

## Modeling Stream Fish Assemblages with Niche Apportionment Models: Patterns, Processes, and Scale Dependence

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**Abstract.**—Understanding patterns in terms of the mechanistic processes that produce them is the essence of ecology. However, many studies merely document nonrandom patterns of species coexistence without providing insight into the structuring mechanisms and their scale dependence. Moreover, few studies address the mechanisms driving functional diversity. The objectives of this study were to document empirical patterns of species coexistence within stream fish assemblages across a broad geographic region, addressing both the functional and taxonomic organization of those assemblages, and to determine whether the structuring mechanisms are scale dependent. We gathered data from a report published by the Texas Parks and Wildlife Department that provided empirical species abundance distributions for 62 assemblages from 7 ecoregions and 18 river basins. For each assemblage, we simulated expected species abundances using five previously published models of niche apportionment. These models generate relative abundances in proportion to niche breadth and are constrained to maintain observed species richness, but they do not include information on species identity. These models included four stochastic variants of a geometric series (dominance preemption, random fraction, broken stick, and dominance decay) in which species abundances relate directly to niche breadth and one model (random assortment) in which abundances are independent of niche partitioning altogether. To assess scale dependence, we repeated the analyses after pooling assemblages by ecoregion, river basin, and the entire state. The patterns of niche apportionment for assemblages pooled according to river basin are more consistent with local assemblages than with assemblages pooled according to ecoregions or the entire state. These results suggest that niche apportionment plays a crucial role in structuring stream fish assemblages and that functional groups divide niche space more evenly than do species.

Two of the major goals in ecology are to determine the factors responsible for species coexistence and to use that information to formulate predictive models of community assembly (May 1975; Drake 1991; Strange and Foin 1999). Species coexistence in stream fishes is often a result of niche partitioning in which species differ along axes of food, habitat, or activity times (Ross 1986; Nishikawa and Nakano 1998; Herder and Freyhof 2006). In this case, species coexistence depends on either the amount of niche space that each species sequesters (i.e., niche breadth) or the total amount of available niche space. For small-scale studies (e.g., stream reach), estimating niche breadth is feasible by quantifying diet selection, habitat selection, and patterns of activity. This is not the case for large-scale studies, however, for which it is more practical to use species abundance distributions as indicators of niche breadth.

Species abundance distributions are a fundamental characteristic of communities. Not only do they

provide the basis for most measures of biodiversity, they also provide insight into how species subdivide niche space to coexist (Whitaker 1965; May 1975; Sugihara 1980; Tokeshi 1990; Magurran 2004). A suite of mechanistic models has been developed to specifically address niche partitioning (Tokeshi 1990). Each of these models conceptualizes niche space as being sequentially divided among the species as they enter the community; however, the amount of niche space that each new species sequesters differs with each model. These models are stochastic variants of a geometric series  $n_i = NC_k K(1 - k)^{i-1}$ , where  $n_i$  is the number of individuals in the  $i$ th species,  $N$  is the total number of individuals in the community,  $k$  is the proportion of the available niche space sequestered by each new species, and  $C_k = [1 - (1 - k)^S]^{-1}$  is a constant that ensures that the total number of individuals equal  $N$  (Magurran 2004). (Although these models are based on the concept of sequential introduction of species, in practice the abundances of all species are estimated simultaneously.) Although these models were originally developed to assess the taxonomic organization of assemblages, they can also be used to assess functional organization.

The functional organization of assemblages is becoming an increasingly important topic in stream fish ecology. First, functional characteristics allow

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comparisons to be made among broad geographic regions where assemblages comprise different taxa (Simberloff and Dayan 1991). For example, Lamouroux et al. (2002) observed intercontinental convergence in functional traits related to hydraulics and geomorphology despite phylogenetic and historical differences in fish assemblages. Second, functional characteristics provide a means of testing theoretical expectations of changes in species traits along environmental gradients, such as those generated from habitat templates (Southwood 1977), the river continuum concept (Vannote et al. 1980), and landscape filters (Poff 1997). For example, habitat templates predict changes in reproductive traits with habitat stability, such as increasing parental care with decreased variability (Townsend and Hildrew 1994). Other studies examined functional organization in various contexts, including longitudinal zonation (Schlosser 1982), hydrological stability (Poff and Allan 1995), landscape variability (Angermeier and Winston 1999), intercontinental convergence (Lamouroux et al. 2002), river size (Goldstein and Meador 2004), and scale-dependency of structuring factors (Hoeinghaus et al. 2007).

The overall goal of this study was to understand how functional groups and taxonomically defined species partition niche space. More specifically, the objectives were to document empirical patterns of functional and taxonomic coexistence within stream fish assemblages across a broad geographic region and to determine the extent to which the structuring mechanisms are scale dependent.

### Methods

**Data.**—We obtained data from fisheries surveys conducted by the Texas Parks and Wildlife Department (Linam et al. 2002). The surveys focused on the least disturbed streams of 11 different ecoregions of Texas—all but one of the ecoregions described by Omernik (1987)—and included 62 localities from 18 drainages. Biologists from the Texas Parks and Wildlife Department sampled fish assemblages, using seines (100% of sites), backpack electrofishing (81% of sites), and boat electrofishing (8% of sites), the gear choice depending on environmental characteristics such as flow regimes, water chemistry, and habitat availability. All sites were sampled with seines, and some sites were also sampled using electrofishing techniques. When a combination of electrofishing and seining was used, the mean duration of shocking was 13 min and the mean number of seine (4.6 m × 1.8 m; 4.8-mm mesh) hauls was 7.4; the mean stream reach (length) sampled was 61 m. At sites where only seines were used to collect fish, the mean number of seine

