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Diversity and stability in Mississippi stream fish assemblages

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Jacob F. Schaefer[1] AND **Scott R. Clark**[2]
University of Southern Mississippi, Department of Biological Sciences, Hattiesburg,
Mississippi 39406 USA

Melvin L. Warren, Jr[3]
US Department of Agriculture Forest Service, Southern Research Station, Center for Bottomland
Hardwoods Research, Oxford, Mississippi 38655 USA

Abstract. Positive correlations between diversity and stability have been reported for a number of ecosystems and are thought to be caused by a stabilizing effect of differential species' responses to environmental perturbation. Empirical field studies in which investigators tested for diversity–stability relationships are lacking for some taxonomic groups and typically have not included tests of the importance of other potential correlates of diversity or assemblage structure. We sampled stream fish assemblages and associated habitat variables at 36 sites over a 10-y period. Quantitative and qualitative measures of stability were correlated with fish diversity at sites. Fish assemblage composition was correlated with a variety of habitat variables, and diversity was correlated with stream size. We used Akaike's Information Criterion to select the models that best predicted qualitative and quantitative stability. Candidate models contained variables describing diversity, stream size, time between samples, and change in habitat variables over time. Models that included diversity and time between samples were the best predictors of stability. Our results support the existence of diversity–stability relationships, and we showed that other predictors of diversity or habitat change were generally poor predictors of stability.

Key words: diversity, stability, insurance hypothesis, stream fish.

> "*…the balance of relatively simple communities of plants and animals is more easily upset than that of richer ones*"
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> *C. Elton (1958, p. 145).*

The relationship between ecosystem diversity and stability has long intrigued ecologists. Observations by Elton (1958) and modeling work by MacArthur (1955) suggested that more diverse communities were less vulnerable to invasions and less variable over time than were less diverse communities (Levine and D'Antonio 1999, McCann 2000, Ives and Carpenter 2007). Models developed by May (1972) contradicted this relationship, and the issue remained contentious for some time. More recent empirical data from terrestrial systems and a variety of mesocosm experiments have yielded fairly broad support for the correlation between ecosystem diversity and stability (Tilman and Downing 1994, Tilman 1996, Tilman et al. 2006, Ives and Carpenter 2007). However, data from field experiments supporting the relationship stems primarily from plant communities, and the broader mechanisms driving the pattern are still debated (Doak et al. 1998, Leary and Petchey 2009). We know of only one study focused on the diversity–stability relationship in freshwater stream fish communities (Franssen et al. 2011) and one for stream macroinvertebrates (Mykrä et al. 2011). Increasing diversity is hypothesized to increase functional redundancy in species that have important stabilizing roles (McCann 2000, Leary and Petchey 2009). Functional redundancy increases the covariance in species responses to perturbation, thereby dampening changes to ecosystem emergent properties. By extension, the documented relationship between diversity and ecosystem function (Dangles et al. 2011, Lecerf and Richardson 2010) is both consistent and expected.

A working definition of stability is an important component of a test of the diversity–stability relationship. Stability can be assessed from functional (composite ecosystem measures; Tilman et al. 2006,

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[1] E-mail addresses: jake.schaefer@usm.edu

[2] scott.r.clark@eagles.usm.edu

[3] mwarren01@fs.fed.us

Ives and Carpenter 2007) or compositional (individual species abundances or turnover; Ross et al. 1985, Sankaran and McNaughton 1999, Shurin 2007, this study) response variables. Functional and compositional measures can be viewed as being dynamically stable (measured as the ability of a system to resist change or return to equilibrium after change) or resilient (measured as the rate of system recovery) (Holling 1973, McCann 2000). In this context, systems are stable if they can resist significant perturbations or return to a steady state soon after. In the absence of perturbations, stable systems should be unchanging at some equilibrium. Compositional stability (hereafter stability) must be observed over an appropriate temporal scale, which has been argued to be the mean generation time of assemblage dominants or the time required for complete turnover of all individuals (Connell and Sousa 1983, Grossman 1990, Doak et al. 1998, Ives and Carpenter 2007). In general, more stable communities should have lower extinction rates and more consistent population densities that result in higher and more consistent measures of quantitative and qualitative assemblage similarity through time.

If diversity–stability relationships are common, the relationship between stability and other documented correlates of diversity are potential predictors of stability (Sankaran and McNaughton 1999). Relationships between diversity and habitat size (area or discharge), time (species–time [STR]), and disturbance regime (intermediate disturbance hypothesis) are fundamental ecological principles (Xenopoulos and Lodge 2006, Shurin 2007, McGarvey and Ward 2008, Scheiner et al. 2011). White et al. (2006) noted that increases in diversity with duration of sampling period (i.e., STR) were ubiquitous across a variety of groups and constituted a fundamental ecological pattern. Temporal autocorrelations among measures of assemblage similarity (Collins 2000) and STR (White et al. 2006) indicate that time might contribute substantially to models predicting stability. Slopes of relationships between STR and stability were lower in more diverse systems, a result indicating that mechanisms that increase diversity reduce rates of species turnover (thereby increasing stability) (White et al. 2006).

Stream ecologists have studied the influence of stochastic vs deterministic processes on fish assemblage dynamics (Grossman 1985, Ebeling et al. 1990, Grossman et al. 1990, Holomuzki and Stevenson 1992, Hansen and Ramm 1994, Snodgrass and Meffe 1998, Micheli et al. 1999, Ostrand and Wilde 2002, Matthews and Marsh-Matthews 2003, 2006, Schweizer and Matlack 2005, Trexler et al. 2005, Chase 2007). Many of these investigators tied fish assemblage composition to habitat structure and aspects of disturbance regimes. Disturbances are expected to alter the physical habitat, thereby changing assemblage composition (Fausch and Bramblett 1991) and decreasing measures of stability. Several investigators have linked disturbance-induced changes in habitat structure to changes in assemblage composition (Matthews 1986, Taylor et al. 1993, Taylor and Warren 2001, Matthews and Marsh-Matthews 2003, Li and Gelwick 2006). Much has been learned about how individual factors (diversity, time, change in habitat, size) may be related to assemblage dynamics and stability, but these factors typically are studied in isolation (Mykrä et al. 2011). Data sets robust enough to allow simultaneous tests of the relative importance of multiple factors are rare.

