Intercontinental comparison of fish ecomorphology: null model tests of community assembly at the patch scale in rivers

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Abstract. Community assembly is affected by environmental filtering that restricts viable phenotypes and by species interactions that impose limits on interspecific trait similarity. Relative influences of these processes should vary according to habitat features and dispersal. Species dispersion within assemblage trait space also should vary in relation to species richness, strength of competition, and the spatiotemporal scale of analysis. We examined ecomorphological diversity of two freshwater fish families (Neotropical Cichlidae, Nearctic Centrarchidae) to test theories of local assembly from regional species pools and theories of species packing within mesohabitat patches. Cichlid and centrarchid assemblages were surveyed in four floodplain rivers (two in South America and two in North America) during low-water periods when fish densities are highest. Surveys were conducted in four mesohabitat types (submerged wood, leaf litter, rocks, sand bank) within river channels and floodplain lakes. We measured 23 morphological traits associated with locomotion and feeding. Principal components analysis was performed on the species × traits matrix, and species axis scores were used to calculate species pairwise Euclidean distances and indices of dispersion within assemblage morphospace: mean nearest-neighbor distance (indicating similarity), mean distance to centroid (assemblage morphospace size), and standard deviation of nearest-neighbor distance (evenness of dispersion within assemblage morphospace). A null model was used to assess whether patterns were significantly nonrandom. When data for all mesohabitat types were combined for each river, species were significantly overdispersed and the assemblage morphospace was larger than predicted at random in every case. Analysis of assemblages within mesohabitat patches of different types revealed, in every case, significant overdispersion of species in morphospace indicative of limiting similarity. The total assemblage morphospace was greater than expected for tropical cichlids, but not for temperate centrarchids. Trends of species dispersion with assemblage morphospace in relation to species richness within mesohabitat patches were not consistent among or within river systems, possibly indicating that patches were already saturated with these perciform fishes. Interregional comparisons suggest an influence from both adaptive diversification and environmental filtering at broad spatial scales. At the scale of mesohabitat patches in lowland rivers, cichlid and centrarchid assemblages revealed patterns of trait complementarity that imply limiting similarity and strong influence of biotic interactions.

Key words: Centrarchidae; Cichlidae; environmental filtering; functional trait; limiting similarity; Neartic; Neotropics; niche complementarity; Peru; species packing; Texas; Venezuela.

INTRODUCTION

Patterns of species richness and community structure derive from interactions between regional and local processes (Cornell and Lawton 1992, Ricklefs 2004, Algar et al. 2011) and constraints set by historical biogeography (Ricklefs and Schluter 1993, Ricklefs and Renner 2012). Different processes may influence assemblage taxonomic and functional structure depending on the spatial scale of analysis (Levin 1992, Oberdorff et al. 1995, Huston 1999, Vellend 2010). At broad scales

(regional to global), abiotic environmental factors and historical biogeography are major determinants of biodiversity (Jackson et al. 2001, Algar et al. 2011), whereas at local scales, community assembly and population persistence should be strongly influenced by productivity, environmental stress, habitat complexity, and species interactions (Huston 1999, Brooker et al. 2009). When biotic interactions are strong, species coexistence may be facilitated by functional trait complementarity that gives rise to resource partitioning (Hutchinson 1959, MacArthur and Levins 1967, Pianka 1974, Losos et al. 2003, Kahmen et al. 2006). The relative importance of regional vs. local processes on community composition has long been hypothesized to differ between tropical and temperate regions (Dobzhansky 1950). In the tropics, species tend to reveal a

Species packing with high niche overlap

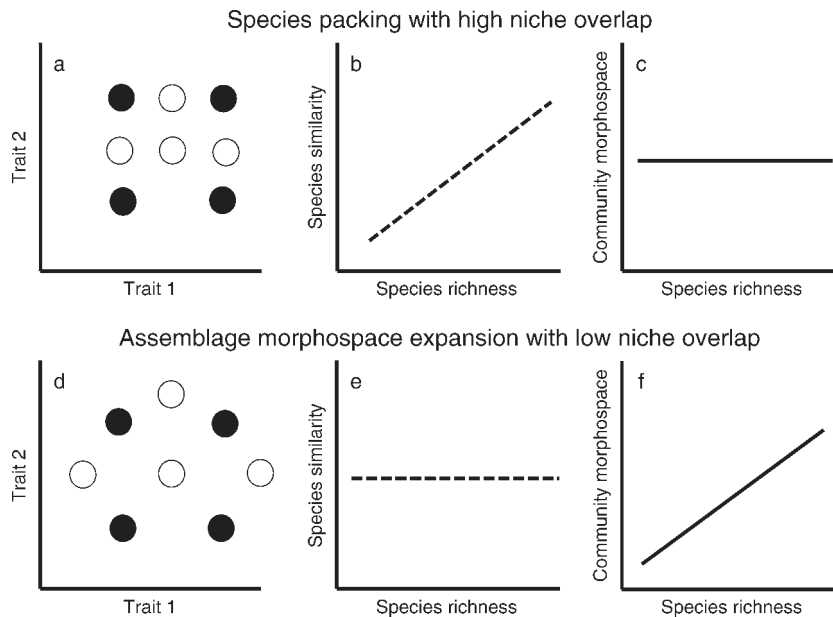## Assemblage morphospace expansion with low niche overlap

Fig. 1. Theoretical models of species distribution in morphological space and the relationships with species richness, showing original species in morphological space (solid circles), new species added (open circles), niche volume (solid lines), and species dissimilarities (dashed lines). (a–c) Under the niche compression model, average similarity among species increases as new species are added to the assemblage, with total morphological niche volume remaining relatively constant. (d–f) Under the niche expansion model, average differences among species remain relatively constant as new species are added, and assemblage morphological niche volume increases as species richness increases.

greater variety of specialized ecological traits that appear to derive from selection associated with species interactions, such as competition, predation, parasitism, and mutalism, whereas in temperate regions, spatial and environmental filters seem to account for a greater proportion of trait variation within local communities, and species interactions may be less influential (Jackson et al. 2001, Ricklefs 2009, Schemske et al. 2009).

Morphological approaches have been used to compare assemblage structure between continents (Ricklefs and Travis 1980, Winemiller 1991, Lamouroux et al. 2002, Silva and Brandao 2010, Inward et al. 2011, Ricklefs 2012), reveal patterns of convergence and divergence (Winemiller et al. 1995, Losos et al. 2003, Gillespie 2004, Stayton 2006), and examine assemblage structure in relation to habitat complexity (Willis et al. 2005, Montaña and Winemiller 2010). Morphological data have been used to infer the relative importance of environmental filtering vs. limiting similarity in structuring species assemblages (Weiher et al. 1998, 2011, Moreno et al. 2006, Mouillot et al. 2007, Ingram and Shurin 2009, Baraloto et al. 2012, Mouchet et al. 2012, Wilson and Stubbs 2012). Environmental filtering results in assemblages of coexisting species that are more similar than expected by chance, either because of shared ancestry or evolutionary convergence. Environmental conditions constrain the sets of functional traits required to achieve positive fitness, and resulting species assemblages have high functional redundancy. In contrast, the limiting similarity theory predicts that

species with sufficiently similar traits and ecological requirements are unable to coexist when resources are limiting, and coexisting species should be less similar than expected by chance and have high functional complementarity to reduce interspecific competition (MacArthur and Levin 1967). Weiher and Keddy (1995) postulated that limiting similarity should have greater importance at smaller spatial scales, whereas environmental filtering should predominate at larger spatial scales. Tests of these predictions for fish assemblages have produced variable results. Schlosser (1987), Peres-Neto (2004), and Mouchet et al. (2012) concluded that habitat features act as local filters regulating co-occurrence of fish species with similar traits. Competition seems to account for structure of fish assemblages in temperate streams (Winston 1995), and predation has been shown to influence fish assemblage structure at the patch (mesohabitat) scale in both tropical rivers (Layman and Winemiller 2004, Petry et al. 2010) and temperate streams (Power and Matthews 1983, Schlosser 1988).