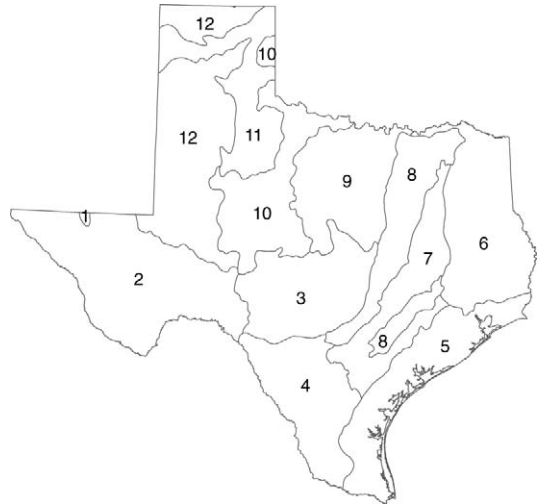


FIGURE 1.—Ecoregions of Texas: (1) Arizona–New Mexico Mountains, (2) Chihuahuan Deserts, (3) Edwards Plateau, (4) Southern Texas Plains, (5) Western Gulf Coast Plains, (6) South Central Plains, (7) East Central Texas Plains, (8) Texas Blackland Prairies, (9) Central Oklahoma–Texas Plains, (10) Central Great Plains, (11) Southwestern Tablelands, and (12) Western High Plains.

hauls was 8.0 and the mean stream reach was 74 m. Although the desired number of seine hauls was 6 and total shocking time was 15 min, each locality was sampled until species accumulation peaked, and all habitats within a locality were sampled in relative proportion to their abundance. The streams were sampled during the summer months (June through September) from 1988 through 1990. Easily identified fish were enumerated and released in the field; the remaining fish were preserved in 10% formalin and transported to the laboratory for positive identification. The data recorded included a description of the sampling site, latitude and longitude, size of drainage basin ( $\text{km}^2$ ), stream discharge ( $\text{m}^3/\text{s}$ ), and abundance of fish species at each site.

**Ecoregions of Texas.**—The state of Texas contains 12 ecoregions (Omernik 1987); however, biologists from the Texas Parks and Wildlife Department incorporated only 11 of them into their study because the Arizona–New Mexico Mountains barely extend into Texas and few perennial streams occur within that ecoregion. The 11 ecoregions studied are the Chihuahuan Desert, Western High Plains, Southwestern Tablelands, Central Great Plains, Central Oklahoma–Texas Plains, Edwards Plateau, Southern Texas Plains, Texas Blackland Prairies, East Central Texas Plains, Western Gulf Coastal Plain, and South Central Plains (Figure 1). However, Linam and Kleinsasser (1998)

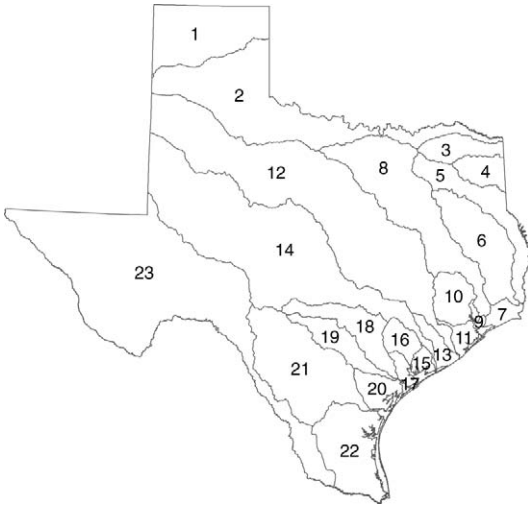


FIGURE 2.—River basins of Texas: (1) Canadian, (2) Red, (3) Sulfur, (4) Cypress, (5) Sabine, (6) Neches, (7) Neches–Trinity, (8) Trinity, (9) Trinity–San Jacinto, (10) San Jacinto, (11) San Jacinto–Brazos, (12) Brazos, (13) Brazos–Colorado, (14) Colorado, (15) Colorado–Lavaca, (16) Lavaca, (17) Lavaca–Guadalupe, (18) Guadalupe, (19) San Antonio, (20) San Antonio–Nueces, (21) Nueces, (22) Nueces–Rio Grande, and (23) Rio Grande.

aggregated some of the ecoregions based on detrended correspondence analysis so that their analysis could more adequately capture the similarities in fish assemblages. They grouped the East Central Texas Plains and the South Central Plains into one ecoregion (Mixed Land Use Region); consolidated the Central Great Plains, Texas Blackland Prairies, and Central Oklahoma–Texas Plains into a single ecoregion (Subhumid Agriculture Plains); and grouped the Western High Plains and Southwestern Tablelands into one ecoregion (Western High Plains). For our analyses, we also pooled species according to their consolidated ecoregions to capture similarity in fish assemblages. More specifically, we simply summed the individuals within a species across all localities within a specific ecoregion.

*River basins of Texas.*—Twenty-three river basins exist within the state of Texas (Figure 2); however, because Linam et al. (2002) focused on streams with entire watersheds located within an ecoregion, fish assemblages from only 18 river basins were sampled for our study: the Brazos River basin (15 sites), Colorado River basin (9 sites), Rio Grande River basin (7 sites), Trinity River basin (5 sites), Red River basin (4 sites), Cypress Creek River basin (3 sites), Sabine River basin (3 sites), Guadalupe River basin (2 sites), Lavaca–Guadalupe River basin (2 sites), Neches River

basin (2 sites), Nueces River basin (2 sites), San Jacinto River basin (2 sites), Brazos–Colorado River basin (1 site), Canadian River basin (1 sites), Colorado–Lavaca River basin (1 site), Lavaca River basin (1 site), San Antonio River basin (1 site), and Sulfur River basin (1 site). Three of these river basins (Brazos–Colorado, Colorado–Lavaca, and Lavaca–Guadalupe) are small basins with rivers that empty directly into the Gulf of Mexico; they are located between major river basins and named accordingly. When pooling species according to river basin, we simply summed the individuals within a species across all localities within a specific river basin.

*Formation of functional groups.*—To classify fish species into functional groups, we used a classification scheme proposed by Matthews (1998) that emphasizes the role of an organism in ecosystem processes. This classification scheme expanded traditional trophic groups (e.g., herbivore, piscivore, and invertivore) to include the manner in which fish affect aquatic ecosystems. Although the designated functional groups have not yet been tested for differences in their effects on ecosystem-level processes (e.g., nutrient cycling), this classification provides an initial framework for examining patterns of functional diversity in stream fishes by examining what the fish eat, where they find food, and how they consume resources (Matthews 1998). This classification scheme imposes an important distinction between fishes that physically disturb substrates and fishes that do not disturb substrates, which should differentially affect ecosystem processes such as nutrient cycling. In addition to this dichotomy, Matthews incorporated information on the manner in which fish feed. For example, he distinguished suction piscivores from biting piscivores because suction piscivores generally swallow prey whole, whereas biting piscivores tend to leave fragments in the environment that other organisms can consume. Hence, this classification scheme is specifically designed to address issues regarding ecosystem function, including aspects of decomposition, primary production, nutrient cycling, and energy flow.