Understanding the processes that yield stability in ecosystem services is critically important for ecological theory and resource management. The promise of more stable ecosystem services is likely to be an appealing justification for policies aimed at conserving diversity. Our goal was to assess patterns of diversity and stability in freshwater stream fish communities. We sampled stream fish communities repeatedly at 36 sites throughout Mississippi. Time between samplings at the same site was as long as 10 y. We measured physicochemical variables associated with each sample to link assemblage composition to habitat structure and to measure change in the physical habitat over the same interval. We asked: 1) Is fish assemblage composition correlated with habitat variables? 2) Are fish diversity and stream size related? 3) Are diversity and stability related? and 4) Is diversity the best predictor of stability or are other variables, such as stream size, sampling interval, or change in physical habitat, important contributors to models predicting stability?

Methods

We sampled 36 first- to fifth-order streams across Mississippi (Fig. 1, Table 1). We selected sites randomly from a database of 366 sites sampled as part of an earlier (1999–2003) survey (Warren et al. 2002a, b). We sampled 1 site 4 times, 2 sites 3 times, and 33 sites twice. This sampling strategy resulted in 46 paired samples of the same site through time. Time between samples ranged from 1 to 10 y (mean = 7.33 y, mode = 7 y). Forty of the 46 paired samples were ≥6 y apart.

We sampled fish assemblages and characterized habitats in summer or early autumn (June–October) with the same methods described by Warren et al. (2002a, b). We sampled when water levels were low enough to allow seining and backpack electrofishing of all habitats (see below). We defined the length of stream sampled as 20 (1999 samples only) or 30 (all other

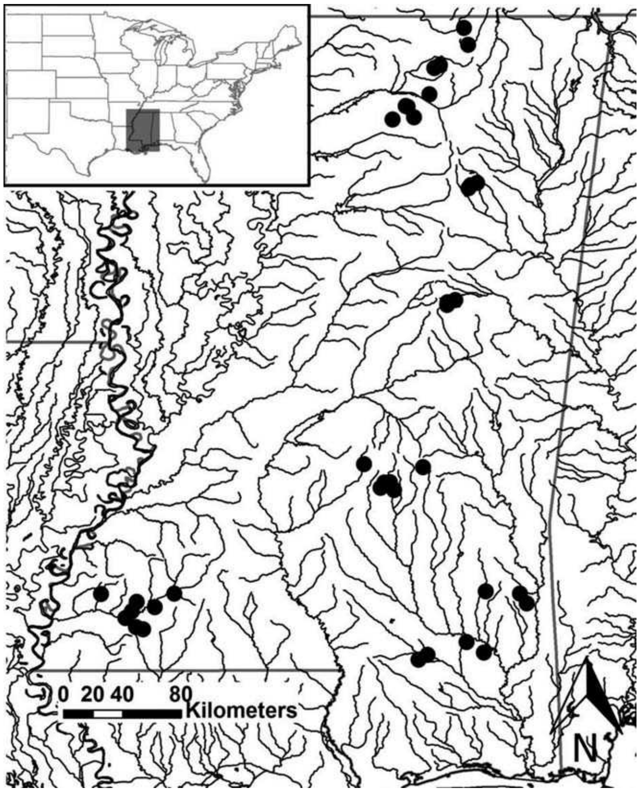

FIG. 1. Sampling locations used to assess fish diversity and stability over time.

samples) times the estimated mean width. Minimum lengths were 80 and 120 m and maximum lengths were 300 and 360 m in 1999 and all other samples, respectively (Walters et al. 2003). This approach ensured that sampling effort was proportional to stream size and that we sampled a variety of habitat types (riffles, runs, and pools). We selected sites in stretches of riffle–run–pool habitat away from bridge crossings, confluences, impoundments, or beaver dams.

We used both backpack electrofishing and seining to sample sites with equal effort. The efficiency of both gears differs by species, but combined they provide an objective method to characterize the assemblage (Patton et al. 1998). We ran preliminary analyses (proportion of species sampled by both, proportion sampled exclusively by one) to quantify sampling efficiency of each gear before pooling data for all subsequent analyses. We set electrofishing effort at 5 s/m of stream length sampled and seining effort to include ≥8 seine hauls spread about evenly along the sampled reach. We defined 1 haul as a sustained drag through a pool or a single kick-set of a riffle. We preserved fishes in 10% formalin, later transferred them to 70% ethanol, and then identified and counted them. We vouchered most of the 2009 collections in the University of Southern Mississippi Ichthyological Collection (database at http://ichthyology.usm.edu/usm/).

We measured habitat variables at each site. We counted the distinct habitat types encountered (number of pools, runs, and riffles) along the entire sampling reach. We placed 12 evenly spaced transects perpendicular to flow along the sampling reach. We recorded depth, current velocity, substrate size (modified Wentworth scale, 6 categories; Cummins 1962), canopy cover (0, 25, 50, 75, 100%), and presence of small and large in-stream wood, detritus, and aquatic vegetation at evenly spaced points along each transect (2-m intervals along transects in streams >10 m wide, 1-m intervals in streams <10 m wide). We also measured wetted width at each transect. We extracted drainage area upstream of each sampled site from the National Hydrology Dataset (NHDPlus; http://www.horizon-systems.com/nhdplus/) for use as a measure of stream size. For analyses, we used mean canopy cover, width, depth, and current velocity at each site and expressed categorical variables as % occurrence (substrate size, detritus, large and small in-stream wood) or, in the case of distinct habitats, as a sum (number of riffles, number of pools, and number of runs). We used the coefficient of variation (CV) for width, depth, current velocity, and canopy cover as measures of habitat heterogeneity at each site.