As species richness within a habitat patch increases, patterns of species dispersion within assemblage morphological space (morphospace) and the size of this space could change in two ways (Fig. 1). When new species are added to a local community, the total assemblage morphospace could remain constant while average similarity of species increases: a pattern that would infer weak competition. Alternatively, under a competition scenario, the addition of species to a habitat

patch could result in resource partitioning (MacArthur 1971, Pianka 1974) associated with no change in average species similarity and an expanded assemblage morphospace, a more even dispersion of species within the morphospace, or both (Fig. 1; Ricklefs and Miles 1994). A classic study by Werner (1977) found that three North American sunfishes (*Lepomis* spp.) had similar niches when occurring alone in ponds, but when stocked in ponds together, these species underwent shifts in habitat use and feeding that resulted in interspecific niche segregation (niche complementarity). Ricklefs and Travis (1980) found that similarity of bird species within assemblage morphospace was relatively constant, but the periphery of assemblage morphospace expanded with increasing species richness. Other studies involving fishes (Winemiller 1991), lizards (Ricklefs et al. 1981), and bats (Stevens et al. 2006) also revealed an expanded morphospace for assemblages with greater species richness.

The expansion of assemblage morphospace has been interpreted as an expansion of niche space (e.g., Douglas and Matthews 1992) or alternatively as morphological diversification associated with ecological specialization and niche partitioning with or without expansion of community niche space (e.g., Winemiller 1991). Ricklefs (2012) estimated assemblage morphospace of passerine birds from 11 zoogeographic regions and found no relationship with species richness at either the scale of local species assemblage or regional avifauna, although there was a weak relationship with average number of species per family. Species of regional faunas were not evenly distributed in morphospace, and regions revealed much convergence. He inferred that species interactions posed little constraint on local and regional assemblage structure, and evolutionary diversification, extinction, and dispersal limitation had greatest influence.

To test ecological theories of community assembly and structure, we analyzed morphological patterns among species of two perciform fish families that are widely distributed and common in rivers of South and North America. We examined patterns at two spatial scales: regional (rivers) and local (mesohabitat patches within the river channel and floodplain lakes). Specifically, we asked whether or not species coexisting in mesohabitats were more or less similar than predicted at random (niche filtering vs. limiting similarity), whether there was evidence of assemblage morphospace expansion, and also whether species similarity and dispersion and the total assemblage morphospace was correlated with species richness at either of the two spatial scales. We chose perciform fishes in the families Cichlidae (South America) and Centrarchidae (North America) as model taxa because of their ecological and morphological similarities (Norton and Brainerd 1993, Montaña and Winemiller 2013) and also because they are diverse and common fishes inhabiting freshwater habitats. The Neotropical clade of the Cichlidae has about 600 species that reveal a high degree of morphological and ecological diversification (López-Fernández et al. 2012), with many species often coexisting at the local scale (e.g., Winemiller et al. 1995, Montaña and Winemiller 2010). The Centrarchidae (sunfishes and black basses) has eight genera and 34 species that are morphologically diverse and inhabit freshwater habitats throughout most of North America (Cook and Phillip 2009). We therefore predicted that Neotropical cichlids could be more tightly packed within local assemblage morphospace or have an expanded morphospace compared with temperate centrarchids within similar habitats. We employed multivariate techniques to quantify the morphological space occupied by species within each macrohabitat and mesohabitat. To test for statistical significance of patterns, we developed null models to contrast observed patterns with those derived from randomized data from computer simulations.

MATERIALS AND METHODS

Study sites and field data collection

We conducted this study in four lowland rivers: two in South America (the Cinaruco and the Tambopata) and two in North America (the Neches and the Brazos). These rivers were chosen for comparison to provide similar environmental conditions in terms of geomorphology, sediments, and water quality. The Cinaruco River (study area centered at approximately 6°32′ N, 67°24′ W) and the Neches (30°35′ N, 94°08′ W) have clear but stained waters, with sandy substrates, low pH, and high transparency (Montoya et al. 2006, Stamatis 2007). The Cinaruco River is a tributary of the Orinoco River in the Venezuelan llanos of Apure, southern Venezuela, whereas the Neches River in Texas (USA) originates in eastern Van Zandt County, and flows to its mouth at Sabine Lake, an inlet of the Gulf of Mexico. The Tambopata River (study area centered at approximately 12°72′ N, 69°28′ W) and the Brazos River (30°37′ N, 96°37′ W) are similar to each other, with neutral pH, high loads of suspended sediments of fine grain size, and high turbidity during high flow conditions that limits aquatic primary production (Barthem et al. 2003, Zeug et al. 2005). The Tambopata River originates in the Andes Mountains and drains into the Madre de Dios River in Peru, then becomes the Beni River in Bolivia before it meets its confluence with the Amazon River. The Brazos River in Texas flows 1485 km from its origin near the Texas–New Mexico border to the Gulf of Mexico.

In all four rivers, we conducted fieldwork during the low-water period (defined as the annual dry season in South America and the summer in North America), because more fishes inhabit habitats in the littoral zone and they can be captured more efficiently under these conditions. As water levels descend in rivers and floodplains, aquatic habitat is reduced, fish densities increase, and most biotic interactions intensify (Lowe-McConnell 1987, Winemiller and Jepsen 1998). Survey methods were standardized to produce comparable

samples of perciform fish assemblages from the same habitats across the four regions. We sampled fishes from a stretch of the river channel (~20 km) and nearby floodplain lakes. In the Cinaruco River, where floodplain lakes were common, we collected cichlids along the shoreline of seven lakes, whereas in the Tambopata, a single large lake was present in the survey region (Lake Tres Chimbadas). In the Brazos River, we sampled two oxbow lakes (Big Bend and Moehlman's Slough; Zeug et al. 2005), and the main river channel ~10 km upstream and 10 km downstream from state Highway 21. Finally, we surveyed the river channel and two floodplain lakes along the Neches River between the towns Evadale and Spurger. Habitats were categorized as macrohabitats (river channel, floodplain lakes) and mesohabitats. Within the two macrohabitats, four mesohabitats were surveyed: sand bank (>95% sand substrate), leaf litter (>90% covered by leaves), rock shoal (>90% covered by rocks), and submerged wood (>95% submerged wood) (see Montaña and Winemiller [2010] for further details).

In the Cinaruco River, we conducted surveys between December of 2005 and May of 2006. We surveyed the Tambopata River during June and July of 2009. Surveys in the Texas rivers were conducted during three summers (May to August, 2009–2011). As a result of the diversity of mesohabitat types in each of the rivers and the logistical difficulties of using certain techniques in the tropical rivers, multiple survey methods were required. Seining was conducted in the Cinaruco, Tambopata, Neches, and Brazos Rivers within mesohabitats classified as sand bank or leaf litter (seine dimensions: 6.4 × 1.8 m, 4-mm mesh). At each survey site (mesohabitat patch), one sample consisted of three hauls that were not overlapping in the area covered (following method of Layman and Winemiller 2004). Seine hauls were initiated from a depth that ranged between 1.0 m to 1.5 m and terminated along the shoreline. In the Cinaruco and Lake Tres Chimbadas (Tambopata), small baited hooks (number 8) were used to capture fish from rock shoals and submerged wood patches where seining was ineffective. A cast net (2 m diameter, 1-cm mesh) also was used in leaf litter and wood substrata in Lake Tres Chimbadas to assess if any additional species were present. Electrofishing (pulsed direct current [DC] from a hand-held boat unit) was conducted in the two Texas rivers within rock or wood patches. Each rock shoal or submerged wood patch was considered sufficiently sampled when no additional perciform species were obtained following 30 min of sustained effort using hooks or 10 min of electrofishing. We assumed that seining effectively captured all cichlid and centrarchid species in sand bank and leaf litter mesohabitats. We assumed that baited hooks did not effectively capture dwarf cichlids (e.g., *Apistogramma*, *Biotoecus*, *Crenicichla* aff. *wallacii*) if they were present in rock shoal or submerged wood patches. Based on comparisons with prior field studies at these sites that used the same plus alternative methods to survey fishes in these mesohabitats of the same rivers (Zeug et al. 2005, Arrington and Winemiller 2006, Layman et al. 2010), our survey methods and degrees of effort yielded reliable estimates of presence or absence of perciform species within mesohabitat patches. The two exceptions were *Crenicichla* aff. *wallacii* in the Cinaruco, a dwarf cichlid we did not capture from rock and submerged wood patches using hooks, but which was present in 15–40% of artificial ceramic brick and woody debris patches sampled with a net in earlier studies (Arrington et al. 2005, Layman et al. 2010), and *Apistogramma* sp., a dwarf cichlid not captured from submerged wood by us, but present in 20–40% of artificial wood patches in the earlier studies. In the tropical rivers, 282 mesohabitat samples (669 total seine hauls, 340.8 hours of fishing with baited hook, and 130 cast net throws) yielded 8705 individual cichlids. In the temperate rivers, 241 mesohabitat samples (516 total seine hauls, 7177 times/second [pulse periods of electrofishing]) yielded 9675 individual centrarchids. Captured specimens were preserved in a 15% formalin solution in the field and transported to the laboratory where they were examined and measured. Voucher specimens were archived in the Museo de Ciencias Naturales at UNELLEZ Guanare, Venezuela, and the Biodiversity Research and Teaching Collections at Texas A&M University, College Station, Texas, USA.

