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SPECIES-AREA RELATIONSHIPS FOR STREAM FISHES¹

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Abstract. We sampled riffle and pool habitats of small streams in Minnesota, Illinois, and Panama to examine variation in species-area relationships within and between the respective fish faunas. For six of the seven streams studied, habitat volume was a better predictor of species richness than was habitat area, and number of individuals was a better predictor of species richness than habitat volume. Slopes of species-volume relationships were similar among regions, but the number of species per unit volume was greater in Panama. Multiple regression analyses indicated that knowledge of habitat complexity and volume did not enhance appreciably the capability of linear models to predict species richness from number of individuals in the sample. These results support the hypothesis that species-area relationships may often be epiphenomena stemming from the more comprehensive community "samples" intercepted by larger habitat patches. Although number of individuals was the best single predictor of species richness, habitat structure and type clearly influenced species' distributions in some streams, thereby indicating that species-area relationships were not strictly sampling phenomena. An index of habitat complexity based on depth, current, and bottom type was correlated with species richness in two Panama streams. Also, the abundance of individual species was more likely to be correlated with habitat volume in Panama than in Illinois or Minnesota, and species relative abundances were more similar between years in Panama than in Illinois or Minnesota streams, especially in pools. These patterns suggest that in streams subject to strong seasonal and annual environmental variation, habitat features are poorer predictors of fish distribution and abundance than in streams subject to less environmental variability. We speculate that annual variability in reproductive success and harsh winters interact to maintain imbalance between the fish assemblages and their habitat in Minnesota. Weak relationships between species richness and habitat volume or complexity may be indicative of population variability and the predominance of extinction/recolonization processes in community organization.

Key words: assemblage organization; fishes; habitat volume; Illinois; Minnesota; Panama; pool; riffle; species-area relationships; streams.

INTRODUCTION

Species-area relationships are ubiquitous in community ecology. They have been discussed in the literature for many years (e.g., Gleason 1922), yet continue to interest ecologists, especially concerning their implications for conservation biology and the fragmentation of once extensive ecosystems (Simberloff and Abele 1982, Boecklen and Gotelli 1984). Two questions are of particular interest: (1) why are species richness and habitat size closely (positively) related? and (2) what are the main sources of variation in slope,

intercept, and scatter of linear characterizations of species-area relationships?

The three most popular hypotheses for why species-area relationships exist have been widely discussed and are reviewed elsewhere (Boecklen 1986, Schoener 1986). One hypothesis invokes the theory of island biogeography (MacArthur and Wilson 1967) and the dependency of species immigration and extinction rates on island size. Such an argument is not very compelling for systems in which habitat islands do not support self-sustaining populations of the species being studied (as for birds in small tracts of woodland), or in which individuals move relatively freely among "islands" because of connecting habitat. A second hypothesis suggests that larger patches of habitat contain a larger array of habitat configurations and food resources, thereby providing more niches and supporting more species (Williams 1964). This hypothesis should be especially

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tenable when increases in habitat size involve additions of different habitat types (e.g., forest and prairie), but could also apply to smaller scales of habitat heterogeneity. The third hypothesis views species-area relationships merely as sampling phenomena, maintaining that larger areas support more individuals, thereby sampling the available pool of species more completely (Connor and McCoy 1979). Although the latter two hypotheses have seldom been directly tested against each other (but see James and Wamer 1982), the relative importance of habitat heterogeneity and area, *per se*, have been extensively studied for forest bird communities. However, interpretations are ambivalent, with habitat structure appearing to be an important determinant of species richness within some sets of woodlots (Boecklen 1986, Freemark and Merriam 1986), but in others accounting for little of the variation in species richness after area is factored out (Martin 1981a, Ambuel and Temple 1983, Blake and Karr 1987).

Variation in the shape and tightness of species-area relationships for a particular taxon has several sources. Among newly formed islands, the slope of species-area relationships may be largely determined by immigration rates (Schoener and Schoener 1981). Among equilibrated habitat patches, different types of habitat of the same size may support different numbers of species (James and Wamer 1982). In any data set, the observed slope of the species-area relationship may be influenced by the range of areas included in the analysis (Martin 1981b). Among zoogeographic regions, the number of species occupying a particular type and size of habitat should reflect historical factors affecting the number of species available for colonization. Diamond and Gilpin (1980) identified numerous sources of scatter in species-area relationships, including between-patch differences in habitat structure, temporal (especially seasonal) variance in species occurrences, and random fluctuation in species richness due to continual immigration and extinction. Studies of bird communities indicate that groups of species with different migratory status (e.g., residents vs. migrants) vary considerably with respect to the scatter in their respective species-area relationships (Schoener and Schoener 1983, Freemark and Merriam 1986, Blake and Karr 1987). Finally, recent evidence indicates that intense predation may result in greater slopes of species-area relationships for forest birds (Martin 1988) and greater scatter in species-area relationships for spiders in oceanic archipelagos (Schoener 1986).

Small streams provide excellent systems in which to examine species-area relationships of fishes. Habitat patches can be clearly defined and the number of species and individual fishes can be accurately estimated. Two habitat types, riffles and pools, are often easily distinguished on the basis of depth and flow characteristics. Riffle-pool patterns of stream geomorphology are consequences of fundamental laws of hydraulics (Yang

1971, Richards 1976), and differences in depth, current velocity, and substrate composition between habitat types profoundly influence the structure and function of animal communities (Brussock et al. 1985, Huryn and Wallace 1987). A series of habitat patches within a stream may be viewed conceptually as an archipelago, albeit with two important differences from true islands. First, single patches of habitat are generally too small to support self-sustaining populations of fish. In this regard, stream habitats are analogous to small woodlots for bird populations. Second, although there are usually no physicochemical barriers to prevent fish from moving freely among habitat patches, predation pressure on those that do may often be severe (Power 1984, Power et al. 1985), and some fishes apparently spend much of their life within single habitat patches (Hill and Grossman 1987). Although some analyses of species-area relationships among river drainages have been reported for fishes (Livingstone et al. 1982, Sheldon 1987) and mussels (Sepkoski and Rex 1974), we know of no studies that examine such relationships among individual habitat patches within streams.