Data analyses

We used nonmetric multidimensional scaling (NMDS) of Bray–Curtis distances (after transformation of absolute to relative abundance) to summarize fish assemblage composition. We obtained starting NMDS configurations from principal coordinates analysis and assessed convergence on a final configuration with Procrustes analysis (Peres-Neto and Jackson 2001) at each iteration. We assessed the final dimensionality by comparing stress values from 2- to 6- dimensional NMDS to stress values from NMDS of 20 randomized data sets (column totals unchanged) following the methods outlined by McCune and Grace (2002). We used Bray–Curtis distance as a quantitative measure of stability (increased variability in fish species abundances decreases Bray–Curtis similarity; Mykrä et al. 2011). We used Jaccard's index as a qualitative measure of stability. The qualitative index was sensitive only to species turnover and insensitive to variability in fish abundance. We measured diversity as rarefied diversity or Shannon's diversity index. We defined diversity at a site as the mean value from samples over time. We used principal components analysis (PCA; singular-value decomposition of variables scaled to unit variance) to summarize habitat data from all collec-

TABLE 1. List of sites sampled, drainage area, stream width, latitude and longitude, and major river drainage. Drainage designations follow Ross (2001).

Site	Drainage area (km^2)	Width (m)	Latitude/longitude	Drainage
Middleton Creek (tributary)	1.76	1.75	31.39°N/90.88°W	Lower Mississippi
Walker Branch	1.94	3.61	31.25°N/90.95°W	Lower Mississippi
Homochitto River (tributary)	3.33	1.49	31.32°N/91.06°W	Lower Mississippi
Brown Branch	5.49	1.70	31.23°N/90.99°W	Lower Mississippi
Pressley Branch (tributary)	5.40	2.17	34.93°N/88.99°W	Lower Mississippi
Richardson Creek	9.03	3.82	31.42°N/90.99°W	Lower Mississippi
West Prong Muddy Creek	18.52	4.60	34.83°N/88.97°W	Lower Mississippi
Sandy Creek	71.39	8.47	31.47°N/91.21°W	Lower Mississippi
Richardson Creek	18.33	4.55	31.36°N/91.02°W	Lower Mississippi
McGehee Creek	160.61	17.73	31.47°N/90.76°W	Lower Mississippi
Redhead Creek	3.44	2.03	32.15°N/89.48°W	Pascagoula
Shongelo Creek	6.21	2.20	32.12°N/89.50°W	Pascagoula
Spring Branch	3.31	2.78	31.48°N/88.86°W	Pascagoula
Tishkill Creek	25.91	4.85	32.15°N/89.44°W	Pascagoula
Leaf River (tributary)	3.67	2.07	31.17°N/88.98°W	Pascagoula
Quarterliah Creek	13.01	4.46	32.24°N/89.24°W	Pascagoula
Griffin Creek	16.94	2.93	31.41°N/88.61°W	Pascagoula
Little Creek	35.47	5.99	31.47°N/88.65°W	Pascagoula
Weldy Creek	19.57	3.99	31.11°N/88.87°W	Pascagoula
Big Creek	80.96	8.16	31.06°N/89.27°W	Pascagoula
Leaf River	267.04	8.57	32.10°N/89.42°W	Pascagoula
Walls Creek	62.54	4.58	31.10°N/89.27°W	Pascagoula
Robinson Creek	37.98	2.80	32.26°N/89.60°W	Pearl
Sand Branch (tributary)	2.97	1.68	33.97°N/88.95°W	Tombigbee
Noxubee River (tributary)	4.90	3.03	33.23°N/89.10°W	Tombigbee
Sand Branch	8.77	2.79	33.95°N/88.96°W	Tombigbee
Dicks Creek	17.98	4.86	33.98°N/88.91°W	Tombigbee
Bearfoot Branch	5.39	1.70	33.26N/89.05°W	Tombigbee
Noxubee River	38.89	6.22	33.25°N/89.09°W	Tombigbee
Cypress Creek	10.38	3.23	34.38°N/89.29°W	Yazoo
Puskus Creek (tributary)	4.36	2.14	34.45°N/89.34°W	Yazoo
South Fork of Chilli Creek	11.95	5.45	34.68°N/89.17°W	Yazoo
Yellow Leaf Creek	15.29	3.40	34.37°N/89.43°W	Yazoo
Mitchell Creek	4.43	2.66	34.52°N/89.20°W	Yazoo
Chilli Creek	4.25	1.59	34.70°N/89.14°W	Yazoo
Puskus Creek	46.73	6.97	34.44°N/89.34°W	Yazoo

tions. We quantified change in habitat at each site as the Euclidean distance in PCA space between paired samples over time.

We used canonical correspondence analysis (CCA) to examine the relationship between fish assemblage composition (log[x + 1]-transformed abundance) and the habitat data. We eliminated any highly correlated habitat variables and then used a stepwise procedure (with Akaike's Information Criterion [AIC] to evaluate addition or elimination of variables) to find the model with the most explanatory power (McCune and Grace 2002). We used Monte Carlo randomizations (1000) to test the significance of the overall CCA, the first 3 CCA axes, and each of the contributing variables (Legendre et al. 2011).

We tested for correlations between sample rarefied diversity and Shannon's index with drainage area to identify relationships between fish diversity and stream size. We tested for correlations between rarified diversity (mean of all samples at a site) and quantitative and qualitative measures of stability (Bray–Curtis and Jaccard's indices of paired samples through time, respectively) to identify a relationship between diversity and stability. Random fluctuations in abundance of individual species can produce diversity–stability relationships in some systems (Doak et al. 1998, Tilman et al. 1998). Therefore, we compared the observed correlation coefficient to a distribution of correlation coefficients calculated in the same way from 1000 simulated communities for which the abundance of individual species was randomly generated based on observed probability of occurrence, mean abundance, and variation in abundance. Thus, all simulated communities had similar levels of overall diversity, individual species abundance, and variation in abundance.