Morphological traits

For all species collected (26 species of cichlids and 12 species of centrarchids; Appendix A), we recorded 23 morphological characters (Appendix B) in five adult specimens per species. Traditional morphometric measurements were made using calipers (to nearest 0.01 mm). We chose measurements to reflect various facets of trophic ecology, swimming behavior, and habitat use (Gatz 1979, Winemiller 1991, Montaña and Winemiller 2010). Twenty-one measurements were converted to proportions of standard length, body depth, body width, or head length following Winemiller (1991), so that descriptors of body and fin shape could be analyzed without the influence of body size. Ratios of body size can introduce allometric bias into shape analysis, but allometric influences should be negligible for interspecific comparisons in which a restricted adult size class is chosen to represent a given species. In our data set, interspecific morphological variation greatly exceeded intraspecific variation, including ontogenetic variation; therefore, bias from failure to account for intraspecific variation (Violle et al. 2012) is not expected to significantly influence overall community patterns. We performed preliminary analysis using three different techniques to remove the effect of body size from components of shape: ratios or proportional standardization based on standard length (SL; Gatz 1979), sheared principal components analysis (PCA; Bookstein et al. 1985), and residuals from analysis of covariance (McCoy et al. 2006), and results from these methods

yielded patterns that essentially were the same. Therefore, we used standardized values of selected ratios as descriptors of shape that have straightforward ecological and functional interpretations (Winemiller 1991).

Data analysis

Analysis of morphospace.—To describe the morphological space occupied by each species assemblage and examine among-species differences in functional traits, we first performed a principal components analysis (PCA) based on the correlation matrix of all species and traits. We eliminated *Centrarchus macropterus* from the Neches River data set, because only one individual was captured during our surveys. All other species from all four rivers (Appendix C) yielded at least 10 individuals during surveys. Morphological data for 130 specimens of cichlids from the Cinaruco and Tambopata Rivers and 120 specimens of centrarchids from the Neches and Brazos Rivers were log-transformed prior to the analyses to enhance the interpretation of the axes and fulfill assumptions of this multivariate approach. Because the measurements of morphological traits made on five adult specimens of a given species were highly consistent, we calculated species means for the 23 morphological attributes. These means were then used for PCA to ordinate species in morphospace. Species loadings on the first four PC axes provided the basis for inter-assemblage comparisons of species distributions in morphological space. The first four PC gradients explained 68.8% of total morphological variation (Appendix B). We used a multivariate MANOVA to test for significant differences among morphospaces occupied by the four regional perciform assemblages as defined by PCA. In addition, a Mantel test was conducted to derive correlations between the matrix of species trait values and matrices of species occurrence in mesohabitat categories. PCA, MANOVA, and Mantel test analyses were performed with PAST.exe (Hammer et al. 2001).

Morphological dissimilarity for every possible species pairing within each regional assemblage was estimated by calculating Euclidean distance using PC scores. To adjust for the different amounts of variation modeled by each axis, we calculated species morphological similarity using weighted Euclidean distance. This method allows more dimensions (gradients) of morphological variation to be included when estimating species similarity for calculation of assemblage morphospace metrics, without biasing the analysis by treating all gradients as having equal influence. The contribution of each PC axis to the Euclidean distance was weighted using the proportion of variance explained by the axis as the weighting factor (w). Euclidean distance between species pairs was computed according to the following formula:

$$d_{(j,k)} = \left[\Sigma^n w_i \left(x_{ij} - x_{ik} \right) \right]^{1/2}$$

where n was the number of attributes i (PC axes), x_{ij} and x_{ik} were standardized values of the same attribute (PC axis scores) for species j and k, and w_i was a weight attached to attribute i.

From the pairwise Euclidean distance values, we determined morphological measures of mean nearest-neighbor distance (NND), an index of species packing in morphological space, the standard deviation (SD) of NND, an index of evenness of species dispersion or packing in morphological space, and the average distance to the assemblage centroid (CD), an index that provides an estimate of the relative size of the morphological hypervolume or total niche space occupied by an assemblage (Gatz 1979, Winemiller 1991). Lower values of the SD of NND indicate that species are more evenly dispersed within morphospace, a pattern that would be consistent with limiting similarity. We performed linear regressions using SPSS 16.0 for Windows (SPSS 2007) to test the relationship between species richness and mean NND, as well as the SD of NND and mean CD. We compiled sub-matrices containing species from individual mesohabitat patches for each river, and then aggregated mesohabitat patch samples to form matrices for mesohabitat categories for each river.

Morphological null model.—To test the hypothesis that assemblage morphological structure differs from random expectations when viewed at different spatial scales, we developed a computer program (Sampler version 1.0; see the Supplement) that generates random species assemblages drawn from the observed species pool and calculates the nearest-neighbor distances (NND) and centroid distances (CD). The input to the program was an n-by-four matrix consisting of the first four PCA axes for each species in an n-species assemblage. The proportion of the variance modeled by each PCA axis was used as input to compute weighted Euclidean distances. For each species assemblage, the program repeatedly generated random samples of k rows (simulated local assemblages) from the n rows, representing the species in the assemblage regional pool, and computed the NND and CD for the k rows. For smaller assemblages, such as the Brazos (11 species) and Tambopata (7 species), the program generated all possible combinations (samples) of k rows from the original n. For large assemblages such as in Cinaruco (n = 19 species), the program generated 1000 random samples of size k. Random assembly of null assemblages implies that all species in the regional pool are ecologically equivalent and have the same probability of colonizing a habitat patch (Hubbell 2001). To generate the random assemblages, species were selected without replacement in the regional species pool. For each mesohabitat category, null assemblages containing the same number of species observed for individual mesohabitat patches within each river were generated. The null model assumes that all species from the rivers macrohabitat species pools have equal probability to colonize a mesohabitat patch within that macrohabitat, which seems reasonable given the high abundance and

dispersal capabilities of all cichlid and centrarchid species in the macrohabitats (again, *C. macropterus*, the only rare species, was eliminated from the Neches data set).

Observed values for mean NND, SD of NND, and mean CD of natural assemblages were compared to values for randomly generated sets of species having the same number of species as the real assemblage. We used Fisher's chi-square summation test of combined probabilities [$\chi^2 = -2 \Sigma \log(P_i)$] to test whether morphological patterns from each mesohabitat type were significantly different from those drawn randomly from the set of species pools. Fisher's summation test (Sokal and Rohlf 1995) combines probabilities (P_i) from all samples within a set of related comparison to determine if the overall difference between observed vs. random values is statistically significant. Relationships of the three assemblage dispersion metrics with species richness were examined using standard linear regression with SPSS 16.0 (SPSS 2007). We also performed analysis of covariance (ANCOVA) using SPSS 16.0 (SPSS 2007) to test for differences in regression slopes and intercepts of observed and randomly generated data sets. The homogeneity of regression (slope) assumption was tested to evaluate interactions between the covariate (i.e., species richness), independent variable (mean NND, SD of NND, and mean CD), and dependent variable (observed vs. random).