In this paper we attempt to identify the basis for species-area relationships among stream fishes and the sources of variation in the shape and scatter of those relationships. Because we seek to identify patterns that apply to a wide variety of streams, we analyze fish species-area relationships from three widely separated geographic locations: Minnesota, Illinois, and Panama. In particular, we examine the relative importance of habitat area, habitat volume, habitat heterogeneity, and number of individuals as determinants of the species richness in a habitat patch. We also identify associations between patterns of scatter in species-area relationships and features specific to different streams and habitat types. Finally, we speculate on what relationships between habitat features and species' distributions may indicate regarding processes of community organization.

METHODS

Study streams

We sampled fishes from two streams in Minnesota, two in Illinois, and three in Panama. All are small streams, with mean channel width between 1 and 7 m. All streams were sampled during low-flow periods when availability of preferred habitat is likely to be especially limited (Orth and Maughan 1982). Sucker Creek and Gould Creek are headwaters of the Mississippi River in north-central Minnesota. They are bordered by mixed coniferous and deciduous forest and support a fish fauna consisting mostly of cyprinids. Highest flows normally occur in spring (April–May), with lower but annually variable flows occurring in summer (June–August; Schlosser and Ebel, 1989). Over 2 yr, we collected 10 riffle and 10 pool samples from Gould Creek, and 8 riffle and 40 pool samples from Sucker Creek. All sites were sampled in August 1983 and 1984.

TABLE 1. Categories of depth, current, and substrate type used to compute an index of habitat complexity for sample sites of study streams.

Variable	Categories					
Depth (cm)	0-5	6-20	21-50	≥ 51		
Current (mm)	0	1	2-7	8-22	≥ 23	
Substrate type	clay	silt	sand	gravel	pebble	rock

Jordan Creek and Range Creek are headwaters of the Vermilion and Embarras rivers, respectively, in east-central Illinois. Upstream areas of Jordan Creek's watershed and channel are highly modified to accommodate intensive agricultural use (Schlosser and Karr 1981), but the downstream area studied here has never been channelized, and like Range Creek, is bordered largely by pasture and deciduous forest. Both streams support rich fish faunas dominated by cyprinids, centrarchids, catostomids, and percids. We have no flow data for Range Creek, but personal observations (P. L. Angermeier) indicate its annual hydrologic pattern is similar to Jordan Creek, which exhibits consistently high flow in spring (March–April), and low, but annually variable flow in late summer or early autumn (September–October; Schlosser 1985). In August 1979, we sampled 1 riffle and 20 pools in Range Creek. Over 2 yr we collected 12 riffle and 24 pool samples from Jordan Creek. All sites were sampled in August 1979 and 1980.

The Quebrada Juan Grande, Rio Frijolito, and one unnamed stream (hereafter Tower Creek) are headwaters of the Rio Chagres in central Panama. These streams are located in Parque Nacional Soberania, a tract of lowland rainforest that has remained largely undisturbed since the early 1900s. The fish fauna is composed largely of characids, loriciariids, and poeciliids. Stream flow reflects rainfall, with the driest months occurring from January through March; <5% of the total annual precipitation falls during this period (Angermeier and Karr 1983). Over 2 yr we collected 7 riffle and 12 pool samples from Quebrada Juan Grande, 14 riffle and 15 pool samples from Rio Frijolito, and 9 riffle and 18 pool samples from Tower Creek. Most (71%) sites were sampled in both January 1980 and March 1981.

Sampling procedures

Up- and downstream limits of sample sites coincided with apparent discontinuities in channel morphology, with each site corresponding to a single pool or riffle. Habitat structure was evaluated on the basis of depth, current velocity, and substrate type, following methods used in Schlosser (1982) and Angermeier and Karr (1983), which were modified from methods introduced by Gorman and Karr (1978). Briefly, depth, current, and substrate were measured at regular intervals along transects perpendicular to the stream channel. Dis-

tances between transects ranged from 1.0 to 3.5 m, and distances between measurement points ranged from 0.5 to 1.0 m, depending on stream size. Distances between transects and measurement points were constant within a particular stream. At each measurement point depth was measured to the nearest centimetre with a metre stick, an index of current was recorded as the distance (in millimetres) that water was forced up the upstream edge of a vertical metre stick, and substrate was classified into one of six categories (Table 1). Depth and current measurements were subsequently divided into four and five categories, respectively (Table 1), to facilitate computation of a habitat complexity index. Depth, current, and substrate categories were constant for all streams. The data from each measurement point represent a particular habitat configuration expressed in three dimensions (depth, current, substrate). The number of unique configurations (based on categories in Table 1) and their frequencies of occurrence were used to compute a Shannon-Wiener index of habitat complexity for each sample site. Area of each site was estimated from length and mean width of the channel. Volume of each site was estimated from area and mean depth.

Each site was blocked prior to sampling at the up- and downstream ends with 0.5-cm mesh nets. Sites in Minnesota and Jordan Creek were sampled using two passes of a 7-m long electric seine powered by a generator with 8.7 A (alternating current) maximum capacity. Stunned fish were collected in dip nets and block nets. The efficiency of this technique has been previously discussed in detail (Larimore 1961, Schlosser 1982). At least 80% of the species and individuals captured after five passes are usually captured in the first two passes. Absolute efficiency of the technique ranges from 10 to 70% for various families of fishes (Larimore 1961).

Pools in Range Creek and in Panama were sampled using three downstream passes of a 1.4 × 6.2 m bag-seine with 0.5-cm mesh. To improve seining efficiency, moveable woody debris and rocks were removed from the channel before seining, but after habitat measurements were completed. Sampling efficiency of a similar technique in Jordan Creek indicated that at least 75% of the species and individuals captured after eight passes were usually captured in the first three passes (Schlosser 1982). Riffles in Range Creek and Panama were sampled by thoroughly "kicking" through the substrate

TABLE 2. Summary of analysis of covariance for total species observed in sites of seven streams. Tabled entries include intercepts, slopes for year, site area, and site volume, and R^2 values for regression models including year and a respective covariate as independent variables.