TABLE 2. Candidate models predicting qualitative and quantitative stability in fish assemblages. Models were selected based on Akaike's Information Criterion. All 2-way interaction terms were included in models, but 3-way interactions were excluded. K = complexity.

Model	K	Hypothesis: Assemblage stability (quantitative or qualitative) is best predicted by:
Null	2	None of the measured variables
Habitat change	3	Change in habitat variables (distance in Principal Components Analysis [PCA] space), sites with greater change should be less stable
Stream size	3	Site drainage area, larger streams are predicted to be more stable
Diversity	3	Species diversity, more diverse sites are predicted to be more stable
Time	3	Years between samples, the amount of assemblage change will be temporally autocorrelated
Habitat change + stream size	5	Change in habitat variables and drainage area or an interaction between these variables
Habitat change + diversity	5	Change in habitat variables and species diversity or an interaction between these variables
Habitat change + time	5	Change in habitat variables and years between samples or an interaction between these variables
Stream size + diversity	5	Drainage area and species diversity or an interaction between these variables
Stream size + time	5	Drainage area and years between samples or an interaction between these variables
Diversity + time	5	Species diversity and years between samples or an interaction between these variables
Stream size + diversity + time	8	Combination or interaction of drainage area, diversity, and years between samples
Habitat change + diversity + time	8	Combination or interaction of change in habitat variables, diversity, and years between samples
Habitat change + stream size + time	8	Combination or interaction of change in habitat variables, drainage area, and years between samples
Habitat change + stream size + diversity	8	Combination or interaction of change in habitat variables, drainage area, and species diversity
Global (all variables)	12	

We used AIC for small sample size ($\mathrm{AIC_c}$) to compare the predictive power of candidate stability models (Anderson et al. 2000). Candidate models included drainage area, rarefied diversity, change in habitat variables, and time (years between samples) as predictor variables and qualitative or quantitative measures of stability as response variables (Table 2). We included 2-way interactions in models with >1 predictor but excluded all higher-order interactions. Models with low $\Delta\mathrm{AIC_c}$ and high Akaike weights (w_i) have the best combination of parsimony (few parameters) and predictive power. We interpreted only models with $\Delta\mathrm{AIC_c} < 2.0$ and $w_i > 10\%$ of the highest w_i score as meaningful (Anderson and Burnham 2002). We ran all analyses in R (version 2.10; R Development Core Team, Vienna, Austria).

Results

We captured a grand total of 17,546 individuals representing 88 species (Appendix). Sample size ranged from 9 to 1396 (mean ± SE, 231 ± 30.9) individuals. Seining was generally less efficient than electrofishing (across all samples, 60.5% of species at a site were collected in seines, 79.4% by electrofishing). Both gears collected species missed by the other (average across all samples of 20.8% species collected by seine alone, 39.6% by electrofishing alone). Both gears sampled similar numbers of individuals (50.2% by seine, 49.8% by electrofishing).

Across all sites, rarefied diversity ranged from 2.97 to 25.0 (12.64 ± 0.61) and Shannon diversity ranged from 0.08 to 2.72 (1.79 ± 0.52). *Luxilus chrysocephalus* and *Cyprinella camura* were the 2 most abundant species (12.25 and 8.77% of all individuals captured, respectively). *Fundulus olivaceus*, *Lepomis megalotis*, *Lepomis macrochirus*, and *Semotilus atromaculatus* were the most commonly sampled species (Appendix) and occurred in 82, 61, 55, and 55% of all samples, respectively. The 30 most abundant species made up 89.5% of individuals sampled. Based on published accounts, those 30 species had an average generation time and lifespan of 1.27 and 2.83 y, respectively. Generation times for these 30 species were all ≤ 3 y. Thus, we are confident that the temporal scale of our study was appropriate for

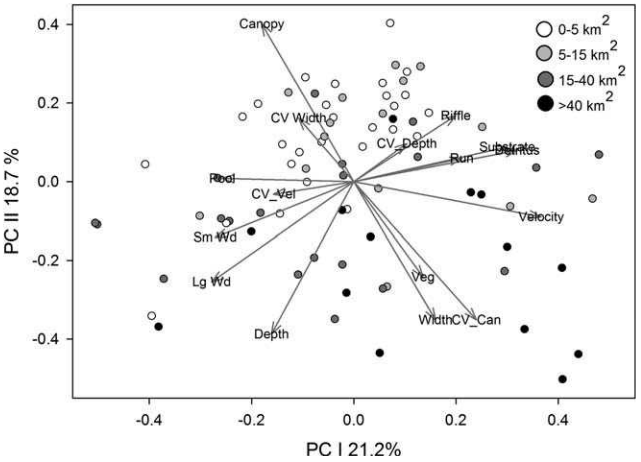

FIG. 2. Principal components (PC) analysis of habitat variables for all sites. Shaded ellipses represent 4 stream size categories based on drainage area. Arrows end at centroids for environmental variables. CV = coefficient of variation, Sm Wd = small wood, Lg Wd = large wood, Veg = vegetation, CV_Can = CV of canopy cover, CV_Vel = CV of current velocity.

the questions asked (Connell and Sousa 1983, Grossman et al. 1990).

Ordination of the habitat data revealed gradients related to stream channel slope and stream size. The first 2 axes of the PCA explained 39.9% of the variation in the habitat data (Fig. 2). The 1st PCA axis described a water-velocity gradient from fast- to slow-flowing streams. Sites with high scores had coarser substrate, greater current velocity, and higher counts of riffles and runs. Sites with lower scores had finer substrate, more in-stream wood (large and small), more detritus, and more pools. The 2nd PCA axis corresponded to stream size. Sites with high scores had greater canopy cover, less aquatic vegetation, and narrower channels. Euclidean distances in PCA space between paired samples in time ranged from 0.79 to 4.72 (2.54 ± 0.14).

