 0.252; Fig. 4B). Stream size and flow variability were also associated with T (r = 0.88, $P <$ **0.001;** r = *-0.74,* P = 0.006; respectively) such that small streams with high flow variability had the strongest nested assemblages.

For individual species, immigration rate was associated positively with mean local abundance (immigration, r = 0.47, P = 0.007; Fig. 5A) and extinction rate was associated negatively with mean local abundance (r = -0.77, $P <$ 0.001; Fig. 5B). There was no significant difference among trophic groups (Kruskal-Wallis test) with respect to immigration and extinction rates (immigration, H = 4.18, P = 0.652; extinction, H = 1.97, P = 0.318), even after statistically controlling for mean local abundance (immigration, H = 3.12, P = 0.794; extinction, H = 6.77, P = 0.343). Neither immigration nor extinction rates were associated with body size (immigration, r = *-0.0003,* P = *0.398; extinction,* r = 0.17, P = 0.370). Overall, species' immigration and extinction rates did not differ (Friedman's test; χ^2 = 1.29, P = 0.26) and the rates were significantly correlated (r = -0.521, P = *0.005).*

DISCUSSION

Nestedness

There are two ways in which this study differs fundamentally from others, regarding the analysis of nested subset community patterns. First, nestedness has traditionally been measured as a spatial phenomenon occurring in a snapshot of time. Space and time scales are very large for the systems traditionally studied (e.g., isolated mountains, landbridge islands); the temporal dynamics are not easy to observe. The dynamics of a stream system operate much faster than those of landbridge islands or isolated mountaintops. Streams rise and fall rapidly due to the vagaries of climate. Precipitation events cause habitats to grow in size and drought causes habitats to shrink or disappear. Connections among habitats also change, leading to isolation or facilitating dispersal events. Given these rapid physical changes, community dynamics are much faster than in the traditional systems and do not necessarily correspond to the population-level processes of colonization and extinction, per se. Nevertheless, the dynamics do represent quantifiable changes in species composition through time, whether due to immigration and emigration, or colonization and extinction. Thus, we were able to quantify the development of nested patterns through time at a given site and then to relate this pattern to estimated immigration and extinction rates.

The second difference refers to the fact that streams are largely continuous systems. Our chosen study sites were neither islands nor isolates (e.g., a mountaintop or forest fragment). Nevertheless, many of our study sites were isolated or quasi-isolated for relatively short periods of time (i.e., weeks to months instead of years to millennia) by virtue of low seasonal flows. However, the prevalence of nested community subsets across a wide variety of taxa and geographic regions suggests

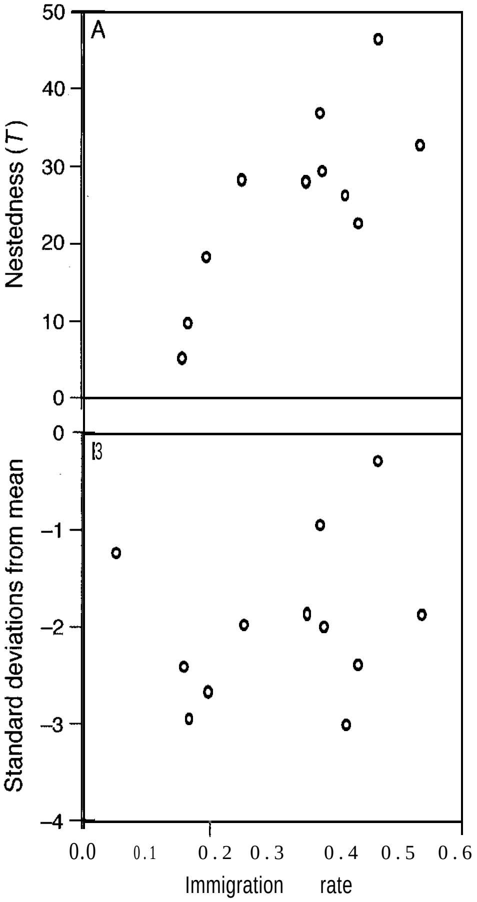

FIG. 4. Relationships of (A) nestedness (T) and (B) sigma (σ) with immigration rate. Sigma (σ) is the number of standard deviation units the observed T lies from the mean of 5000 randomly generated T values.

that it may be a general ecological property worthy of investigating in a wide variety of systems that operate at different space and time scales (Patterson and Brown 1991). Stream systems offer a very dynamic model to test competing hypotheses concerning mechanisms leading to nestedness.