Stream	Parameter estimate				Model R^2	Parameter estimate			
	Intercept	Slope		Intercept		Slope		Model R^2	
		Year	Area			Year	Volume		
Gould	-1.28	0.11	4.41	0.132	-5.65	-0.42	5.12*	0.367	
Sucker	9.66*	-2.18*	4.22*	0.202	-0.20	-2.28*	5.68***,†	0.324	
Range	-10.55	...	7.04*	0.323	-6.51	...	5.18*	0.426	
Jordan	-1.16	-0.34*	7.17***	0.464	-0.35	-0.39*	4.25*	0.357	
Frijolito	-9.96*	1.21	11.22***	0.583	-13.07***	1.89*	7.68***	0.727	
Tower	-1.90	-0.35	8.70***	0.773	-3.28*	0.02	5.14***	0.797	
Grande	-9.40*	1.88	12.33***	0.652	-6.98*	1.39	6.23***	0.721	

* Probability (parameter = 0) < .05.

*** Probability (parameter = 0) < .001.

† The year × volume interaction was omitted from the model, though barely significant ($P = .041$).

upstream of a stationary net (0.5-cm mesh). The net was repositioned at 2–3 m intervals down the length of a riffle, and the entire riffle was “kicked” three times.

Although the methods we used to sample fish were not equivalent in all streams, we believe our respective sampling efforts achieved efficiencies within 10–20% of each other, with electrofishing usually providing more complete samples. Differences in efficiencies of sampling procedures could influence the robustness of our interpretations of inter-regional patterns (see Results), but should not affect our interpretations of relationships derived within a particular stream.

Statistical analyses

Relationships among number of individuals, number of species, habitat area, habitat volume, and habitat complexity were examined using correlation, linear regression, analysis of variance, and analysis of covariance. We used Type II sums of squares in multiple linear regression models to assess relative predictive capabilities of independent variables. That is, each variable’s predictive capability was judged on the basis of the proportion residual variation explained after all other variables were included in the model. Analyses of covariance proceeded in two steps to ensure homogeneity of slopes within the covariance models. First, we tested a model including a class variable, an interaction term (class × covariate), and a covariate as independent variables. Except where otherwise indicated, the interaction term did not account for a significant proportion of the variance ($P > .05$) in the dependent variable. Thus, the interaction term was omitted from the second covariance model for that dependent variable. Because distributions of the data variables were commonly non-normal, we corroborated parametric statistical analyses with distribution-free statistical analyses where appropriate. Interpretations of these paired analyses were typically identical. Habitat area, habitat volume, and numbers of individual fishes were

\log_{10} -transformed in all analyses in order to minimize effects of non-normality.

RESULTS

Relationships between species richness and site characteristics

We used a combination of statistical techniques to distinguish the relative effects of number of individuals, site area, site volume, and site complexity on species richness. First, we determined which measure of habitat size, volume or area, was the better predictor of species richness. Then, we compared the capability of habitat size, habitat complexity, and number of individuals to predict species richness. These relationships were examined for different habitat types, for habitat types combined, and among geographic regions.

We compared effects of site area and site volume on fish species richness using analysis of covariance models with “year” as a class variable. We reasoned that because between-year differences in species’ distributions or abundances could be significant, data from separate years should not be pooled. Covariance models containing site volume as the covariate consistently accounted for a greater proportion of the variance in species richness than models with site area as the covariate (Table 2); Jordan Creek in Illinois was the only exception. Sucker Creek and Jordan Creek exhibited significant ($P < .05$) annual differences in species richness at sites regardless of which measure of habitat size was in the model. Because site volume was judged to be a better predictor of species richness than site area, only site volume was used in subsequent analyses of species-area type patterns.

Relationships between species richness and site characteristics (i.e., volume, complexity, and number of individuals) were examined using bivariate correlations (Pearson’s r and Kendall’s τ ; Table 3) and mul-

TABLE 3. Correlation coefficients (Pearson's *r*) between species richness and three other variables, and between site volume and habitat complexity, at sites from seven streams. Coefficients were computed for individual years and with years combined.

Stream	Year	N	Species richness vs.			Complexity vs. volume
			Individuals	Volume	Complexity	
Gould	1983	10	0.983	...*
	1984	10	0.942	0.772
	Overall	20	0.957	0.602
Sucker	1983	24	0.630	0.415†
	1984	24	0.836	0.585
	Overall	48	0.805	0.432
Range	1979	21	...	0.653
Jordan	1979	18	0.731	0.607†	0.568†	0.692
	1980	18	0.620	0.494	...	0.518†
	Overall	36	0.719	0.401†	...	0.620
Frijolito	1980	16	0.888	0.794	0.569	0.729
	1981	13	0.888	0.895	0.759	0.929
	Overall	29	0.877	0.822	0.647	0.833
Tower	1980	14	0.969	0.915	0.686	0.800
	1981	13	0.930	0.867	0.654	0.891
	Overall	27	0.951	0.893	0.637	0.794
Grande	1980	8	0.982	0.740
	1981	11	0.892	0.923	...	0.706
	Overall	19	0.917	0.838	0.496†	0.720

* Absent entries indicate the coefficients were not significant ($P > .05$).

† Correlations were not significant when an analogous nonparametric test (Kendall's τ) was performed.

multiple linear regression (Table 4). Species richness was correlated ($P < .05$) with number of individuals for all streams in all years except in Range Creek in 1979. Species richness was correlated with site volume for all streams in all years except Gould Creek in 1983. However, three of the correlations did not achieve significance ($P < .05$) using Kendall's τ , a nonparametric correlation coefficient. In 16 of 19 cases, the correlation between species richness and number of individuals was stronger than between species richness and site volume (Table 3). Correlations between species richness and number of individuals were generally weaker in Illinois than in Minnesota or Panama, whereas correlations between species richness and site volume were weaker in Minnesota and Illinois than in Panama (Table 3).