The NMDS effectively summarized variability in fish assemblage composition among samples (3-axis best solution, stress = 15.0%; McCune and Grace 2002; Fig. 3). The distance in NMDS space between paired samples in time ranged from 0.139 to 1.643 (0.507 ± 0.047). Jaccard's similarity between paired samples in time ranged from 0.11 to 0.84 (0.42 ± 0.022).

Habitat variables explained a relatively small but significant proportion of the variance in fish assemblage composition along gradients congruent with those for the PCA of habitat variables. The full CCA model (16 variables) explained 35.0% of the variance in fish assemblage composition. Elimination of less informative and redundant variables resulted in a final CCA model with 9 variables (depth, width, velocity, small in-stream wood, canopy, riffles, substrate, $CV_{velocity}$, CV_{depth}) that explained 23.4% of the variation. The final CCA model explained a significant amount of the variation (pseudo-$F_{9,66} = 2.25$, $p < 0.005$), as did the first 3 axes (CCA1 pseudo-$F_{1,68} = 5.49$, $p < 0.005$; CCA2 pseudo-$F_{1,68} = 4.90$, $p < 0.005$; CCA3 pseudo-$F_{1,68} = 2.41$, $p < 0.005$). Five of the 9 model variables (all but canopy, velocity, small in-stream wood, and CV_{depth}) were significant. CCA axes were generally similar to PCA axes. Current velocity, substrate, and number of riffles, indicators of stream channel gradient, were correlated with the CCA1, and width and depth, indicators of stream size, were correlated most closely with CCA2.

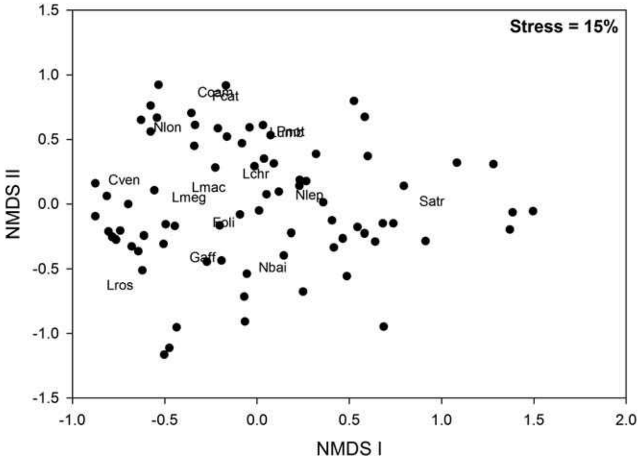

FIG. 3. Nonmetric multidimensional scaling (NMDS) analysis of fish assemblage data. Weighted average scores for the 15 most abundant species are also plotted in NMDS space. See Appendix for species abbreviations.

Both measures of diversity were positively related to drainage area (rarefied diversity: $F_{1,75} = 27.01$, $p < 0.001$, $R^2 = 0.26$; Shannon diversity: $F_{1,75} = 14.9$, $p < 0.002$, $R^2 = 0.16$; Fig. 4A, B). Quantitative and qualitative site stability were positively related to rarefied diversity ($F_{1,43} = 7.32$, $p < 0.009$, $R^2 = 0.15$ and $F_{1,43} = 4.86$, $p < 0.032$, $R^2{=}0.10$, respectively). Observed correlation coefficients (r) were greater than simulated r in 96.0% (quantitative: observed $r = 0.39$, simulated mean = 0.14, simulated range = −0.39–0.62) and 92.6% (qualitative: observed $r = 0.32$, simulated mean = 0.18, simulated range = −0.35–0.55) of simulated communities.

AIC analysis of stability models identified diversity (quantitative $F_{1,43} = 7.32$, $p < 0.009$; qualitative $F_{1,43} = 4.86$, $p < 0.033$) and diversity + time + diversity × time (diversity*time) (quantitative $F_{3,41} = 4.26$, $p < 0.01$; qualitative $F_{1,43} = 2.61$, $p < 0.06$) as the 2 best models predicting both qualitative and quantitative measures of stability. For quantitative stability, diversity*time

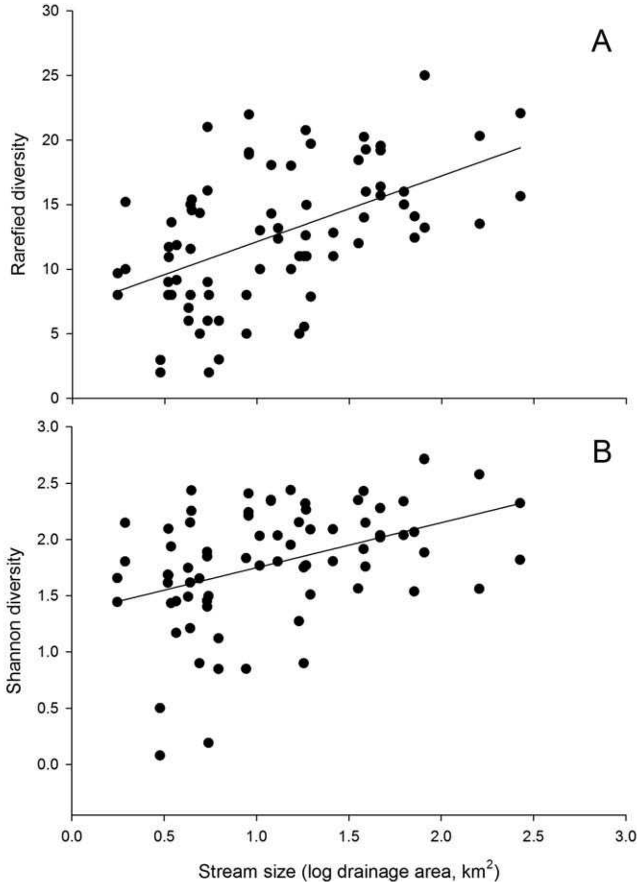

FIG. 4. Relationship between stream size (drainage area) and rarefied diversity (A) and Shannon's index of diversity (B) for all samples.

was the best model, but diversity alone was nearly as good and was the only other interpretable model (Table 3, Fig. 5A, B). For qualitative stability, diversity alone was the best predictor by far, but the null (marginally) and diversity*time models were interpretable. Stream size (cumulative drainage area) and change in habitat variables (Euclidean distance in PCA space) were not part of any interpretable model. Models with >2 parameters suffered from excessive complexity and were of low quality.