The specific functional groups used in this study were (1) grazers, (2) browsers, (3) benthic detritivores, (4) mud or sand sifters, (5) disturbance pickers, (6) scavengers, (7) egg eaters, (8) filter feeders, (9) surface feeders, (10) water column particulate feeders, (11) benthic pickers, (12) snail crushers, (13) suction piscivores, and (14) biting piscivores. For specific descriptions of these function groups, refer to the original depictions provided in Matthews (1998). Fish species were assigned to one or more functional groups on the basis of literature accounts that documented feeding habits, reproductive strategies, or habitat

requirements (Scott and Crossman 1973; Sublette et al. 1990; Tomelleri 1990; Page and Burr 1991; Ross 2001; Miller and Robison 2004). Many species were classified into multiple functional groups to reflect opportunistic feeding strategies and ontogenetic shifts in diet. For these fishes, we partitioned the total number of individuals sampled into the multiple functional groups equally so as not to artificially inflate the ecological importance of generalist species. Species comprising only one functional group had all individuals placed into that group.

*Species abundance distributions.*—The species abundance distributions used in this study were based on variations of the geometric series in which niche apportionment is the primary focus of the model (Tokeshi 1990, 1999). Each model assumes that the fraction of niche space sequestered by a species is proportional to its relative abundance and that the relative proportions of the species are in equilibrium. The models differ in how the available niche space is subdivided, resulting in differing degrees of evenness (Figure 3). The random-assortment model results in abundances that vary independently from 1. Because in this model abundances are unrelated to niche breadth, it explicitly serves as the null model with which to compare the remaining models. The dominance decay model is a stochastic model in which each new species sequesters less than one-half of remaining available niche space, but the specific amount is uniformly random between 0 and 0.5. Dominance decay describes a situation in which a new species occupies a portion of the niche space of the most abundant species, thereby decreasing the amount of dominance within an assemblage. The broken-stick model is a stochastic model in which niche space is divided in a probabilistic manner, although it is often viewed as representing an assemblage of species of equal competitive ability that are vying for niche space (Tokeshi 1993; Magurran 2004). The random-fraction model is similar to the broken-stick model except that each additional species uniformly chooses which available niche to sequester, based on all available niches not just those suited to the species, thereby creating an abundance distribution with several numerically dominant species. The dominance preemption model is the converse of the dominance decay model: each additional species sequesters more than half of the available niche, but the specific amount is uniformly random between 0.5 and 1. That is, dominance preemption describes a situation in which each additional species sequesters less niche space than its predecessors and consequently has a lower abundance.

*Simulations.*—For each empirical abundance distribution, whether taxonomic or functional, we simulated

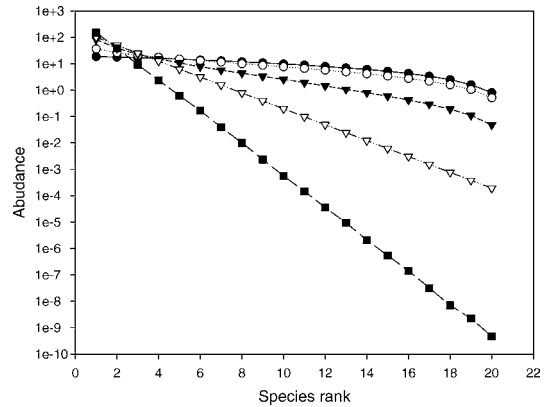


FIGURE 3.—Diagrammatic representation of the differences in form among five niche-partitioning models: dominance decay (closed circles), broken stick (open circles), random fraction (closed triangles), random assortment (open triangles), and dominance preemption (solid squares).

five theoretical distributions according to the different niche-partitioning models. We assessed lack of fit by using sum-of-squared differences between empirical (observed) and theoretical (expected) abundances. We used the sum-of-squared differences as the basis for calculating the Akaike information criterion (AIC) for each model; AIC not only rewards goodness of fit but also includes a penalty for the number of estimated parameters, which discourages overfitting (Hilborn and Mangel 1997). The dominance decay, broken-stick, random-assortment, and dominance preemption models each had three parameters, and the random-fraction model had four parameters. Because the niche-partitioning models were stochastic, we repeated this process 1,000 times and used the mean AIC value for each model to determine which one best fit the data. More specifically, we subtracted the lowest AIC value from the remaining four values for each analysis to provide a relative difference in lack of fit among models. Thus, the model with the AIC value of 0 was deemed to be the best-fitting model. All simulations were conducted with MATLAB version 6.0 software (MathWorks 1997).

## Results

The niche-partitioning models differed in their fits with empirical data, whether local assemblages were analyzed separately or pooled by river basin, ecoregion, or the entire state (Figure 4). Moreover, the best-fitting models were different for functional and taxonomic organization of assemblages (Table 1). When we combined all of the assemblages from across the state, the broken-stick model produced abundances