Habitat complexity was not correlated with site volume in Range Creek or in the Minnesota streams (Table 3). Species richness was consistently correlated with habitat complexity only in Rio Frijolito and Tower Creek, and correlations were always weaker than those between species richness and the other two variables. In Jordan Creek and Quebrada Juan Grande, habitat complexity was correlated with site volume, but not with species richness.

Correlation analyses demonstrate that site volume, site complexity, and number of individuals all have some capability of "predicting" species richness. However, because site variables tend to be intercorrelated, these analyses cannot identify unambiguously which is the best single predictor of species richness. To assess the relative usefulness of number of individuals, site

TABLE 4. Summary of multiple regression analyses of species richness vs. number of individuals, site volume, and site complexity in seven streams. Tabled entries include intercepts, slopes (based on Type II ss), and the proportion of variance in species richness accounted for by the models.

Stream	Model 1					Model 2			
	Intercept	Slope			Model R^2	Intercept	Slope		Model R^2
		Individuals	Volume	Complexity			Individuals	Volume	
Gould	3.60	5.68***	-0.64	-1.24	0.930	1.21	5.88***	-0.63	0.919
Sucker	1.44	5.10***	0.69	-1.53	0.675	-0.59	5.34***	0.13	0.648
Range	-18.35*	4.01*	5.23***	1.76	0.586	-13.68*	3.24*	5.33***	0.561
Jordan	-8.35*	5.27***	3.45*	-0.52	0.686	-8.75*	5.28***	3.31***	0.685
Frijolito	1.21	5.96*	0.46	-1.40	0.775	0.99	5.94*	-0.50	0.770
Tower	0.56	4.87***	0.13	-0.37	0.906	0.56	5.00***	-0.24	0.905
Grande	-1.92	4.14***	2.62	-1.36	0.872	-2.21	4.29***	1.74	0.862

* Probability (parameter = 0) < .05.

*** Probability (parameter = 0) < .001.

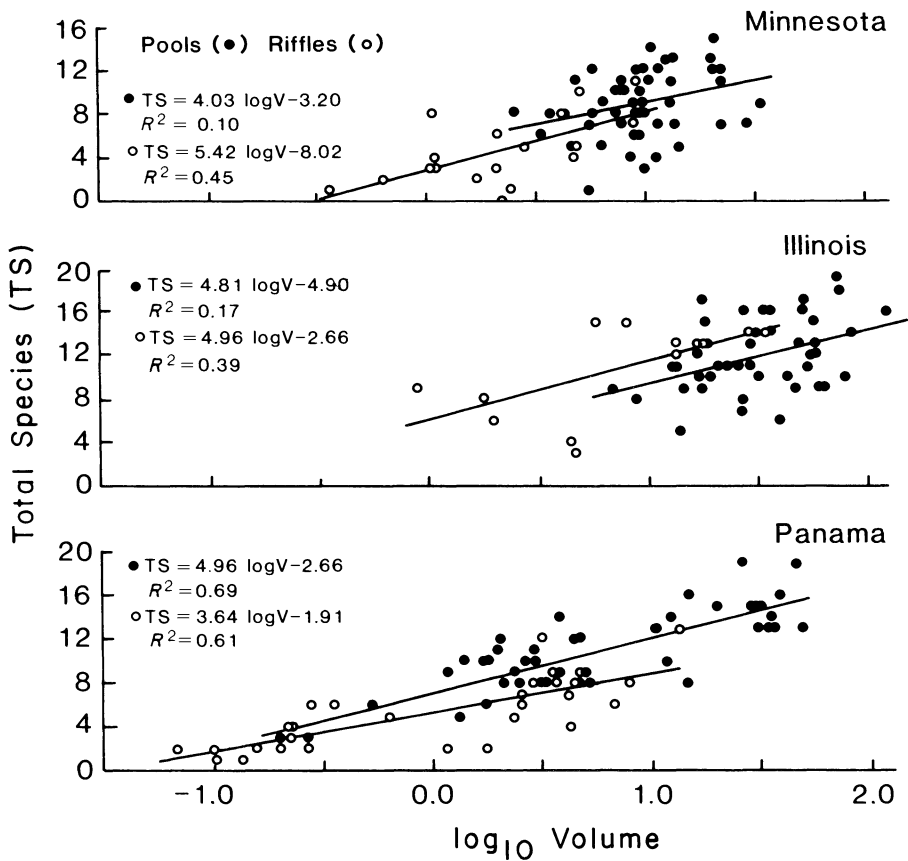


FIG. 1. Plots of species richness against site volume (in cubic metres) for streams from three geographic regions. Sites are classified as pools or riffles. Lines represent the simple regressions that are given. See text for discussion of analyses of covariance.

volume, and habitat complexity as predictors of species richness in sites of each stream, we used two multiple regression models (Table 4). Because between-year differences in species richness were not important in most study streams (Table 2), we combined data from different years for these analyses. The first model regressed species richness on number of individuals, site volume, and site complexity. Site complexity did not contribute a significant proportion of the sums of squares (Type II ss) for any of the streams, and removing it from the models reduced R^2 values by <3% in each stream. The second model included only number of individuals and site volume as independent variables. The number of individuals from a site contributed a significant ($P < .05$) proportion of the sums of squares (Type II ss) to all models, whereas site volume contributed a significant proportion of the sums of squares only in the two Illinois streams (Table 4). Thus, although simple correlations between species richness and habitat volume were widespread, volume was generally not a useful predictor of species richness after adjusting for the number of individuals captured at a site. With the exception of Gould Creek, models including number of individuals and site volume ac-

counted for less of the variance in species richness in Minnesota and Illinois streams than in Panama (Table 4).