Results

Regional and local species richness

The Cinaruco River had 19 cichlid species, the Neches River had 12 centrarchid species, the Brazos River had 10 centrarchids, and the Tambopata River had 7 cichlids. Surveys in the turbid channel of the Tambopata River did not yield any cichlids; all specimens were collected from Tres Chimbadas, a connected floodplain lake. Ten centrarchids were common to the Neches and Brazos, and *Centrarchus macropterus* (rare and therefore eliminated from analyses) and *Pomoxis nigromaculatus* (common) were only present in the Neches. Species richness of cichlids and centrarchids tended to be higher in floodplain lakes than the corresponding river channel (Appendix C). In the Cinaruco, most cichlid species were captured in both the river channel and floodplain lakes, with only two species restricted to specific macrohabitats; *Cichla intermedia* was restricted to the river channel, and *Satanoperca mapiritensis* was captured only from floodplain lakes.

Ecomorphological gradients

Species of both families were strongly differentiated on the basis of head and body shape, mouth width and position, and fin dimensions. PCA resulted in four axes (PC1–4) explaining 68.8% of the total variation in species morphology (Appendix B). PC1 described a gradient that reflected differences in morphological traits associated with locomotion, such as body size and shape, and fin dimensions. Species with positive scores on PC1 had relatively deep and laterally compressed bodies and short snouts (e.g., sunfishes and heroine and cichlasomatine cichlids). Negative values on PC1 were associated with large mouths and large dorsal and anal fins, features possessed by *Cichla* spp. and *Crenicichla lugubris* (Cichlidae), as well as *Micropterus* spp. and *Pomoxis* spp. (Centrarchidae). PC2 was strongly influenced by traits directly involved with feeding such as head height, eye diameter, eye position, and snout length. Species with large positive scores on PC2 had relatively long and dorso-ventrally compressed heads (e.g., *Crenicichla* spp.), short snouts, and terminally to superiorly positioned mouths (e.g., *Apistogramma* spp. and *Biotoecus*). High negative scores on PC2 were associated with relatively large eyes and narrow heads (e.g., *Lepomis* and *Pomoxis* spp.). PC3 and PC4 accounted for 17.2% of morphological variation. PC3 was mostly associated with body shape, fin dimensions, and other traits that directly affect locomotion; species with high positive scores on PC3 had laterally compressed bodies, long dorsal fins, and short snouts (e.g., *Lepomis* spp. and heroine and cichlasomatine cichlids). PC4 described a gradient of traits associated with feeding; species with relatively short heads, long snouts, and highly protrusible jaws (e.g., geophagine cichlids) had high positive scores on PC4.

MANOVA performed on the assemblage PCA coordinates for the four rivers indicated that regional species assemblages occupied significantly different areas within the total perciform morphospace (Wilks's $\lambda = 0.004$, $F = 4.46$, $P < 0.0001$). The Mantel test revealed a significant correlation between ecomorphological structure of local species assemblages and mesohabitat categories ($r = 0.10$, $P = 0.04$).

Ecomorphological dispersion within perciform assemblages

Interregional comparisons.—Results from comparisons of observed data with randomized data from the null model indicated nonrandom distributions within ecomorphological space of perciform assemblages for each of the four rivers when data for all mesohabitat types were combined (Fig. 2). Most observed data were above the upper 95% confidence interval for random data, and Fisher's summation χ^2 analysis yielded statistically significant differences for nearly all comparisons (Table 1). Assemblages of all four rivers had mean nearest-neighbor distances (NND) that were significantly greater than predicted at random. The mean distance to the assemblage centroid (CD) also was significantly greater than the random prediction for each river. The standard deviation of NND was significantly greater than the random prediction for every river except the Tambopata ($P = 0.06$), which indicates that species dispersion within assemblage ecomorphological space was less even than expected by chance in those three rivers.
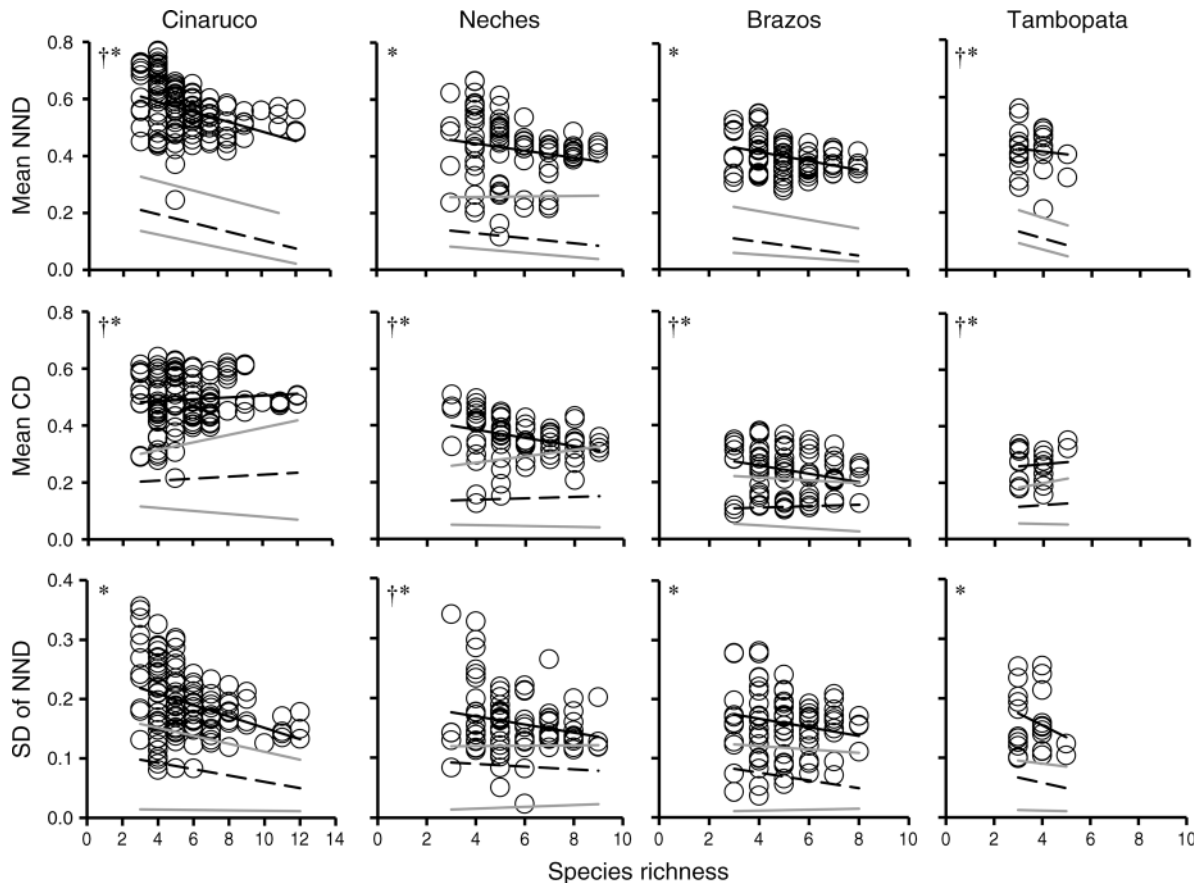
Fig. 2. Values of three morphological dispersion indices (mean and standard deviation [SD] of nearest-neighbor distance [NND], and mean distance to centroid [CD]) for perciform assemblages in mesohabitats of four floodplain rivers: the Cinaruco and the Tambopata in South America (Peru) and the Neches and the Brazos in North America (USA). Distances between species in the morphospace were plotted as a function of the number of species for every river. Open circles represent observed data, solid lines represent the mean of observed data, dashed lines represent the mean of the randomly generated assemblages, and gray solid lines represent 95% confidence intervals for random assemblages.

* Differences in the means (results from chi-square, χ^2) of observed samples were significantly greater ($P < 0.05$) than random expectation.

† Regression slopes (results from ANCOVA) of observed samples were significantly greater ($P < 0.05$) than random expectation.

Comparisons among mesohabitats within rivers.— Mean NND of most assemblages plotted above the upper 95% confidence interval for the distribution of means from null assemblages drawn at random from the corresponding regional species pool (Fig. 3). Results from Fisher's summation χ^2 indicated that all but one of 20 mesohabitats had assemblages with mean NND values significantly greater than means derived from null

TABLE 1. Results of Fisher's summation χ^2 for differences in indices of ecomorphological dispersion between observed vs. randomly generated perciform fish assemblages from four rivers (nearest-neighbor distance, NND; distance to centroid, CD).