Discussion

Our data support a diversity–stability relationship in Mississippi streams similar to those found in other systems (Levine and D'Antonio 1999, Ives and Carpenter 2007, Franssen et al. 2011). Our data are unique in that we assessed stability with field data and considered other known correlates of assemblage composition or diversity as predictors of stability. Stream size and habitat variables were correlated with diversity and assemblage structure, respectively, but neither was a predictor of stability. Stability was best predicted by models incorporating diversity and the time between samples. Time between samples was more important for quantitative stability (i.e., decreased stability with time), a result indicating that patterns of abundance degraded over time (ecological drift). Time between samples was not as important to qualitative stability, perhaps because the temporal scale of the study was too limited to quantify local extinction and colonization processes (Table 3). Results associated with time between samples were consistent with those of other studies documenting temporal autocorrelations (Collins 2000) or general models of ecological drift (Hubble 2006).

Given the correlation between habitat variables and assemblage composition, the absence of a relationship between habitat change and stability was unexpected (Mykrä et al. 2011). Other investigators have found that fish assemblage structure is not coupled to disturbance-induced change in physical habitat. In 2 notable studies, stream fish assemblages were quite resilient and returned to predisturbance levels within 1 y. Fish assemblage composition was largely unchanged from predisturbance composition 11 mo after a major hurricane altered streambed sediment and stream morphology and doubled the amount of instream wood (Dolloff et al. 1994). Catastrophic flooding altered fish assemblage composition beyond expected levels (seasonal variability based on long-term data set) in areas where pools were scoured and significantly altered by the disturbance (Matthews 1986), but assemblages recovered rapidly over the next 8 mo. Matthews (1986) attributed the short-term dramatic changes to differential redistribution and recruitment immediately after the flood. He noted that the site slowest to recover was a low-diversity site and had not returned to preflood assemblage composition 1 y later. Matthews (1986) also noted the importance of the interaction between the timing of disturbance and life-history dynamics of individual species. Thus, stability may be less related to large (from a human perspective) individual disturbances than to predictability of disturbances.

Relationships between disturbance predictability and assemblage variability often are tied to habitat size and complexity. Unpredictable hydrology can induce variability in fish assemblages in small, more homogeneous habitats (Fausch and Bramblett 1991) or can increase local extinction rates (Taylor and Warren 2001). In other studies, the general harshness of disturbance regimes was the best predictor of stability (Ross et al. 1985). Our data captured change in physical habitat based on ≥2 surveys in time, and we were unable to quantify disturbance predictability or any

TABLE 3. Candidate models predicting qualitative and quantitative stability in fish assemblages. For each model, complexity (K), Akaike Information Criterion (AIC) score corrected for small sample size (AIC_c), ΔAICc, and weights (w_i) are given for both qualitative and quantitative measures of stability. Interpretable models ($\Delta AIC_c < 2.0$, $w_i > 10\%$ of largest weight) are bolded.

		Quantitative stability				Qualitative stability			
Model	K	AIC_c	ΔAIC_c	w_i	r^2	AIC_c	ΔAIC_c	w_i	r^2
Null	2	−43	5	0.035	–	−41.9	2.5	0.115	–
Habitat change	3	−41.0	7.2	0.013	0.00	−40.0	4.8	0.044	0.01
Stream size	3	−42.7	5.3	0.031	0.04	−40.6	3.8	0.060	0.03
Diversity	3	**−47.8**	**0.2**	**0.380**	**0.15**	**−44.5**	**0.0**	**0.407**	**0.10**
Time	3	−40.7	7.3	0.011	0.00	−39.6	4.8	0.037	0.00
Habitat change + stream size	5	−38.0	9.9	0.003	0.05	−36.1	8.4	0.006	0.02
Habitat change + diversity	5	−43.4	4.5	0.043	0.15	−40.5	4.0	0.055	0.12
Habitat change + time	5	−36.1	11.8	0.001	0.01	−35.1	9.7	0.003	0.01
Stream size + diversity	5	−43.2	4.7	0.039	0.15	−41.1	3.3	0.078	0.13
Stream size + time	5	−39.1	8.9	0.005	0.07	−35.7	8.7	0.005	0.02
Diversity + time	5	**−48.0**	**0.0**	**0.421**	**0.24**	**−42.6**	**1.9**	**0.159**	**0.16**
Stream size + diversity + time	8	−40.5	7.4	0.010	0.25	−38.6	5.8	0.023	0.24
Habitat change + diversity + time	8	−39.9	8.1	0.007	0.24	−34.4	10.1	0.003	0.16
Habitat change + stream size + time	8	−31.2	16.7	0.001	0.08	−27.7	16.7	0.001	0.03
Habitat change + stream size + diversity	8	−36.0	11.9	0.001	0.18	−35.7	8.7	0.005	0.19
Global (all variables)	12	−27.2	20.7	0.001	0.26	−26.5	17.9	0.001	0.26