We also examined relationships between species richness and number of individuals, site volume, and site complexity with respect to how they might differ between pool and riffle habitats. Because our sample sizes of pools or riffles from each stream were inadequate for meaningful statistical analyses, we grouped pools and riffles from Minnesota, Illinois, and Panama, respectively. Species richness was more strongly correlated with number of individuals than with site volume in all regions and habitats (Table 5). Species richness was more strongly correlated with habitat complexity and site volume in Panama habitats than in Minnesota and Illinois (Table 5 and Fig. 1). Species richness patterns in pools and riffles were also examined using multiple regression models with number of individuals, site volume, and site complexity as independent variables (Table 6). Between-year effects were again omitted for simplicity. Effects of site volume and complexity were significant ($P < .05$) after accounting for number of individuals only in Illinois pools, whereas number of individuals was significant for all six

TABLE 5. Correlation coefficients (Pearson's r) between species richness and three other variables from streams in three regions. Two habitat types were analyzed separately.

Region	Habitat	N	Species richness vs.		
			Individuals	Volume	Complexity
Minnesota	Pool	50	0.786	0.315	...*
	Riffle	18	0.976	0.668	...
Illinois	Pool	44	0.487	0.408	...
	Riffle	13	0.836	0.624†	...
Panama	Pool	45	0.875	0.833	0.648
	Riffle	30	0.885	0.782	0.681

* Missing entries indicate that the coefficients were not significant ($P > .05$).

† Indicates that an analogous nonparametric test (Kendall's τ) yielded a nonsignificant coefficient.

models (Table 6). Species richness was predicted more precisely in riffles than in pools for all three regions.

The relationship between total fish density (number per cubic metre) and species richness varied among regions and habitats (Table 6). In pools, fish density was positively correlated (Kendall's τ) with species richness in Minnesota, uncorrelated in Illinois and negatively correlated in Panama. Fish densities in riffles were unrelated to species richness except in Minnesota, where a positive correlation was observed.

Analysis of covariance was used to test for variation in the species–volume relationship between habitat types within each geographic region (Fig. 1). Differences in intercept between species–volume relationships in pools and those in riffles were significant ($P < .05$) only in Panama, where pools supported approximately two more species per unit volume than did riffles (Fig. 1). A similar analysis was performed to compare species–volume relationships among geographic regions. Although slopes of species–volume relationships did not differ significantly ($P > .05$) among regions, the number of species per unit volume was 1–2 species greater in Panama ($P < .05$) for both habitat types (Fig. 1). Regional variation in number of species per unit volume would probably have been even great-

er if our sampling efficiency in Panama had been as high as in Illinois and Minnesota.

In summary, site volume was usually a better “predictor” of species richness than was site area, and the number of individuals in a sample was usually a better “predictor” of species richness than were site volume or habitat complexity. Furthermore, correlations between species richness and site volume or habitat complexity were more apparent in Panama streams than in Minnesota or Illinois. These patterns obtained whether habitat types were analyzed together or separately. Between-habitat differences in species richness were apparent only in Panama, and Panama sites supported the most species per unit volume.

Species abundance patterns

The number of species per unit volume was shown earlier (Table 2) to vary between years in some streams. We performed additional analyses to determine whether site volume could predict abundances of individual species and whether predictive capability varied between years. For each stream and each year, we selected all species occurring in six or more sites. Correlations between a species' abundance and site volume were then tested for all sites in that stream and year where the species occurred (i.e., zero-abundances were omitted). Most species tested exhibited no positive correlation between abundance and site volume, but species abundances in Panama streams were more likely to be correlated with site volume than those in Illinois or Minnesota. Only 7 of the 79 tests performed (9%) on species in Illinois and Minnesota yielded positive correlations (Kendall's τ ; $P < .05$), whereas 20 of the 57 correlations tested (35%) on Panama species were significant. Abundances of species for which correlations were significant were then regressed against site volume to determine whether those species recognized a minimum volume for the habitats they occupied. Inspection of the abundance–volume plots (\log_{10} -transformed) indicated that these relationships were generally linear. Thus, species were judged to recognize thresholds of habitat volume if the y -intercept of the regres-

TABLE 6. Summary of multiple regression analysis of species richness vs. number of individuals, site volume, and site complexity in two habitat types in three geographic regions (entries as in Table 4). Also given are correlation coefficients (Kendall's τ) between fish density (number per cubic metre) and species richness.

Region, habitat	Intercept	Slope			Model R^2	Correlation between fish density and species richness
		Individuals	Volume	Complexity		
Minnesota pools	1.65	5.48***	0.42	-1.58	0.651	0.515***
Minnesota riffles	1.68	5.08***	0.11	-0.88	0.959	0.635***
Illinois pools	-22.86***	5.74***	5.27***	2.54*	0.564	0.122
Illinois riffles	-5.87	4.82*	2.49	-0.30	0.751	0.119
Panama pools	-2.43	6.40*	0.82	-0.96	0.772	-0.283*
Panama riffles	-0.69	4.24***	1.91*	-1.17	0.816	-0.131

* Probability (parameter = 0) < .05.

*** Probability (parameter = 0) < .001.

TABLE 7. Coefficients of concordance (Kendall's τ) of species relative abundance between two sample years for six streams. The percentage of species captured in only 1 of the 2 yr is also given. The analysis was performed for two habitat types separately and for habitats combined.

Stream	Habitats combined			Riffles			Pools		
	No. species	τ	% species in only 1 yr	No. species	τ	% species in only 1 yr	No. species	τ	% species in only 1 yr
Gould	18	0.131	38.9	13	0.016	46.2	18	0.132	38.9
Sucker	24	0.482*	37.5	13	0.124	38.5	24	0.490*	37.5
Jordan	28	0.749***	17.9	20	0.578***	20.0	28	0.663***	17.9
Frijolito	24	0.804***	4.2	17	0.425*	17.6	23	0.760***	13.0
Tower	15	0.706***	26.7	11	0.174	45.5	15	0.725***	26.7
Grande	19	0.452	10.5	12	-0.112	75.0	18	0.527*	11.1

* $P < .05$.

*** $P < .001$.

sion line was significantly ($P < .05$) less than one fish. Slopes of regression lines were significantly ($P < .05$) greater than zero for all models tested except one from Gould Creek. All species with significantly positive regression slopes appeared to recognize minimum thresholds of habitat volume (i.e., their y -intercepts were < 1 fish).