River	Mean NND		Mean CD		SD of NND	
	χ^2 P, obs/ran	Regression slope P	χ^2 P, obs/ran	Regression slope P	χ^2 P, obs/ran	Regression slope P
Cinaruco	0.001	0.02	0.001	0.04	0.001	0.07
Neches	0.008	0.07	0.001	0.01	0.002	0.01
Brazos	0.001	0.34	0.002	0.005	0.02	0.06
Tambopata	0.002	0.02	0.001	0.03	0.06	0.17

Notes: ANCOVA was used to test for statistical significance of differences between regression slopes of observed vs. random (obs/ran) assemblages for ecomorphological indices as a function of species richness. Data for local assemblages from diverse mesohabitats in both channel and floodplain lake macrohabitats were pooled for each river. The Cinaruco and the Tambopata are located in South America (Peru), and the Neches and the Brazos are found in North America (USA).
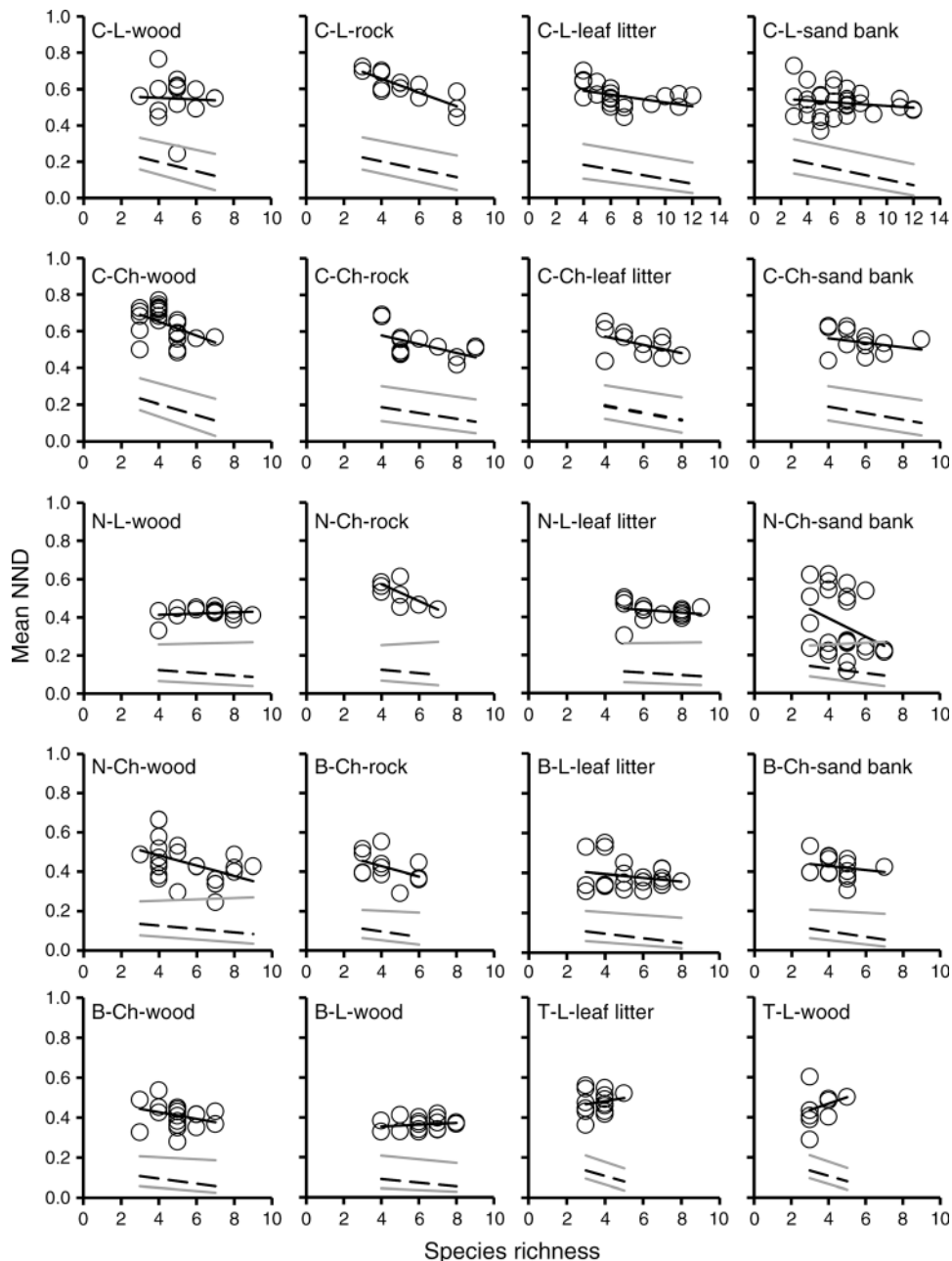
Fig. 3. Observed and simulated mean nearest-neighbor distance (NND) in perciform assemblages (river, macrohabitat, and mesohabitat) inhabiting local mesohabitats in four floodplain rivers. Abbreviations for the rivers are: C, Cinaruco; N, Neches; B, Brazos; and T, Tambopata. Abbreviations for the macrohabitats are: L, floodplain lake; and Ch, river channel. Distances between species in the morphospace were plotted as a function of number of species for every mesohabitat type. Open circles represent observed data, solid lines represent the mean of observed data, dashed lines represent the mean of the randomly generated assemblages, and gray solid lines represent 95% confidence intervals for random assemblages.

model randomizations (Table 2), which means that species were less similar within local assemblages than expected by chance.

The mean distance to the assemblage centroid was significantly greater than expected at random for all eight mesohabitats of the Cinaruco, for wood patches of the Tambopata floodplain lake, and for sand bank patches in the channel of the Neches, but not for any of the Brazos and the remaining mesohabitats in the Neches (Fig. 4, Table 2). Mean CD values were smaller for centrarchid assemblages (ranging from 0.33–0.41 in the Neches and 0.19–0.31 in Brazos) when compared with cichlids (ranging from 0.42–0.57 in the Cinaruco).

TABLE 2. Results of Fisher's summation χ^2 for combined probabilities for significance of differences between ecomorphological indices for observed vs. randomly generated samples from each of 20 perciform assemblages surveyed in mesohabitats of tropical and temperate floodplain rivers.

River and macrohabitat	Mesohabitat category	Mean NND		Mean CD		SD of NND	
		χ^2 P, obs/ran	Regression slope P	χ^2 P, obs/ran	Regression slope P	χ^2 P, obs/ran	Regression slope P
Cinaruco							
Floodplain lake	wood	<0.001	0.33	<0.001	0.19	0.10	0.15
Floodplain lake	rocks	<0.001	0.009	<0.001	0.22	0.10	0.03
Floodplain lake	leaf litter	<0.001	0.02	0.05	0.98	0.02	0.14
Floodplain lake	sand bank	<0.001	0.001	0.01	0.19	0.05	0.04
Channel	wood	<0.001	0.17	<0.001	0.42	0.01	0.62
Channel	rocks	<0.001	0.02	<0.001	0.02	0.001	0.01
Channel	leaf litter	<0.001	0.04	0.01	0.66	0.01	0.28
Channel	sand bank	<0.001	0.58	0.01	0.78	0.02	0.26
Neches							
Floodplain lake	wood	<0.001	0.88	0.50	0.77	0.90	0.73
Channel	rocks	<0.001	0.11	0.10	0.12	0.01	0.09
Floodplain lake	leaf litter	<0.001	0.12	0.90	0.69	0.90	0.53
Channel	sand bank	0.99	0.05	<0.001	0.07	0.90	0.84
Channel	wood	0.05	0.03	0.90	0.24	0.90	0.02
Brazos							
Channel	rocks	<0.001	0.001	0.97	0.88	0.50	0.04
Floodplain lake	leaf litter	<0.001	0.001	0.97	0.29	0.97	0.03
Channel	sand bank	<0.001	0.001	0.50	0.21	0.90	0.59
Channel	wood	<0.001	0.03	0.97	0.53	0.50	0.21
Floodplain lake	wood	<0.001	0.001	0.97	0.73	0.90	0.01
Tambopata							
Floodplain lake	leaf litter	<0.001	0.68	0.50	0.66	0.90	0.52
Floodplain lake	wood	<0.001	0.61	<0.001	0.51	0.90	0.69

Note: ANCOVA tested for statistical significance of differences between regression slopes of observed vs. random assemblages for ecomorphological indices as a function of species richness.