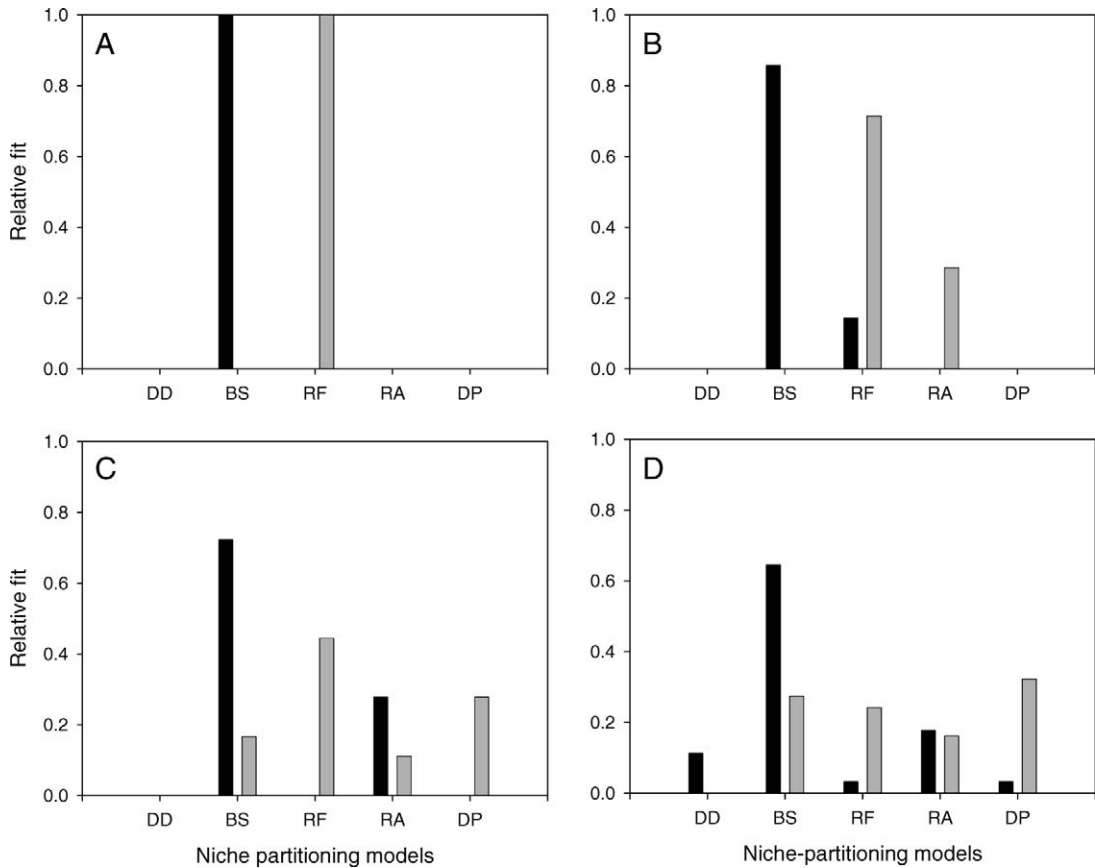


FIGURE 4.—Relative fits of five niche-partitioning models to empirical data across (A) the entire state of Texas, (B) ecoregions, (C) river basins, and (D) individual sites. Model abbreviations are as follows: DD = dominance decay, BS = broken stick, RF = random fraction, RA = random assignment, and DP = dominance preemption. The black bars correspond to functional groups, the gray bars to species.

that closely matched the empirical functional-abundance distribution. This suggests that niche breadth is approximately equal among functional groups and that larger niches are generally subdivided to facilitate coexistence. Surface feeders were, on average, the most abundant functional group, having a mean relative abundance of 23%, followed by water column particulate feeders (20%), egg eaters (14%), benthic pickers (12%), and browsers (10%). The random-fraction model best fit the species abundance distribution, suggesting that fish sequester a random proportion of niche space. This is not to imply that certain common species (e.g., western mosquitofish *Gambusia affinis* 22%, red shiner *Cyprinella lutrensis* 14%, and blacktail shiner *C. venusta* 13%) are not consistently abundant across the region, but rather that fish as a whole, irrespective of species identities, do not consistently have specific niche breadths.

The broken-stick model best fit functional-abun-

dance distributions from all ecoregions except the Western High Plains, for which the random-fraction model was the best. The random-fraction model results in a more uneven distribution than the broken-stick model which accounted for the high relative abundance of surface feeders (42%, primarily plains killifish *Fundulus zebrinus*). Surface feeders were also the most abundant functional group in the Western Gulf Coast Plains, Mixed Land Use Region, and Southern Deserts, although their relative abundances were much less (29, 27, and 29%, respectively). Browsers were the most abundant functional group in the Southern Texas Plains (26%), and water column particulate feeders were the most abundant group in the Central Texas Plains and Subhumid Agriculture Plains (22% and 26%, respectively). The lower relative abundance of the most numerically dominant functional group in these ecoregions allowed the broken-stick model to be the best fit.

The random-fraction model best fit the species abundance distributions in five of the seven ecoregions. The numerically dominant fishes in the Mixed Land Use Region were western mosquitofish (28%), blacktail shiner (12%), and ribbon shiner *Lythrurus fumeus* (11%). The Southern Texas Plains were dominated by western mosquitofish (32%), roundnose minnow *Dionda episcopa* (16%), and red shiner (15%). The dominant fishes in the Central Texas Plains were blacktail shiner (25%), central stoneroller *Camptostoma anomalum* (20%), mimic shiner *Notropis volucellus* (13%), and Texas shiner *N. amabilis* (12%). Red shiner (35%), western mosquitofish (24%), and blacktail shiner (16%) were the most abundant fishes in the Subhumid Agriculture Plains. The Southern Deserts were dominated by roundnose minnow (27%), western mosquitofish (22%), and Texas shiner (17%). Hence, a vast majority of the fish in these ecoregions were cyprinids and poeciliids. The remaining two ecoregions (Western Gulf Coast Plains and Western High Plains) had empirical species abundance distributions that closely matched those produced by the random-assortment model, primarily a result of the greater abundance of the most numerically dominant species. Western mosquitofish (56%) and red shiner (34%) were numerically the most abundant fishes in Western Gulf Coast Plains, and plains killifish (57%) and red shiner (22%) dominated the Western High Plains.

The broken-stick model best fit functional-abundance distributions in 13 of the 18 river basins examined. Water column particulate feeders were the most abundant functional group in 7 of the 13 river basins, including the Colorado–Lavaca (37%), Guadalupe (32%), San Jacinto (29%), Canadian (25%), Brazos (23%), Colorado (23%), and Trinity (22%) river basins. Surface feeders were the most abundant group in 4 of the 13 river basins, including the Neches (30%), Guadalupe (28%), Cypress Creek (26%), and Sabine (24%) river basins. Browsers were most abundant in the River Grande River basin (30%), whereas benthic pickers were most abundant in the Nueces River basin (24%). The only other functional groups with relative abundances greater than 10% were egg eaters and benthic detritivores. The remaining five river basins (Brazos–Colorado, Lavaca–Guadalupe, Red, Rio Grande, and Sulfur River basins), were most strongly associated with the random-assortment model. This suggests that functional abundances are independent of niche breadth in these particular systems.