Habitat volume was a better predictor of fish abundance in Panama than in Minnesota or Illinois. Linear models with habitat volume as the independent variable accounted for 41–93% ($\bar{X} = 78\%$) of the variance in abundance of Panama species tested, but only 35–61% ($\bar{X} = 45\%$) of the variance in abundance of temperate species tested. Furthermore, the predictive capability of habitat volume was more consistent among streams and years in Panama than in Minnesota and Illinois. Only one temperate species (*Notropis cornutus*) exhibited significant regressions of abundance on habitat volume in a stream (Sucker Creek) for both sample years. No temperate species exhibited such relationships in more than one stream. Abundances of four other species (*Semotilus atromaculatus*, *Hybognathus*, *Fundulus*, and *Cottus*) were correlated with habitat volume in only one stream and 1 yr. In contrast, abundances of four species (*Neoheterandria*, *Brycon*, *Hyphessobrycon*, *Astyanax*) were correlated with habitat volume during both sample years in Rio Frijolito. Two of those species (*Hyphessobrycon*, *Astyanax*) exhibited similar correlations during both sample years in Tower Creek. Five species (*Neoheterandria*, *Astyanax*, *Brachyrhaphis cascajalensis*, *Aequidens*, *Hyphessobrycon*) exhibited correlations between abundance and habitat volume in two or more Panama streams, and two species (*Gephyrocarax*, *Geophagus*) exhibited such correlations in only one stream and 1 yr.

We also examined annual variation in species relative abundances within streams using Kendall's τ as a measure of concordance. Abundances from all sites in a stream and sample year were summed for each species. Species captured in only 1 yr were included in the analysis. Annual comparisons were made for each stream except Range Creek, which was sampled in only 1 yr. With habitats combined, relative abundances of

species were strongly correlated ($P < .01$) between years in all streams except Gould Creek (Table 7). The proportion of species captured in only 1 of the 2 yr was relatively high in both Minnesota streams, and lowest in Rio Frijolito (Table 7). Separate analyses for pools and riffles showed that relative abundances in pools were more constant between years than were those in riffles. Indeed, only Jordan Creek and Rio Frijolito exhibited between-year correlations in species relative abundances in riffles. These streams also featured the most well-developed pool-riffle morphology of the streams studied. Panama pools tended to exhibit more consistent relative abundances between years than did temperate pools, especially those in Minnesota.

In summary, abundances of some species were correlated with the volume of the habitats they occupied. This pattern was observed for more species and with more consistency between years and among streams in Panama than in Minnesota or Illinois. Over all habitats, relative abundances of species were correlated between years, but correlations were stronger in pools than in riffles, especially in Panama.

DISCUSSION

Basis for species-area relationships

Larger patches of habitat generally contain more species than smaller patches. Most studies regarding this phenomenon have been conducted on terrestrial systems, where patch area is a simple, convenient measure of patch size. However, in aquatic environments, where a third spatial dimension (i.e., depth) can be accurately measured, patch volume becomes an appropriate measure of patch size. Although correlations between fish species richness and habitat area were usually significant in the streams we studied (Table 2), habitat volume "predicted" species richness more precisely than did habitat area, thereby suggesting that the area and depth of stream habitats influence distributions of stream fishes. It is unclear whether or not volumetric measures of patch size could improve the predictability of species richness for certain terrestrial systems (e.g., birds in woodlots), where unexplained

variance in species number often limits the management utility of species-area relationships (Boecklen and Gotelli 1984). Although not explicitly expressed as a volume term, canopy height is an analogous feature commonly measured when characterizing forest habitat (James and Wamer 1982, Blake and Karr 1987).

The number of individuals in a patch was generally an even better predictor of fish species richness than patch volume (Tables 2 and 3). In contrast, habitat complexity was correlated with species richness in only two of seven streams, and correlations were never as strong as between species richness and habitat volume. Moreover, in two streams habitat complexity was correlated with habitat volume, but not with species richness. These patterns were corroborated in stepwise regression analyses (Table 4), where number of individuals was the only variable consistently correlated with species richness. Furthermore, the superiority of number of individuals as a predictor of species richness was corroborated when habitat types were considered separately (Table 5). Thus, our results support the hypothesis that the positive relationship between species richness and patch size is largely an epiphenomenon associated with sampling effort (Connor and McCoy 1979). That is, larger patches contained more individuals, and thus sampled the available species pool more completely. However, the relative influence of habitat features on fish distribution varied considerably among streams.

If the number of individuals in a habitat patch is the sole determinant of species-volume relationships, then the number of species (and individuals) intercepted by any volume of habitat should be closely related to patch size, but not influenced by other habitat features. Exceptions might include those features that act to concentrate individuals by virtue of providing limited resources (e.g., food, shelter, reproductive sites). Given this premise, the correlation between patch size and the number of individuals in a patch should be stronger than the correlation between patch size and the number of species in a patch. Using volume as a measure of patch size, this condition was not met in any of our study streams (test of homogeneity among correlation coefficients; Sokal and Rohlf 1981). This pattern, along with the numerous relationships we observed between fish distribution and habitat features (Tables 3–6), strongly indicate that species-volume relationships are not strictly sampling phenomena. Indeed, the influence of habitat features on fish distribution and abundance within streams has been extensively studied (Gorman and Karr 1978, Schlosser 1982), although effects of habitat area or volume on those relationships remains unclear. We suggest that only rarely is the distribution of species among a system of habitat patches completely attributable to passive sampling or to any other single phenomenon. Rather, patterns of species assembly and distribution may implicate immigration-extinction dynamics, habitat diversity, and passive sam-

pling, each to varying degrees. This hypothesis is supported by our results, where effects of number of individuals, habitat volume, and habitat complexity on species richness varied considerably among streams. The extent to which species-volume relationships are explained by passive sampling phenomena may depend on the variability of the assemblage's environment (see Scatter in Species-Volume Relationships).