Evenness of species dispersion in morphospace varied according to habitat type. In the Cinaruco, six of eight mesohabitats had assemblages less evenly dispersed within morphospace than expected at random (i.e., observed SD of NND was significantly greater than expected at random; Table 2). In the two temperate rivers, only 1 of 10 mesohabitats (Neches channel rock shoals) revealed dispersion of species within morphospace that was less even than expected at random (Fig. 5, Table 2). Species dispersion within assemblage morphospace in the two mesohabitats of the Tambopata was not significantly different than predicted at random (Table 2).

Ecomorphological similarity in relation to local species richness

Interregional comparisons.—Linear regressions were calculated for each of the morphological dispersion metrics in relation to local assemblage richness (species coexisting within a mesohabitat), and slopes for observed vs. randomized data were compared (Fig. 2, Table 1; Appendix D). For mean NND, the Cinaruco and Tambopata had negative slopes that were significantly steeper than expect at random, the Neches and Brazos had negative slopes, but not significantly different from random. For mean CD, regression slopes for all four rivers were significant greater than expected

at random. Slopes for the Brazos and Neches were more negative than those of the two tropical rivers. The regression slope for SD of NND for the Neches was the only one that was significantly different (greater) than expected at random.

Comparisons among mesohabitats within rivers.— Regression slopes for mean NND in relation to species richness within mesohabitats of floodplain lakes were low and negative with the exception of the Tambopata (Fig. 3; Appendix E). Mesohabitats in the river channel of the Cinaruco, Neches, and Brazos Rivers showed a general pattern of lower morphological similarity with increasing species richness of local assemblages within patches (Fig. 3), but this relationship was only statistically significant for leaf litter and rock shoal mesohabitats in floodplain lakes of the Cinaruco, and submerged wood and rock shoal mesohabitats in the channel of the Neches (Appendix E). Slopes of regressions for observed data were not significantly lower than slopes from random data in 8 of 20 cases (Table 2).

Regression slopes of mean CD were low and positive for cichlid assemblages in mesohabitats of the Cinaruco River (Fig. 4; Appendix E), but low and negative for assemblages in mesohabitats of the Tambopata floodplain lake and for centrarchids in most mesohabitats of the two temperate rivers. Among the 20 cases in which
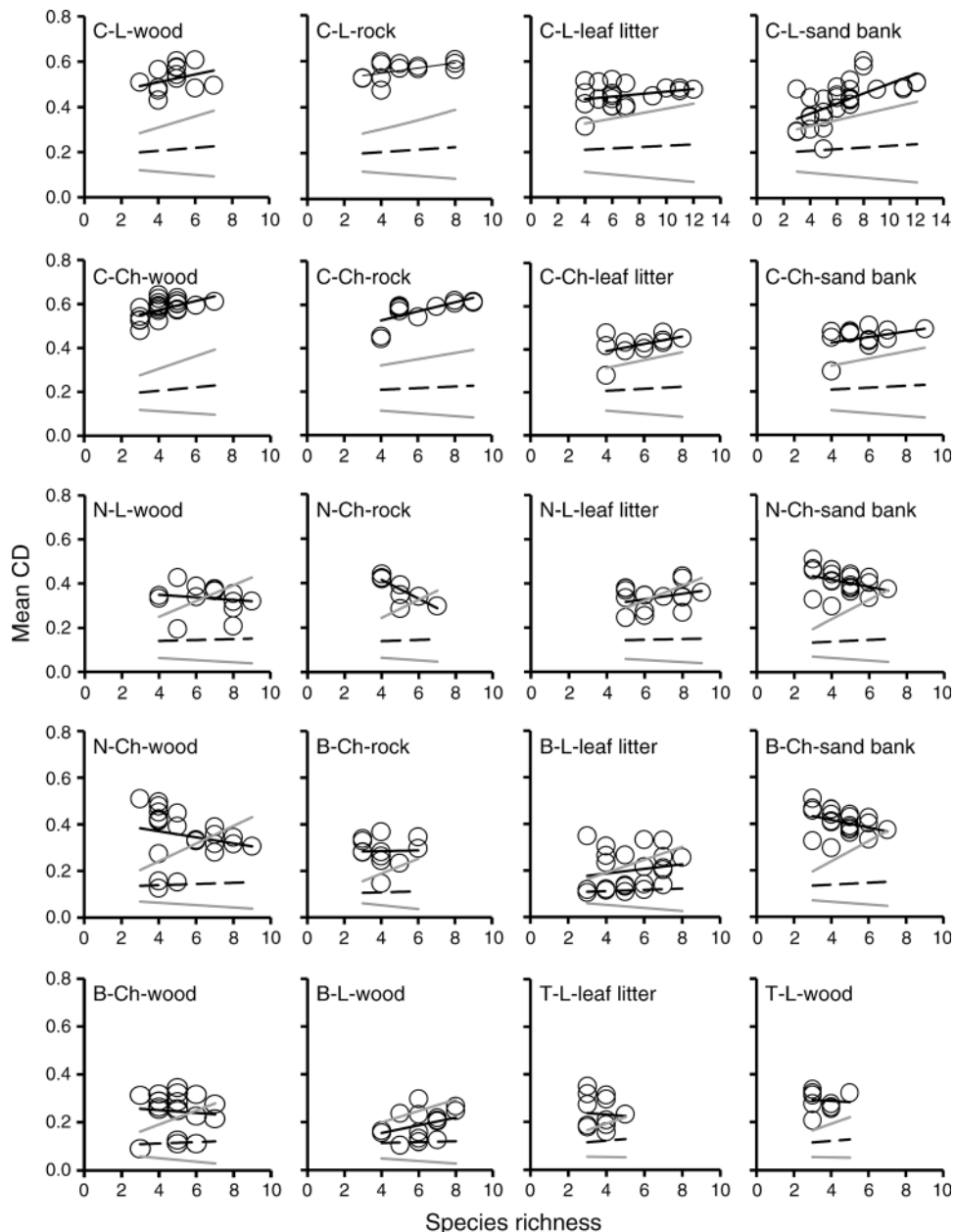
Fig. 4. Observed and simulated mean distance to centroid in perciform assemblages inhabiting local mesohabitats in floodplain lakes and river channels of the Cinaruco, Tambopata, Neches, and Brazos rivers. See Fig. 3 for clarification of the assemblages. Open circles represent observed data, solid lines represent the mean of observed data, dashed lines represent the mean of the randomly generated assemblages, and gray solid lines represent 95% confidence intervals for random assemblages.

the observed regression slope was compared with the regression slope based on random data, only one (Cinaruco channel rock shoal) was significantly different (Table 2).