The broken-stick, random-fraction, random-assortment, and dominance preemption models all accounted for species abundance distributions in more than one basin when pooled according to river basin. The broken-stick model best fit the species abundances in

the Canadian, Sabine, and Trinity river basins. An assemblage from the Canadian River consisted primarily of red shiner (34%), western mosquitofish (28%), sand shiner *N. stramineus* (19%), and plains killifish (11%). Assemblages from the Sabine River basin consisted primarily of weed shiner *N. texanus* (19%), western mosquitofish (18%), and pirate perch *Aphredoderus sayanus* (12%). Red shiner (14%), blacktail shiner (14%), and ribbon shiner (10%) were the most abundant fishes in assemblages from the Trinity River basin. The random-fraction model fit 7 of the 18 river basins, including the Colorado, Cypress Creek, Guadalupe, Neches, Rio Grande, San Antonio, and San Jacinto river basins. For each basin, species abundances are proportional to niche breadth, but the amount of niche space each species sequesters is random. Several of the common species in these river basins include western mosquitofish, Texas shiner, blacktail shiner, and red shiner. The random-assortment model best described species abundances in the Lavaca and Red river basins; hence, species abundances are independent of niche breadth in these basins. Western mosquitofish (55%) and red shiner (33%) were the most abundant species in the Lavaca River basin, and plains killifish (60%), red shiner (21%), and Red River pupfish *Cyprinodon rubrofluviatilis* (11%) were abundant in the Red River basin. The dominance preemption model was the best-fitting model for five river basins, three of which are contained entirely within the Western Gulf Coast Plains: the Brazos–Colorado, Colorado–Lavaca, and Lavaca–Guadalupe river basins. These river basins are heavily dominated by either western mosquitofish (78, 23, and 89%, respectively) or red shiner (73% of fishes in the Colorado–Lavaca River basin). In fact, the overwhelming abundance of these two species is the reason the dominance preemption model is the best-fitting model in the Nueces River basin (75% of fishes are western mosquitofish) and Sulfur River basin (78% of fishes are red shiner) as well.

When examining individual sampling localities (i.e., without pooling data), all five niche-partitioning models best fit the functional-abundance distributions. However, the broken-stick model accounted for a substantial majority (65%) of the functional organization of assemblages. Typically, the most abundant functional group in these localities consisted of water column particulate feeders (mean relative abundance, 23%). Surface feeders averaged 20% of overall abundance, benthic pickers averaged 15%, and egg eaters averaged 11%. The random-assortment model best fit functional abundances in 11 of the 62 localities. Surface feeders were the most abundant, with a mean relative abundance of 39%, but egg eaters (28%) and

TABLE 1.—Relative differences between the niche-partitioning models with respect to the functional and taxonomic organization of stream fish assemblages. Abbreviations for models are as follows: DD, dominance decay; BS, broken stick; RF, random fraction; RA, random assortment; and DP, dominance preemption. Numbers in bold italics indicate the best-fitting models.