Although number of individuals was generally the best single predictor of fish species richness, the importance of habitat features to fish distribution and abundance was apparent in several streams. Influences of habitat configuration become especially apparent in comparisons of riffle and pool assemblages. For example, Panama pools supported more species per volume than riffles, and earlier work in Minnesota and Panama streams demonstrated that fish densities are often greater in pools than in riffles (Schlosser and Ebel 1989, Angermeier and Karr 1983). Our data indicate that riffles are occupied less readily by most species than are pools, and that juveniles of many species are more likely than adults to inhabit riffles, especially if piscivores are abundant in the pools (Schlosser 1987a). It appeared that many species occupying riffles in our study streams were doing so opportunistically rather than as highly adapted riffle specialists. The relatively large degree of variation in rank orders of riffle species' abundances between years is consistent with this hypothesis. Several features of riffles make them less hospitable environments for fish than are pools. Difficulties of riffle living include energy costs of maintaining position against strong currents and risks of exposure to desiccation and predation by birds and mammals during low-flow conditions (Power 1984). In addition, riffle fishes are afforded fewer opportunities for trophic diversification than pool fishes. Riffle fishes are generally restricted to eating algae, aquatic invertebrates, or other fish (Schlosser 1982, Angermeier and Karr 1983, Angermeier 1985), whereas additional foods such as terrestrial invertebrates and terrestrial plant material (Zaret and Rand 1971, Goulding 1980, Angermeier and Karr 1983) are often available to pool fishes. Indeed, in Panama pools, where species per volume ratios were higher than in any other habitats, many species consume significant amounts of allochthonous foods. All eight species that recognized thresholds of minimum habitat volume in Panama are known to consume terrestrial invertebrates or plant material (Angermeier and Karr 1983). Thus, although structural complexity of stream habitats may not consistently predict fish species richness, habitat features that distinguish habitat types are critical to fishes' interactions with their physical and biological environment.

Scatter in species-volume relationships

Diamond and Gilpin (1980) defined turnover noise as the fluctuation in species richness expected in a constant environment due to immigration and extinction,

and suggested that this fluctuation might be a significant source of variance in species-area relationships of islands. Intuitively, fluctuations in species richness due to immigration and extinction should become increasingly pronounced as environmental variability or species' vagility (or both) increase. In systems where the environment frequently shifts between physically harsh and benign conditions, species composition and population densities may remain in continual flux as mobile opportunists immigrate and emigrate in response to current conditions. Consequently, habitats may often support more or fewer individuals and species than expected on the basis of structural features such as patch size or complexity. In our study streams, the proximity of patches within each "archipelago" and the general mobility of fishes enhance the ability of populations to expand or contract their ranges over small spatiotemporal scales, and the ability of individuals to opportunistically occupy different patches. Our results suggest that empirical relationships between species richness and habitat volume and habitat complexity reflect the importance of immigration/extinction dynamics to the structure of stream fish communities. Based on our correlation analyses (Tables 3 and 5), relationships between species richness, habitat volume, and habitat complexity were stronger (less statistical variance) in Panama than in Minnesota or Illinois. In addition, correlations between species' abundances and habitat volume were more frequent, statistically stronger, and more consistent through space and time in Panama than in Minnesota or Illinois. Thus, we suspect that immigration/extinction dynamics play a larger role in organizing the fish communities in our Minnesota and Illinois streams than in our Panama streams.

Statistical variance in relationships between species distribution and abundance and habitat features (e.g., volume, complexity) may reflect population variability, which is closely linked to variability in stream flow and temperature for many fishes (Schlosser and Toth 1984, Ross et al. 1985, Schlosser 1985, 1987b). Seasonal and annual variation in stream flow and temperature, especially during spawning periods, can induce striking seasonal and annual variation in fish reproductive success, density, species composition, and species richness (Starrett 1951, Schlosser 1982, 1985, 1987b). Annual fluctuations in reproductive success of stream fishes are likely to be more pronounced in Minnesota than Panama (with Illinois intermediate) because the seasonal "window" during which spawning is physiologically feasible is shortest in Minnesota. All species in the Minnesota streams spawn between mid-May and July, while reproductive periodicity of Panama species is very diverse, with the seasonal timing and duration varying considerably among species (Kramer 1978). Even if the likelihood of unfavorable flow or temperature conditions occurring during a given spawning period is similar among geographic regions,

opportunities for fish to delay or repeat spawning are especially limited in Minnesota. In addition, stream fishes in Minnesota consistently face extremely harsh winters, with few fish overwintering in small streams (I. J. Schlosser, *personal observation*). Fish apparently recolonize these streams each spring from downstream reaches or connecting lakes. In contrast, most fishes in the Illinois and Panama streams we studied appeared to be year-round residents.

Two additional patterns are consistent with the hypothesis that cycles of emigration and colonization are especially important in Minnesota. First, correlations of species relative abundances between years were generally weakest in Minnesota and the proportion of species occurring in only 1 yr was relatively high (Table 7). If recolonization is viewed as a largely random draw of species from the source pool, then we would expect little similarity in the draws for different years. Second, total fish density was positively correlated with species richness in Minnesota sites (Table 6). Intensity of resource competition is likely to be low in recently colonized habitats, with densities and species richness both increasing until saturation is approached. An inverse relationship between total density and species richness, such as that observed in Panama pools, is analogous to the density compensation phenomenon previously reported for insular faunas (Case 1975). Occurrence of this phenomenon is generally associated with intense competition for resource, especially food (Case et al. 1979).