The general trend was for the SD of NND to remain relatively constant or decline in relation to higher species richness (Table 2), but the regression was statistically significant only for rock shoal habitats in floodplain lakes of the Cinaruco and submerged wood in the channel of the Neches (Appendix E). Regression slopes

for observed data were significantly different than regression slopes for random data in 7 of 20 cases, and each of these had more negative slopes than the regression from random data (Table 2; Appendix E). This indicates that species within local assemblages in these mesohabitats were more evenly dispersed within morphospace than expected at random. Three of these mesohabitats were in the Cinaruco River, two were in the Neches River, and two were in the Brazos River.
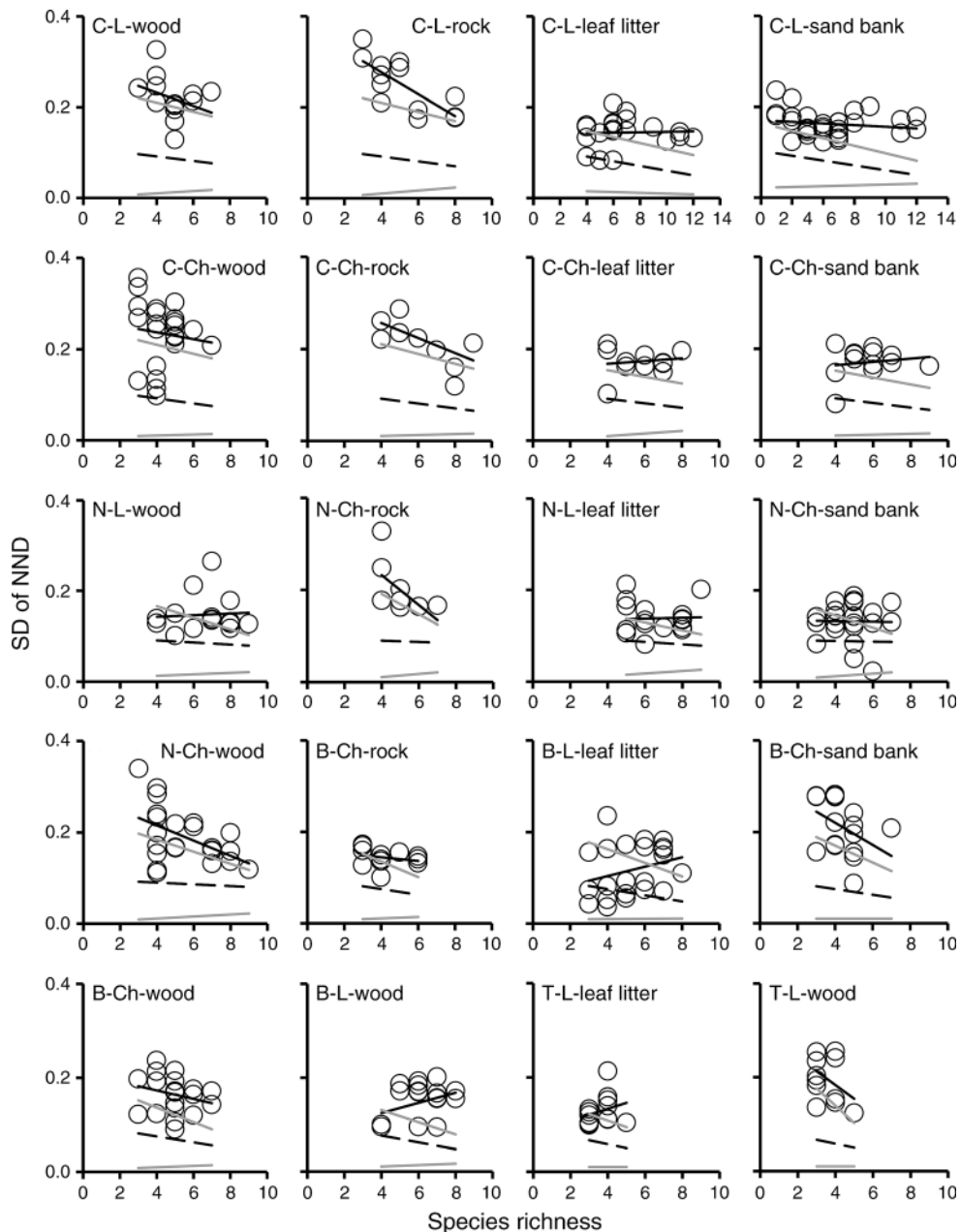
FIG. 5. Observed and simulated standard deviation of nearest-neighbor distance in perciform assemblages inhabiting local mesohabitats in the Cinaruco, Tambopata, Neches, and Brazos Rivers. See Fig. 3 for clarification of the assemblages. Open circles represent observed data, solid lines represent the mean of observed data, dashed lines represent the mean of the randomly generated assemblages, and gray solid lines represent 95% confidence intervals for random assemblages.

DISCUSSION

Environmental filtering or limiting similarity? Among-region comparisons

Both cichlids and centrarchids are common in floodplain lakes and low-velocity habitats within river channels, and they frequently are associated with structurally complex mesohabitats. These two perciform lineages have species that are convergent in many aspects of functional morphology and trophic ecology (Montaña and Winemiller 2013). The distribution of functional traits in these assemblages should reflect modes of maneuvering and feeding within similar habitats. Given findings from an earlier study that found a strong inverse relationship between latitude and the morphospace occupied by river fish assemblages from similar macrohabitats (Winemiller 1991), we expected to see greater centroid distances among

tropical cichlid assemblages than temperate centrarchid assemblages when the same mesohabitats of lowland rivers were compared. The morphospace (average CD) was larger for species-rich cichlid assemblages of the Cinaruco River in Venezuela, but the species-poor cichlid assemblages of the Tambopata floodplain lake in Peru did not have larger morphospaces than centrarchid assemblages. Certain ecomorphotypes among the Neotropical cichlids, such as elongate piscivores (*Crenicichla* spp.) and dwarf invertivores (*Apistogramma* and *Biotoecus* spp.), were absent from the centrarchid assemblages. If we can assume that our morphological traits determine performance, then morphological space serves as a proxy for niche space, and species-rich cichlid assemblages are more ecologically diverse than temperate centrarchid assemblages, as well as cichlid assemblages in regions with low diversity.

In addition to revealing differences in evolutionary niche diversification, interregional comparisons of assemblage functional traits also reflect the influence of environmental filtering. For example, the absence of molluscivorous cichlids in the Cinaruco and Tambopata Rivers is explained by the absence of mollusks, which, in turn, is explained by low water hardness in these rivers (Montaña and Winemiller 2013). The apparent absence of cichlids in the Tambopata River channel can be explained by high concentrations of suspended sediments that made the water turbid, which impairs visually mediated activities that are important for cichlids (Lowe-McConnell 1987). Similarly, centrarchid species richness and abundance was higher in littoral habitats of the Neches River channel than the same types of habitat of the Brazos River, suggesting that the high turbidity of the Brazos negatively affects these fishes (Gardner 1981).

Substrate composition and heterogeneity also influences the use of space by species of both groups. For example, dwarf cichlids, including *Apistogramma* spp. and *Crenicichla* aff. *wallacii*, were most common in leaf litter mesohabitats. Geophagine cichlids that winnow small benthic invertebrates and substrate particles within their oropharyngeal chamber (*Geophagus* spp. and *Satanoperca* spp.) were more common on sandbanks. Piscivorous cichlids (*Cichla* spp., *Crenicichla lugubris*) tended to be associated with mesohabitats containing large structures, such as thick branches or rocks. Jepsen et al. (1997) found that three *Cichla* species in the Cinaruco River subdivided habitat and food resources in a manner that indicated niche complementarity.

Centrarchids also were segregated in space according substrate types and water depth. Many sunfishes (*Lepomis* spp.) were captured in shallow areas with submerged leaf litter or submerged wood, whereas larger piscivores, such as *Micropterus* and *Pomoxis* spp., usually occupied areas of the river channel that contained structures with less density and complexity (e.g., tree trunks, large rocks) or lacked structure (sand banks). Habitat segregation by centrarchids in lentic systems has been shown to be associated with

resource availability (Werner 1977, Werner and Hall 1977) and size-dependent threat of predation (Hall and Werner 1977). Thus, even though limiting similarity (niche complementarity) was strongly supported by our analysis at the patch scale (discussed below in *Trait dispersion in relation to species richness at the patch scale: Species packing or assemblage niche expansion?*), findings at broader scales are consistent with the idea that fish functional traits are associated with habitat features that influence not only foraging success but survival (Winemiller et al. 1995, Wood and Bain 1995, Willis et al. 2005, Carlson and Wainright 2010, Montaña and Winemiller 2010). Evenness of species dispersion within assemblage morphospace was not different among the four regions, so this metric provided no insight about factors structuring assemblages at broad scales.