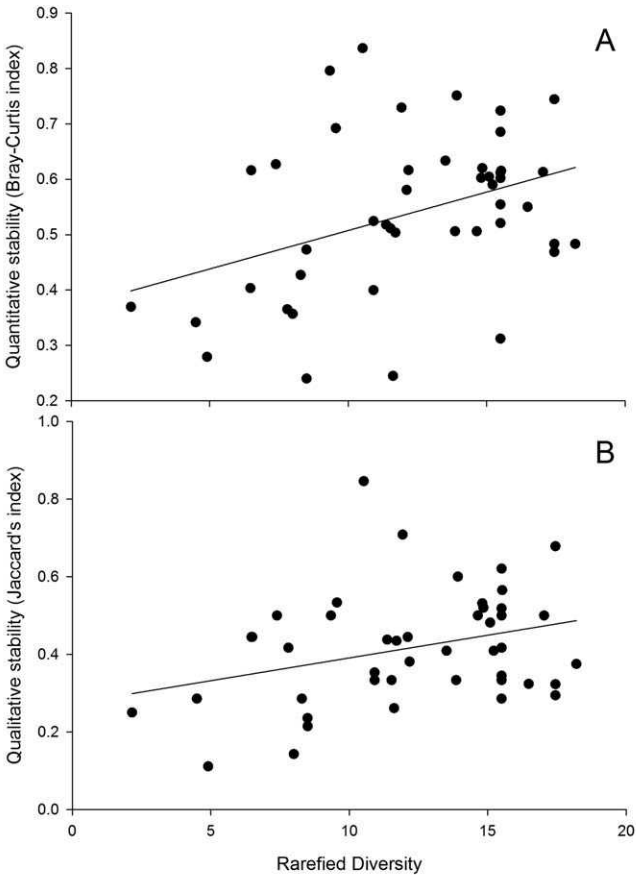

FIG. 5. Relationship between site diversity (rarefied) and quantitative (A) and qualitative (B) measures of stability.

finer-scale properties of disturbance. At least 1 large disturbance occurred that probably altered habitat structure at many sites. Four years before the 2009 surveys, a large category-5 hurricane (Katrina, August 2005) made landfall near the mouth of the Pearl River and traveled northeast over the headwaters of the Pascagoula River. Sustained winds >150 km/h led to high allochthonous input, low dissolved O_2, and fish kills immediately after the storm. However, headwater-stream fish assemblages sampled 1 mo later were no different than usual, and downstream areas (where fish kills were reported) recovered rapidly over the next year (Schaefer et al. 2006).

The prevailing mechanism thought to support diversity–stability relationships is the insurance hypothesis. This hypothesis posits that species respond differently to environmental perturbation, and greater levels of diversity will, on average, dampen effects of perturbations to increase stability (Ives and Carpenter 2007). Experimental evidence for this mechanism is mixed (reviewed in Leary and Petchey 2009), but a key component is that species' differential responses lead to negative covariance (in biomass or abundance) among species. Our data do not allow a direct test of the insurance hypothesis. However, field tests of the diversity–stability relationship are generally rare (Doak et al. 1998, Ives and Carpenter 2007, Franssen et al. 2011) and patterns should be consistent with proposed mechanisms. In our data set, species diversity was positively correlated with species mean abundance ($r = 0.51$, $F_{1,74} = 27.39$, $p < 0.001$) and Shannon's equitability

($r = 0.26$, $F_{1,74} = 5.17$, $p < 0.025$). In long-term data sets for stream fish assemblages, mean abundance through time is negatively correlated with CV for abundance (Schaefer et al. 2005). By extension, one would predict lower CV for abundance in the more diverse sites in our study, resulting in increased stability. Doak et al. (1998) argued that this statistical property alone, in the absence of any ecological interactions, is sufficient to produce a diversity–stability relationship. Thus, low CV of abundance probably contributed to stability in our assemblages. However, our analyses of randomly generated assemblage data (based on observed abundance–CV of abundance patterns) did not produce diversity–stability relationships as strong as those observed indicating ecological interactions also contribute to the pattern.

Stability concepts include the cumulative vs individual species measures described above and they have a stable-state component. Our working assumption was that streams had a single stable state. A perturbation would displace the system from the stable state, and greater stability would be expected to lead to greater resistance to change or more rapid return to the stable state. We cannot discount the possibility of multiple stable states, a phenomena documented in some systems (Scheffer et al. 1997). In our analysis, a shift between 2 stable states would have been interpreted as change in assemblage composition indicative of low stability. If large changes in assemblage composition were commonly the result of shifts between stable states, our data would be consistent with the notion that less diverse systems are more likely to have multiple steady states, a pattern that is generally consistent with current theory. More diverse systems are thought to have fewer steady states or greater difficulty in switching among states (Holling 1973, Ives and Carpenter 2007).

Our data support the hypothesis that increased diversity stabilizes stream fish assemblages and that other correlates of diversity or assemblage structure are poor predictors of stability. Thus, maintaining diversity is the best practice for preserving ecosystem services. Studies demonstrating empirical support for the mechanisms responsible for observed diversity—stability relationships are needed (Leary and Petchey 2009). These studies should include scrutiny of the relative importance of statistical averaging or biotic interactions and further our understanding of assemblage dynamics (Doak et al. 1998).

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APPENDIX. List of species sampled, number of occurrences, total abundance, mean abundance across all sites, mean % abundance across all sites, rank occurrence, and rank abundance. Abbreviations (given in parentheses after species name) for the 15 most abundant (by abundance) species match those in Fig. 3.