Area	Taxonomic organization					Functional organization				
	DD	BS	RF	RA	DP	DD	BS	RF	RA	DP
Texas	170.8	140.9	<b>0.0</b>	160.5	243.5	11.8	<b>0.0</b>	23.1	34.0	47.0
Ecoregions										
Western Gulf Coast Plains	43.4	36.0	13.3	<b>0.0</b>	0.5	8.4	<b>0.0</b>	5.8	9.0	23.6
Mixed Land Use	84.9	56.8	<b>0.0</b>	107.7	151.0	10.6	<b>0.0</b>	13.6	22.6	37.4
Southern Texas Plains	39.6	20.1	<b>0.0</b>	37.4	65.8	10.2	<b>0.0</b>	15.1	22.4	36.3
Central Texas Plains	25.7	3.6	<b>0.0</b>	34.9	63.1	4.2	<b>0.0</b>	21.6	29.0	40.1
Subhumid Agriculture Plains	77.6	60.2	<b>0.0</b>	27.8	81.4	12.9	<b>0.0</b>	19.3	29.2	43.1
Western High Plains	27.9	20.0	4.1	<b>0.0</b>	4.6	13.1	3.7	<b>0.0</b>	0.9	14.2
Southern Deserts	35.9	15.7	<b>0.0</b>	36.6	68.8	11.3	<b>0.0</b>	6.2	14.3	29.5
River basins										
Brazos	58.0	40.4	<b>0.0</b>	32.2	79.7	10.7	<b>0.0</b>	23.6	35.0	48.4
Brazos–Colorado	43.0	38.2	23.8	14.5	<b>0.0</b>	16.5	9.9	5.1	<b>0.0</b>	10.8
Canadian	5.5	<b>0.0</b>	8.8	9.7	18.8	0.3	<b>0.0</b>	14.3	17.4	26.9
Colorado	25.6	1.0	<b>0.0</b>	51.3	81.8	10.5	<b>0.0</b>	24.2	35.5	47.7
Colorado–Lavaca	35.1	30.2	20.3	10.9	<b>0.0</b>	7.0	<b>0.0</b>	0.5	0.3	12.1
Cypress Creek	36.6	17.7	<b>0.0</b>	32.4	59.4	9.2	<b>0.0</b>	15.1	21.5	34.4
Guadalupe	22.8	7.6	<b>0.0</b>	16.6	35.5	13.4	<b>0.0</b>	13.3	20.2	34.4
Lavaca	20.8	14.4	6.1	<b>0.0</b>	2.0	6.6	<b>0.0</b>	9.1	12.6	24.3
Lavaca–Guadalupe	35.5	32.0	23.2	15.4	<b>0.0</b>	8.5	4.3	3.6	<b>0.0</b>	4.2
Neches	28.9	12.1	<b>0.0</b>	33.2	54.4	12.3	<b>0.0</b>	12.3	19.2	33.7
Nueces	37.6	32.8	18.5	11.2	<b>0.0</b>	12.7	6.1	3.2	<b>0.0</b>	10.9
Red	25.1	18.2	5.3	<b>0.0</b>	0.4	12.4	4.1	1.8	<b>0.0</b>	11.4
Rio Grande	48.0	24.1	<b>0.0</b>	51.7	88.1	13.1	<b>0.0</b>	7.0	16.6	31.9
Sabine	32.3	<b>0.0</b>	15.7	72.2	105.0	11.1	<b>0.0</b>	16.0	25.0	39.7
San Antonio	19.8	11.4	<b>0.0</b>	1.7	9.6	5.2	<b>0.0</b>	8.1	10.2	21.2
San Jacinto	50.2	33.5	<b>0.0</b>	30.7	59.4	10.0	<b>0.0</b>	7.2	12.8	27.5
Sulfur	27.0	22.8	13.8	9.3	<b>0.0</b>	5.7	0.5	1.2	<b>0.0</b>	6.0
Trinity	43.4	<b>0.0</b>	58.5	121.6	147.3	9.2	<b>0.0</b>	24.4	34.8	47.2
Localities										
West Bernard Creek	41.8	37.1	21.8	12.9	<b>0.0</b>	14.9	8.2	2.4	<b>0.0</b>	8.6
West Mustang Creek	21.3	14.5	6.4	<b>0.0</b>	2.4	6.5	<b>0.0</b>	9.1	11.8	24.8
Arenosa Creek	26.0	23.1	16.1	12.0	<b>0.0</b>	6.4	2.8	3.3	<b>0.0</b>	2.6
Big Creek	15.3	4.7	<b>0.0</b>	3.6	19.9	<b>0.0</b>	0.6	20.6	25.7	36.5
West Carancahua Creek	35.3	30.4	20.0	12.2	<b>0.0</b>	7.1	0.2	0.6	<b>0.0</b>	11.8
Placedo Creek	28.3	24.6	17.5	12.9	<b>0.0</b>	6.4	2.5	3.0	<b>0.0</b>	5.3
Lake Creek	37.3	23.3	<b>0.0</b>	15.1	37.6	7.8	<b>0.0</b>	7.0	9.5	23.8
Little Cypress Creek	35.7	24.0	<b>0.0</b>	9.7	23.9	6.9	<b>0.0</b>	13.6	19.3	30.9
Catfish Creek	28.0	<b>0.0</b>	31.9	59.8	80.4	5.5	<b>0.0</b>	16.2	22.1	32.5
Big Cypress Creek	28.8	10.9	<b>0.0</b>	25.4	51.6	10.5	<b>0.0</b>	15.3	22.3	35.4
East Fork of the San Jacinto River	20.2	<b>0.0</b>	1.6	26.6	49.7	5.1	<b>0.0</b>	17.1	21.1	32.1
Keechi Creek	19.0	<b>0.0</b>	21.7	39.0	54.5	4.4	<b>0.0</b>	16.0	19.5	29.9
Piney Creek	30.6	21.9	<b>0.0</b>	2.8	8.2	11.2	<b>0.0</b>	2.8	6.9	22.2
Irons Bayou	29.8	<b>0.0</b>	47.9	71.6	88.5	9.5	<b>0.0</b>	17.2	24.0	35.2
Frazier Creek	20.2	<b>0.0</b>	6.5	29.3	45.6	7.6	<b>0.0</b>	14.8	21.3	32.9
White Oak Creek	19.2	<b>0.0</b>	4.8	26.4	47.2	6.2	<b>0.0</b>	10.7	14.7	26.8
Beech Creek	31.1	<b>0.0</b>	57.0	84.7	103.0	6.7	<b>0.0</b>	14.5	19.8	32.6
Black Cypress Creek	32.3	18.2	<b>0.0</b>	17.6	36.4	9.7	<b>0.0</b>	11.5	15.7	29.0
Wheelock Creek	16.0	<b>0.0</b>	6.9	19.5	34.1	8.1	<b>0.0</b>	15.9	21.2	32.9
Ponds Creek	37.0	33.2	23.4	13.8	<b>0.0</b>	6.7	2.7	3.4	<b>0.0</b>	4.7
San Miguel Creek	32.0	27.0	14.2	7.8	<b>0.0</b>	10.4	3.2	1.1	<b>0.0</b>	10.4
Sycamore Creek	20.4	6.3	<b>0.0</b>	15.2	29.9	12.0	1.1	<b>0.0</b>	3.5	12.5
Metate Creek	20.2	16.4	10.4	7.1	<b>0.0</b>	8.6	3.0	2.2	<b>0.0</b>	7.2
Pinto Creek	18.2	11.1	<b>0.0</b>	1.3	4.6	8.0	<b>0.0</b>	6.5	8.4	18.1
Cowhouse Creek	10.1	0.1	<b>0.0</b>	3.7	12.2	7.0	<b>0.0</b>	15.2	18.7	28.1
Medina River	21.1	12.2	<b>0.0</b>	2.7	10.5	4.9	<b>0.0</b>	9.2	9.9	21.3
South Llano River	25.2	17.6	5.4	<b>0.0</b>	5.1	3.3	<b>0.0</b>	9.8	10.6	19.7
Onion Creek	10.0	<b>0.0</b>	1.2	3.9	16.0	6.5	<b>0.0</b>	18.5	24.9	34.2
Rocky Creek	17.6	9.0	1.8	<b>0.0</b>	11.3	9.2	<b>0.0</b>	2.6	6.5	13.1
Barton Creek	3.7	<b>0.0</b>	12.0	14.8	26.0	<b>0.0</b>	3.7	20.4	23.9	32.1
Little Blanco River	11.6	0.6	<b>0.0</b>	2.8	17.4	7.6	<b>0.0</b>	15.3	19.4	30.5
Oatmeal Creek	6.9	<b>0.0</b>	1.6	0.2	5.6	9.5	1.6	<b>0.0</b>	0.9	5.5
Little Barton Creek	14.1	4.8	<b>0.0</b>	1.0	9.9	<b>0.0</b>	8.5	23.2	25.3	32.0
Elm Creek	20.6	12.8	3.6	<b>0.0</b>	8.6	9.6	<b>0.0</b>	12.5	20.9	33.1
Spring Creek	20.5	14.7	3.6	1.3	<b>0.0</b>	7.2	<b>0.0</b>	11.9	15.9	26.8

TABLE 1.—Continued.