Thus, we hypothesize that relatively high annual variability in reproductive success and harsh winters interact to maintain nearly continual imbalance between the Minnesota fish assemblages and their available habitat. The weak relationships we observed between species richness and habitat structure were manifestations of that imbalance. We expect seasonal and annual stability in community structure and intensity of species' interactions in Minnesota to be less pronounced than in Panama streams, with Illinois intermediate. The scenario we describe is analogous to one described by Schoener (1986) for spider populations on Bahama islands. Schoener (1986) argued that spider populations exposed to heavy predation by lizards were more susceptible to local extinction due to climatic factors than were populations on islands without lizards. Consequently, spider populations on islands with high local extinction rates were less likely to exhibit strong species-area relationships or other associations between habitat size or structure and species distribution or abundance (Schoener 1986). Thus, patterns from populations of fishes in streams and spiders on islands suggest that in systems where emigration/extinction and recolonization are especially important to population dynamics, we should not expect strong relationships between habitat features and species distributions. Conversely, we might expect strong correlations between species richness and hab-

itat size and complexity (as observed in Panama) to reflect relatively consistent reproductive success between years and relatively benign seasonality. However, we emphasize that latitudinal position of a stream probably has little to do with the observed strength of relationships between habitat features and species distributions. For example, species richness relationships of Quebrada Juan Grande resembled the temperate streams more closely than other Panama streams. In fact, many tropical streams undergo extreme annual fluctuations in physicochemical features (Lowe-McConnell 1975, 1987), and we expect their fish assemblages to exhibit patterns similar to those in our Minnesota streams. Finally, we offer an important caveat regarding the limitations of interpreting and comparing patterns without experimental corroboration. Recent modeling efforts indicate that a variety of mechanisms of species coexistence can yield identical population dynamics (Chesson 1986, Chesson and Case 1986). Thus, our interpretations of community patterns should be viewed as hypotheses still awaiting rigorous testing.

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APPENDIX

Fish species collected from seven study streams. Numbers indicate the number of sample periods in which a species was captured.

Species	Stream						
	Gould	Sucker	Range	Jordan	Frijolito	Tower	Grande
<i>Umbra limi</i>	2	2					
<i>Culaea inconstans</i>	1	2					
<i>Esox lucius</i>		1					
<i>Esox americanus</i>				2			
<i>Salvelinus fontinalis</i>		2					
<i>Pimephales promelas</i>	2	2	1				
<i>Pimephales notatus</i>		1	1	2			
<i>Semotilus atromaculatus</i>	2	2	1	2			
<i>Semotilus margarita</i>		1					
<i>Hybognathus hankinsoni</i>	1	2					
<i>Phoxinus eos</i>		2					
<i>Phoxinus neogaeus</i>	2	1					
<i>Rhinichthys atratulus</i>	1	2					
<i>Notropis cornutus</i>	2	2					
<i>Notropis stramineus</i>		2					
<i>Notropis heterolepis</i>	2	2					
<i>Notropis heterodon</i>	1						
<i>Notropis chrysocephalus</i>			1	2			
<i>Notropis atherinoides</i>			1				
<i>Notropis umbratilis</i>			1				
<i>Notropis spilopterus</i>			1	2			
<i>Phenacobius mirabilis</i>			1				
<i>Ericymba buccata</i>			1				
<i>Campostoma anomalum</i>			1	2			
<i>Notemigonus crysoleucas</i>			1	2			
<i>Nocomis biguttatus</i>				2			
<i>Catostomus commersoni</i>		2	1	2			

APPENDIX. Continued.

Species	Stream						
	Gould	Sucker	Range	Jordan	Frijolito	Tower	Grande
<i>Erimyzon oblongus</i>			1	2			
<i>Moxostoma erythrurum</i>		2					
<i>Carpionodes cyprinus</i>				1			
<i>Hypentelium nigricans</i>				2			
<i>Ictalurus melas</i>	2			1			
<i>Ictalurus natalis</i>			1	2			
<i>Noturus gyrinus</i>	2	1					
<i>Noturus flavus</i>				2			
<i>Micropterus salmoides</i>	2	2	1	1			
<i>Micropterus dolomieu</i>				2			
<i>Micropterus punctulatus</i>			1				
<i>Lepomis macrochirus</i>		1	1	2			
<i>Lepomis gibbosus</i>	1	1					
<i>Lepomis cyanellus</i>			1	2			
<i>Lepomis gulosus</i>			1				
<i>Lepomis megalotis</i>			1	2			
<i>Pomoxis nigromaculatus</i>			1				
<i>Ambloplites rupestris</i>				2			
<i>Perca flavescens</i>	1	1					
<i>Etheostoma nigrum</i>	2	1	1	2			
<i>Etheostoma exile</i>	2	2					
<i>Etheostoma spectabile</i>			1	2			
<i>Etheostoma gracile</i>			1				
<i>Etheostoma flabellare</i>				2			
<i>Etheostoma blennioides</i>				2			
<i>Etheostoma caeruleum</i>				2			
<i>Percina maculata</i>			1	1			
<i>Cottus bairdi</i>		2					
<i>Dorosoma cepedianum</i>			1				
<i>Aphredoderus sayanus</i>			1				
<i>Fundulus notatus</i>			1	1			
<i>Rivulus brunneus</i>					2	2	2
<i>Trichomycterus striatum</i>					2		1
<i>Hypopomus occidentalis</i>					2	1	2
<i>Hoplias microlepis</i>					2	1	2
<i>Piabucina panamensis</i>					2	2	2
<i>Cheirodon gorgonae</i>					1		2
<i>Gephyrocarax atricaudata</i>					2	2	2
<i>Astyanax ruberrimus</i>					2	2	2
<i>Hyphessobrycon panamensis</i>					2	2	2
<i>Roeboides guatemalensis</i>					2		2
<i>Brycon petrosus</i>					2		
<i>Rhamdia wagneri</i>					2		2
<i>Pimelodella chagresi</i>					2		
<i>Imparales panamensis</i>					2		
<i>Hypostomus plecostomus</i>					2		
<i>Chaetostoma fischeri</i>					2		
<i>Ancistrus spinosus</i>					2		1
<i>Rineloricaria uracantha</i>					2	1	2
<i>Poecilia sphenops</i>					2	2	2
<i>Neoheterandria tridentiger</i>					2	2	2
<i>Brachyrhaphis episcopali</i>					2	2	2
<i>Brachyrhaphis cascajalensis</i>					2	2	2
<i>Aequidens caeruleopunctatus</i>					2	2	2
<i>Geophagus crassilabris</i>					2	2	
<i>Cichlasoma panamensis</i>							2