Species	Total occurrences	Total abundance	Mean abundance	% abundance	Rank occurrence	Rank abundance
Ambloplites ariommus	8	16	0.21	0.09	43	62
Ameiurus melas	2	17	0.22	0.10	68	61
Ameiurus natalis	23	112	1.47	0.64	12	31
Ammocrypta beani	5	8	0.11	0.05	59	67
Ammocrypta meridiana	1	1	0.01	0.01	77	84
Ammocrypta vivax	2	5	0.07	0.03	68	69
Aphredoderus sayanus	19	54	0.71	0.31	21	42
Cyprinella camura (Ccam)	23	1538	20.24	8.77	12	2
Cyprinella lutrensis	1	3	0.04	0.02	77	77
Cyprinella venusta (Cven)	28	775	10.20	4.42	7	9
Dorosoma cepedianum	1	4	0.05	0.02	77	72
Elassoma zonatum	5	12	0.16	0.07	59	64
Erimyzon oblongus	23	120	1.58	0.68	12	28
Erimyzon succetta	1	2	0.03	0.01	77	81
Esox americanus	7	14	0.18	0.08	48	63
Etheostoma artesiae	26	284	3.74	1.62	8	16
Etheostoma caeruleum	6	53	0.70	0.30	55	44
Etheostoma chlorosomum	8	102	1.34	0.58	43	34
Etheostoma gracile	2	6	0.08	0.03	68	68
Etheostoma histrio	2	3	0.04	0.02	68	77
Etheostoma lachneri	4	11	0.14	0.06	63	66
Etheostoma lynceum	17	145	1.91	0.83	25	26
Etheostoma nigrum	12	113	1.49	0.64	34	30
Etheostoma parvipinne	22	173	2.28	0.99	15	22
Etheostoma proeliare	5	18	0.24	0.10	59	60
Etheostoma raneyi	10	53	0.70	0.30	36	44
Etheostoma rupestre	1	1	0.01	0.01	77	84
Etheostoma stigmaeum	18	96	1.26	0.55	22	37
Etheostoma swaini	16	71	0.93	0.40	26	39
Fundulus catenatus (Fcat)	10	338	4.45	1.93	36	15
Fundulus notatus	7	23	0.30	0.13	48	56
Fundulus olivaceus (Foli)	62	664	8.74	3.78	1	10
Gambusia affinis (Gaff)	26	783	10.30	4.46	8	8
Hybognathus hayi	1	1	0.01	0.01	77	84
Hybognathus nuchalis	7	100	1.32	0.57	48	35
Hybopsis winchelli	14	177	2.33	1.01	30	21
Hypentelium nigricans	15	53	0.70	0.30	28	44
Ichthyomyzon gagei	7	12	0.16	0.07	48	64
Ictalurus punctatus	3	4	0.05	0.02	67	72
Labidesthes sicculus	9	264	3.47	1.50	39	17
Ichthyomyzon sp.	18	69	0.91	0.39	22	41
Lepisosteus oculatus	2	4	0.05	0.02	68	72
Lepomis cyanellus	37	158	2.08	0.90	6	23
Lepomis gulosus	14	71	0.93	0.40	30	39
Lepomis humilis	1	4	0.05	0.02	77	72
Lepomis macrochirus (Lmac)	42	555	7.30	3.16	3	12
Lepomis marginatus	6	20	0.26	0.11	55	59
Lepomis megalotis (Lmeg)	46	1079	14.20	6.15	2	3
Lepomis microlophus	4	5	0.07	0.03	63	69
Lepomis miniatus	10	39	0.51	0.22	36	48
Luxilus chrysocephalus (Lchr)	38	2149	28.28	12.25	5	1
Lythrurus bellus	6	155	2.04	0.88	55	24
Lythrurus fumeus	1	3	0.04	0.02	77	77
Lythrurus roseipinnis (Lros)	18	953	12.54	5.43	22	6
Lythrurus umbratilis (Lumb)	16	342	4.50	1.95	26	14
Macrhybopsis storeriana	1	2	0.03	0.01	77	81
Micropterus punctulatus	25	107	1.41	0.61	10	33

Appendix. Continued.

Species	Total occurrences	Total abundance	Mean abundance	% abundance	Rank occurrence	Rank abundance
Micropterus salmoides	20	33	0.43	0.19	19	49
Minytrema melanops	1	1	0.01	0.01	77	84
Moxostoma erythrurum	1	3	0.04	0.02	77	77
Moxostoma poecilurum	14	49	0.64	0.28	30	47
Nocomis leptocephalus (Nlep)	25	487	6.41	2.78	10	13
Notemigonus crysoleucas	8	125	1.64	0.71	43	27
Notropis ammophilus	11	234	3.08	1.33	35	18
Notropis amplamala	7	21	0.28	0.12	48	58
Notropis atherinoides	4	182	2.39	1.04	63	20
Notropis baileyi (Nbai)	13	977	12.86	5.57	33	5
Notropis longirostris (Nlon)	20	1004	13.21	5.72	19	4
Notropis rafinesquei	5	83	1.09	0.47	59	38
Notropis texanus	8	99	1.30	0.56	43	36
Notropis volucellus	4	29	0.38	0.17	63	53
Noturus funebris	7	33	0.43	0.19	48	49
Noturus gyrinus	8	25	0.33	0.14	43	54
Noturus hildebrandi	1	1	0.01	0.01	77	84
Noturus leptacanthus	6	25	0.33	0.14	55	54
Noturus miurus	9	30	0.39	0.17	39	51
Noturus nocturnus	9	22	0.29	0.13	39	57
Noturus phaeus	22	151	1.99	0.86	15	25
Opsopoeodus emiliae	9	195	2.57	1.11	39	19
Percina nigrofasciata	15	112	1.47	0.64	28	31
Percina sciera	21	114	1.50	0.65	18	29
Percina vigil	2	30	0.39	0.17	68	51
Pimephales notatus (Pnot)	22	564	7.42	3.21	15	11
Pimephales vigilax	7	54	0.71	0.31	48	42
Pomoxis annularis	2	5	0.07	0.03	68	69
Pomoxis nigromaculatus	2	4	0.05	0.02	68	72
Pylodictis olivaris	2	2	0.03	0.01	68	81
Semotilus atromaculatus (Satr)	42	908	11.95	5.17	3	7