Area	Taxonomic organization					Functional organization				
	DD	BS	RF	RA	DP	DD	BS	RF	RA	DP
Localities										
Cummins Creek	42.4	34.4	11.7	0.3	<b>0.0</b>	8.8	<b>0.0</b>	5.8	8.3	20.4
Mill Creek	28.4	16.7	<b>0.0</b>	8.1	24.5	9.0	<b>0.0</b>	10.2	14.8	28.9
Clear Creek	22.8	14.6	<b>0.0</b>	2.8	9.3	11.5	<b>0.0</b>	9.0	15.6	28.6
Cottonwood Creek	22.1	16.7	8.9	2.8	<b>0.0</b>	6.8	<b>0.0</b>	5.5	6.5	19.3
Neils Creek	27.1	21.7	8.8	4.2	<b>0.0</b>	3.6	<b>0.0</b>	12.8	14.8	24.8
Deer Creek	19.1	11.6	0.2	<b>0.0</b>	5.0	11.0	<b>0.0</b>	7.0	13.1	26.3
West Rocky Creek	6.1	<b>0.0</b>	15.3	19.6	31.2	<b>0.0</b>	6.1	22.5	23.7	32.3
Steele Creek	23.3	17.8	5.5	3.6	<b>0.0</b>	3.2	<b>0.0</b>	11.6	14.6	24.2
Colony Creek	12.4	<b>0.0</b>	6.8	13.3	29.1	9.0	<b>0.0</b>	16.6	23.1	33.8
Deadman Creek	16.1	9.4	0.8	<b>0.0</b>	1.4	8.0	<b>0.0</b>	5.9	7.5	19.4
Auds Creek	27.3	23.2	14.5	9.1	<b>0.0</b>	5.8	0.5	2.0	<b>0.0</b>	6.4
Bluff Creek <sup>a</sup>	5.7	<b>0.0</b>	11.7	14.1	24.9	1.8	<b>0.0</b>	13.2	15.9	25.8
Wilson Creek	12.5	<b>0.0</b>	6.2	12.0	26.9	0.0	5.7	27.0	32.4	40.5
Ioni Creek	9.0	0.4	<b>0.0</b>	2.0	8.8	0.0	1.2	16.0	17.8	25.9
Bluff Creek <sup>b</sup>	10.5	4.6	2.5	0.5	<b>0.0</b>	5.1	<b>0.0</b>	6.9	5.6	15.4
Willis Creek	21.7	17.7	11.2	7.5	<b>0.0</b>	7.3	1.9	1.9	<b>0.0</b>	7.8
Geronimo Creek	8.0	<b>0.0</b>	1.6	2.9	12.8	8.7	<b>0.0</b>	8.8	12.8	23.8
Wolf Creek	5.1	<b>0.0</b>	8.5	9.3	19.3	0.4	<b>0.0</b>	15.5	17.4	26.9
McClellan Creek	7.7	3.3	2.8	<b>0.0</b>	3.9	<b>0.0</b>	0.8	10.0	9.7	17.6
Whitefish Creek	17.2	13.6	10.0	7.6	<b>0.0</b>	6.2	2.7	3.1	<b>0.0</b>	0.0
Lelia Lake Creek	4.5	1.4	2.7	<b>0.0</b>	2.0	1.4	<b>0.0</b>	8.8	9.6	17.9
Saddlers Creek	7.4	1.7	2.3	<b>0.0</b>	2.9	14.7	8.3	2.9	<b>0.0</b>	0.4
Devils River	30.0	25.5	14.3	9.4	<b>0.0</b>	2.9	<b>0.0</b>	6.6	7.1	16.5
Independence Creek	28.9	24.2	13.0	8.1	<b>0.0</b>	25.2	20.8	12.2	7.7	<b>0.0</b>
Alamito Creek	16.7	10.6	4.5	2.7	<b>0.0</b>	6.1	<b>0.0</b>	2.6	2.1	11.7
Terlingua Creek	12.5	5.2	2.0	<b>0.0</b>	8.9	8.5	<b>0.0</b>	12.8	18.7	31.6
Live Oak Creek	22.0	19.0	13.3	10.0	<b>0.0</b>	29.8	26.4	18.6	12.1	<b>0.0</b>

<sup>a</sup> Scurry County<sup>b</sup> McLennan County

water column particulate feeders (11%) were also fairly abundant. The dominance decay model produced abundances that closely matched seven assemblages with water column particulate feeders (20%), surface feeders (17%), and benthic pickers (10%)—all being approximately equal in mean relative abundance. The random-fraction model and dominance preemption model each best fit two localities. The most abundant functional groups present in assemblages modeled by the random-fraction model were grazers (28%), browsers (23%), and water column particulate feeders (14%), whereas the dominance preemption model explained the high abundance of browsers (49%) and surface feeders (39%).

The dominance preemption model best fit 32% of the species abundance distributions in individual assemblages, followed by the broken-stick model (27%), random-fraction model (24%), and random-assortment model (16%). The dominance preemption model produced highly uneven abundances corresponding to assemblages in which western mosquitofish, red shiner, and blacktail shiner were very abundant. In fact, the mean relative abundance of western mosquitofish in these assemblages was 42%.

Red shiner and blacktail shiner each had a mean relative abundance of 12%. These three species were also important constituents of assemblages in which the random-fraction model was the best fit, except their abundances in these assemblages were more evenly distributed (western mosquitofish, 17%; red shiner, 17%; and blacktail shiner, 13%). Red shiner (28%) and western mosquitofish (15%) were also important species in assemblages modeled by the random-assortment model, except that blacktail shiner (5%) were replaced by plains killifish (19%) as an abundant species. However, the blacktail shiner (15%) was the only species with a relative abundance greater than 10% in assemblages in which the broken-stick model was the best-fitting model.

### Discussion

Studies of niche partitioning in stream fish assemblages have produced conflicting results. Some studies have shown that species are able to coexist without much resource partitioning (Matthews and Hill 1980; Angermeier 1982, 1987); these studies found some degree of niche partitioning, whether it was habitat use or food consumption, but there were no consistent

patterns. However, most studies on niche partitioning suggest that species consistently differ along axes of food, habitat, or activity times (Ross 1986; Nishikawa and Nakano 1998; Herder and Freyhof 2006). Although some of the abundance distributions in our study were more consistent with the random-assortment model, suggesting that niche partitioning does not play a major role in structuring fish assemblages, only in one sampling locality (Saddlers Creek in the Red River basin) and one river basin (the Red River basin) were functional and taxonomic organization both accounted for by the random-assortment model. In all other cases, either functional organization or taxonomic organization was consistent with some mechanism of niche partitioning. Indeed, our results suggest that niche partitioning is an important structuring mechanism across a variety of spatial scales.