The mechanistic basis for nested community patterns has been an area of controversy in recent years (Cook and Quinn 1995, Lomolino 1996, Taylor 1997). Three conditions appear to be necessary for a nested community structure to develop: a common biogeographic history, similar habitats occupied by the communities, such that species turnover (beta diversity) is limited, and a hierarchical set of ecological relationships among the species (Patterson and Brown 1991). Because we are examining the formation of nested subsets for site-specific assemblages, the first two conditions are implicitly met for our system.

The last of the conditions is the most controversial and concerns the role that immigration and extinction play in governing community composition. Differential extinction is often considered to be the primary force leading to nested species subsets. Evidence comes from systems considered to be relaxation faunas, such as landbridge archipelagos (Wright et al. 1998), where extinction rates exceed immigration rates. However, there is also evidence suggesting that immigration can lead to nested subset patterns (Cook and Quinn 1995, Kadmon 1995, Lomolino 1996, Taylor 1997), and the possibility for "dispersal structures" (dispersal-driven community patterns) to develop in stream systems has been suggested (Downes and Keough 1998).

We acknowledge that differential dispersal abilities of species could lead to nested species subsets, but only in a temporary sense if all conditions are met. Given enough time (assuming no local population differentiation) all species will have the opportunity to disperse throughout the system, even the poorest dispersers. The higher the rate of immigration, the more ambiguous and less stable the nested pattern should be. Thus, the final filtering process will be the differential ability of species to avoid extinction at a given locality.

No study to date has directly assessed the association between development of nested subset patterns, and rates of immigration and extinction. As a result, rec-

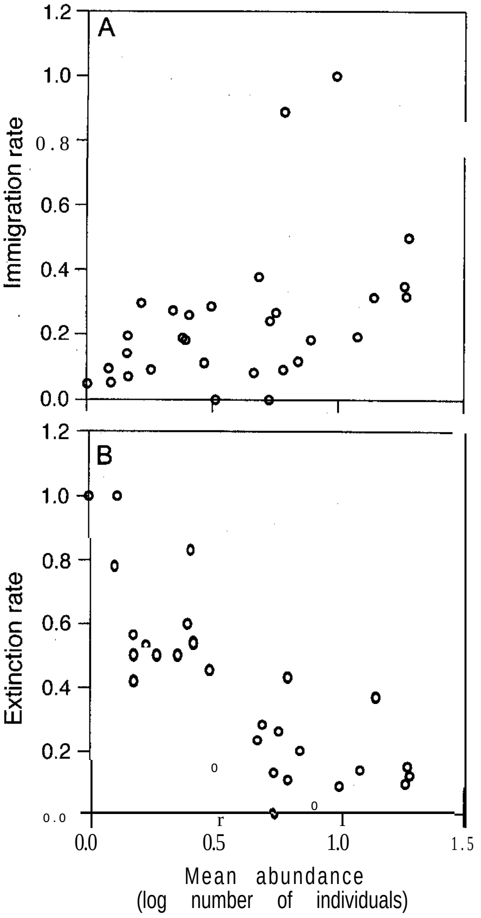

FIG. 5. (A) Immigration and (B) extinction rates of species expressed as functions of mean abundance.

onciliation of the importance of these two mechanisms has been problematic. Our system comprised 12 localities that varied with regard to hydrologic disturbance frequency. This gradient in flow regime allowed us to assess differences among localities regarding the formation of nested species subsets. We did not rely on surrogate measures of immigration and extinction (habitat isolation and size). Instead, we calculated immigration and extinction rates for 12 fish assemblages to assess the cause of nested subset patterns. Our hypotheses were supported. Nestedness increased with increasing extinction rate (Fig. 3A) and decreased with increasing immigration rate (Fig. 4A). Furthermore, at high extinction rates, such an ordered arrangement was less likely to occur by chance (Fig. 3B).

Immigration and extinction rates

The importance of immigration and extinction dynamics in structuring stream fish assemblages is apparent from a number of studies. Angermeier and Schlosser (1989) attributed the scatter in stream fish species-area relationships to immigration and extinction dynamics, and stated that pronounced local fluctuations in species numbers should occur in variable environments. Osborne and Wiley (1992) attributed low fish species richness of isolated streams, relative to similar-sized nonisolated streams, to lower immigration rates in isolated situations, a result predicted by the equilibrium model of MacArthur and Wilson (1967). These studies allude to the importance of immigration and extinction dynamics, but fall short of providing actual rates for assemblages under varying environmental conditions. Our calculated rates and their associations with stream size and hydrologic variability are consistent with Schlosser's (1987) model of how fish assemblages and habitat heterogeneity change along the downstream continuum. We found that mean local immigration and extinction rates for fish assemblages were predictable along environmental gradients considered important in Schlosser's (1987) model. Mean immigration rates were positively associated with stream size and negatively associated with flow variability (Fig. 2). Downstream areas had larger, more stable habitats and a greater number of potential colonists than upstream areas. Extinction rates were positively associated with variation in the flow regime and negatively associated with stream size (Fig. 2). Thus, in accordance with Schlosser's model, stream size and flow variability were both important variables associated with immigration and extinction dynamics that, in part, determined the species composition of local assemblages in our system.