The taxonomic organization of assemblages, in general, was best characterized by the random-fraction model. According to the "requirement" niche concept (see Leibold 1995), this suggests that as new species enter an assemblage, they sequester random proportions of the overall niche space regardless of whether a particular niche is already occupied by a preexisting species. This was particularly true for statewide and ecosystem level of analyses; however, several individual localities and even some river basins were best characterized by the dominance preemption model of niche apportionment. In these systems, new species sequester most of the available niche space and do not affect niches of preexisting species, resulting in highly uneven abundance distributions. These abundance distributions corresponded well with systems in which either western mosquitofish, red shiner, or blacktail shiner had a relative abundance greater than 50%. Of course, because individuals of these species are small, they would not be as abundant if biomass had been assessed instead of abundance. In this case, species biomass distributions would be much more even than species abundance distributions. We do not know exactly how this would affect the identity of the best-fitting model, but we hypothesize that the broken-stick model would have the best fit because the emphasis is no longer on species identity but rather on energy flow.

Overall, the functional organization of stream fish assemblages seems to be most consistent with the broken-stick model of niche apportionment, regardless of spatial scale. That is, the broken-stick model consistently outperformed the other models of niche partitioning whether local assemblages were analyzed separately or aggregated according to ecoregion, river basin, or the entire state. In terms of the "impact" niche concept (Leibold 1995), this suggests that as each new functional group enters an assemblage, its affect on the

environment is such that it generally will alter some of the ecological influences of the most abundant functional group already present. For example, suppose a fish assemblage consisted primarily of filter feeders, which affect primary productivity by removing phytoplankton from the water column. If a new functional group, disturbance pickers, were to enter the assemblage and begin to increase the suspension of fine particulate organic matter, the abundance of filter feeders would decrease and the amount of phytoplankton in the water column would increase because of the addition of the new functional group. In this case, the addition of a new functional group would alter the effects on the environment such that the changes become beneficial to the ecosystem. If the same two functional groups were added in reverse sequence, however, the resulting effects would become detrimental to the ecosystem. That is, the abundance of disturbance pickers would decrease with the addition of filter feeders, less of the fine particulate matter would be suspended in the water column, and less primary productivity would occur as a result of increased removal of phytoplankton. Hence, the order in which assemblages are created may greatly affect ecosystem level processes.

Although one might question whether the evenness of functional-abundance distributions is merely an artifact of evenly splitting individuals within species into multiple functional groups, we believe it is an accurate representation of nature. Eighty-one percent of the species in this study were classified into more than one functional group: 34% of the species were assigned to two functional groups, 35% to three functional groups, 11% to four functional groups, and only 1% to five functional groups. However, when we divided species abundances by the number of functional groups to which each belonged—which decreased species abundance in a fashion similar to that of functional abundance—and reran the analyses on taxonomic organization, we obtained a pattern very similar to that obtained before. The broken-stick model best fit 17 sites, the random-fraction model 11 sites, the random-assortment model 12 sites, and the dominance preemption model 22 of the 62 sites. Moreover, neither the number of functional groups nor the number of species affected the identities of the models that best fit the data. As a result, we do not believe the evenness of functional groups is merely an artifact of our methodology; rather, we believe that communities, regardless of specific locality, must maintain a certain degree of ecosystem functioning and that fish serve as a driving force in those processes.

Alternative functional groupings have been used to assess the functional organization of assemblages. For

example, some authors (e.g., Poff and Allan 1995; Goldstein and Meador 2004) utilized a combination of various species traits, such as trophic ecology, reproductive biology, substrate preference, geomorphic preference, locomotion, body morphology, and reproductive strategy, in their assessment of the relationship between functional organization and hydrological variability. Others (e.g., Hoeinghaus et al. 2007) used a combination of trophic ecology and life history characteristics in their examination of scale dependency in structuring factors associated with functional and taxonomic organization of stream fish assemblages. We believe these different functional groupings will have abundances that closely match the corresponding species abundance distributions because the functional groups are more concerned with how species respond to the environment than with the effects of species on the environment. As a result, we predict the same niche-partitioning models will fit both the functional and the taxonomic organization of assemblages, at least when the requirement niche instead of the impact niche is the primary focus.

One of the advantages of using abundance distributions in multiscale analyses is that species identity does not factor into the shape of the distributions; only the ranks of species abundances are important. This circumvents issues associated with phylogenetic differences among fish assemblages across broad geographic regions. For example, a highly even species abundance distribution that is best described with the dominance decay model will have the same basic shape in any fish assemblage anywhere in the world, and the same mechanism of niche partitioning can be ascribed to it. The same holds true for increasing spatial scale. For example, San Miguel Creek had a species abundance distribution consistent with the dominance preemption model, which also accounted for the abundance distribution across the entire Nueces River basin. Despite the difference in spatial scale, both species abundance distributions indicate that each new species entering an assemblage sequesters more than half of the available niche space. Thus, it becomes more difficult for additional species to coexist in areas where dominance preemption is the primary mechanism of niche apportionment.

Certain functional groups have approximately the same effect on the environment regardless of their specific location, at least as based on consistent relative abundances across the state (see the tables in appendix available in the online version of this article). The specific species composition of the assemblages may change, but the impact of the species on the environment remains the same. Apparently, to maintain "proper" ecosystem functioning, aquatic environments

require certain functional groups to be present in particular abundances. In fact, this phenomenon appears to hold even as the spatial scale increases.

### Acknowledgments

We thank Christopher P. Bloch, Dale A. McCullough, Kenneth A. Schmidt, Gene R. Wilde, Michael R. Willig, and Kirk O. Winemiller for valuable comments and insight regarding this manuscript. This work was submitted in partial fulfillment of the requirements for a doctor of philosophy degree from Texas Tech University.

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