Across all species, local abundance was a strong predictor of immigration and extinction rates. Species that maintained high local abundances tended to have high immigration rates and low extinction rates (e.g., *Etheostoma radiosum* and *Lepomis megalotis),* whereas species with low mean abundances had lower immigration rates and higher extinction rates (e.g., *E. blennioides* and *L. macrochirus;* Table 1). Other studies have also identified the importance of local abundance in determining species immigration and extinction rates (Lima et al. 1996, Gotelli and Taylor 19996). In contrast, body size and trophic status had no detectable effect on immigration and extinction rates. However, our classification was based only on simple trophic attributes, and our body size data did not account for the wide range of sizes we encountered in the field for most species. As we learn more about the life histories of these fishes, it will be possible to group species based on other trait characteristics (e.g., reproductive, tolerance, habitat-based traits) that may affect immigration rates or extinction risks (see Townsend and Hildrew 1994).

Predicting immigration and extinction rates along environmental gradients is challenging because processes and patterns vary at different spatial and temporal scales (Wiens et al. 1986, Lohr and Fausch 1997). The most dynamic property of a stream is its flow regime, which can change very rapidly (Power and Stewart 1987). Habitat size and patterns of connectivity can have a strong affect on local species composition in aquatic systems (Taylor 1997, Magnuson et al. 1998, Pfister 1998). Because we quantified changes in stream size and flow variation on a seasonal basis, we have only captured a crude picture of variability through time. This variability was probably very conservative in that peak flows and rates of rise and fall were not incorporated. However, these seasonal snapshots allowed us to calculate relative measures of variation through time that were comparable across all sites.

Our extinction patterns dictate consideration of refugia in mediating the extinction process (see Sedell et al. 1990). For all tests involving extinction rates we first needed to consider an outlier site that obscured otherwise strong, linear relationships (see Fig. 2). This site was the smallest and one of the most variable with respect to flow; however, it also had the lowest mean extinction rate. This particular locality had a permanent refuge pool that held water throughout the study period and contained submergent plant cover and overhanging rock ledges. The realized species pool at this site was comprised only four species: *E. whipplei, Erimyzon oblongus, Semotilus atromaculatus,* and *L. cyanellus.* The latter two were present in this pool at every census. Although extinction rates mostly increased with increasing variation in the flow regime, refugia habitat moderated the local extinction process at this site, even under conditions of high environmental variability. Similarly, for physically harsh and intermittent Great Plains streams, high species persistence was attributed to deep, complex pool habitats that provided refugia during drought (Fausch and Bramblett 1991).

Conclusions

This work helps to illustrate how immigration and extinction dynamics interact with the spatiotemporal pattern of environmental change to determine, in part, the local composition of stream fish assemblages. Assemblages in small, highly variable streams had high extinction rates and showed strong nested subset patterns, suggesting that local extinction was a structured and orderly process. Sites with high immigration rates did not exhibit significant nested subset patterns. These localities were larger, downstream sites where environmental variability was lowest and the pool of potential colonists was highest. At these sites, species appeared to move in more or less at random without any hierarchy of differences. These findings are in accord with Schlosser's (1987) conceptual model explaining spatial and temporal trends in fish assemblage variability and habitat heterogeneity, and other studies that have implicated the relative importance of immigration vs. extinction dynamics in structuring stream fish assemblages (Angermeier and Schlosser 1989, Osborne and Wiley 1992, Gotelli and Taylor 1999*a*, b).

Finally, the spatiotemporal interaction between the abiotic environment and the composition of local fish assemblages illustrates the importance of maintaining natural flow regimes (see Poff et al. 1997). Anthropogenic modification to small stream systems (e.g., road culverts, poor watershed management practices) may influence rates of local immigration or extinction, with predictable consequences to the distribution and abundance of fish species. If our results represent general ecological phenomena, it may be possible to better understand and predict the community-level effects of disturbance (such as fragmentation) in a variety of systems.

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