Comparisons among mesohabitat types within macrohabitats and regions

When perciform assemblages were analyzed according to mesohabitat patches of various types within a given macrohabitat, species were significantly overdispersed in all 20 cases (Table 3), which supports the limiting similarity model. Overdispersion of coexisting species based on functional traits is evidence that species interactions, competition in particular, influence community assembly (Weiher et al. 1998). The size of the morphospace of cichlid assemblages on patches was greater than expected at random for all eight mesohabitat types examined in the Cinaruco River, and one (submerged wood) of two mesohabitat types that were examined in the Tambopata floodplain lake. In contrast, the morphospace of centrarchid assemblages was not significantly greater than expected at random for 9 of 10 mesohabitat types examined in the two temperate rivers (Table 3). Thus, overdispersion of cichlids within morphospace at the patch scale was accomplished, in part, by expansion of assemblage morphospace (addition of more divergent morphologies). Centrarchid assemblages at the patch scale were significantly overdispersed, but without having a total assemblage morphospace significantly greater than expected by chance. None of the 20 cases revealed species dispersion patterns that were significantly more or less even than expected at random (Table 3); therefore, the evenness metric was not informative.

Body size and shape variation have long been considered to play an important role in niche partitioning (Brown and Wilson 1956, Hutchinson 1959). In our study, body size and features of the mouth accounted for much of the interspecific morphological variation in cichlids and centrarchids, suggesting that trophic niche differentiation plays a role in species coexistence (Werner 1977, Werner and Hall 1977, Mittelbach 1984, Winemiller et al. 1995, Jepsen et al. 1997, Montaña and Winemiller 2009). If competition indeed shapes the structure of local species assemblages during low-water periods, morphological differences among coexisting species that reflect niche partitioning (niche

TABLE 3. Summary of nonrandom ecomorphological patterns of perciform assemblages within mesohabitats and macrohabitats of four rivers from temperate and tropical regions.

| River and macrohabitat | Mesohabitat category | Nearest-neighbor distance | | Size of morphospace | | Greater evenness |
		Packed	Overdispersed	No difference	Expansion	
Cinaruco						
Floodplain lake	wood		√		√	
Floodplain lake	leaf litter		√		√	
Floodplain lake	rocks		√		√	
Floodplain lake	sand bank		√		√	
Channel	wood		√		√	
Channel	leaf litter		√		√	
Channel	rocks		√		√	
Channel	sand bank		√		√	
Tambopata						
Floodplain lake	leaf litter		√	√		
Floodplain lake	wood		√		√	
Neches						
Floodplain lake	wood		√	√		
Channel	rocks		√	√		
Floodplain lake	leaf litter		√	√		
Channel	sand bank		√	√		
Channel	wood		√	√		
Brazos						
Channel	rocks		√	√		
Floodplain lake	leaf litter		√	√		
Channel	sand bank		√	√		
Channel	wood		√	√		
Floodplain lake	wood		√	√		
Number of cases		0	20	11	9	0

Note: A check mark (√) indicates support for the pattern.

complementarity) would be expected (Ricklefs and Miles 1994). For example, *Cichla* and *Crenicichla* species, piscivores that co-occur in many habitats in the Cinaruco River, plot within the same region of cichlid morphospace, but *Crencichla* have more elongate bodies, and *Cichla* have larger mouth gapes and body sizes. Competition among these piscivores likely intensifies during the latter stages of the annual low-water period when densities of prey fishes are greatly reduced by predation mortality (Montaña et al. 2011). Among centrarchids, *Micropterus salmoides*, *Lepomis cyanellus*, and *L. macrochirus* coexist in diverse habitats throughout much of North America. These species differ in morphology and body size, and dietary segregation occurs largely on the basis of prey size (Werner 1977, Werner and Hall 1977). *Micropterus salmoides* is more piscivorous than the two sunfishes, *L. macrochirus* consumes mostly small aquatic invertebrates, but occasionally small fishes, and *L. cyanellus* is a generalist that consumes both invertebrates and fishes at sizes smaller than those consumed by *Micropterus* and larger than those consumed by *L. macrochirus* (Werner 1977, Montaña and Winemiller 2013).

Trait dispersion in relation to species richness at the patch scale: Species packing or assemblage niche expansion?

Several mechanisms could allow a given habitat patch to support more species. If population densities are reduced by predation or disturbance, the ratio of resource demand/supply could be sufficiently low such that competition is no longer a limiting factor for species coexistence. In this case, the total assemblage morphospace might be constant with species more crowded (underdispersed) within it (Fig. 1). On the other hand, if resource demand/supply is high enough to cause competition, the available niche space may be subdivided as new species are added (Pianka 1974). In this case, higher species richness might be associated with a constant assemblage morphospace and a more even dispersion of species within it. Alternatively, species that can exploit different kinds of resources, or the same resources but in novel ways, may be added to the habitat, and this case, the assemblage morphospace (niche space) would expand while species similarity remains unchanged (Fig. 1; Ricklefs and Travis 1980, Winemiller 1991).

When regression slopes of morphological indices vs. assemblage species richness were compared between real and random assemblages of mesohabitat types within macrohabitats, only one case among 20 revealed significant assemblage morphospace expansion (Table 4). Five cases revealed greater packing of species within assemblage mophospace than predicted at random as species richness increased, and seven cases revealed less species packing than predicted at random (Table 4). Thus, our findings at the scale of the local habitat patch are not consistent with those from analyses of morphology in

TABLE 4. Summary of support for alternative ecomorphological patterns in relation to species richness of perciform assemblages within mesohabitat patches in tropical and temperate rivers.

River and macrohabitat	Mesohabitat category	Nearest-neighbor distance		Size of morphospace		Greater evenness
		Packed	Overdispersed	No difference	Expansion	
Cinaruco						
Floodplain lake	wood			√		
Floodplain lake	leaf litter		√	√		
Floodplain lake	rocks	√		√		√
Floodplain lake	sand bank		√	√		√
Channel	wood			√		
Channel	leaf litter		√	√		
Channel	rocks	√			√	√
Channel	sand bank			√		
Tambopata						
Floodplain lake	leaf litter			√		
Floodplain lake	wood			√		
Neches						
Floodplain lake	wood			√		
Channel	rocks	√		√		√
Floodplain lake	leaf litter			√		
Channel	sand bank		√	√		√
Channel	wood			√		√
Brazos						
Channel	rocks	√		√		√
Floodplain lake	leaf litter		√	√		
Channel	sand bank		√	√		
Channel	wood	√		√		
Floodplain lake	wood		√	√		√
Number of cases		5	7	19	1	8

Notes: When the regression for mean nearest-neighbor distance (NND) had a statistically lower slope than expected at random, species packing with high niche overlap is supported (average similarity increases with species richness); if the regression slope has a significantly higher slope than expected at random, then limiting similarity is supported. When the regression slope of mean distance to the assemblage centroid (CD) was significantly higher than expected at random, greater species richness was associated with expansion of assemblage morphospace. Increased evenness of species dispersion within ecomorphological space with increasing species richness was supported by a negative trend in standard deviation of NND with a regression slope lower than expected at random. A check mark (√) indicates support for the pattern.

freshwater fish (Winemiller 1991) and bird communities (Ricklefs and Travis 1980, Travis and Ricklefs 1983) made at much larger spatial scales (e.g., stream reaches, forests, islands) in which species tended to join the periphery of morphological space as species richness increased and species morphological similarity remained relatively constant. It is important to note that these earlier studies conducted at broader spatial scales also compared patterns among more diverse taxa, and they did not use null models to determine whether or not the trends were significantly different from trends expected at random. In 8 of 20 cases, more species-rich cichlid and centrarchid assemblages had greater evenness of species dispersion within assemblage morphospace (Table 3), a pattern suggesting that species interactions play a role. One reason why significant trends in relation to species richness were not observed at the patch scale is that these local species assemblages were influenced by biotic interactions, irrespective of species richness in the local patch. In other words, mesohabitat patches could have been supporting the maximum possible number of cichlids and centrarchids during the low-water period when fish densities are highest. A high degree of mesohabitat patch saturation would be inferred from

the significant overdispersion that was found in every case (Tables 1–3). It would be informative to repeat this study at the same sites when water levels are sustained at high levels. We predict that local assemblages may be more randomly assembled, or responsive to environmental filtering under high-water conditions of expanded aquatic habitat and reduced per-unit-area fish densities. Arrington et al. (2005) determined that fish assemblages in littoral zones of the Cinaruco River are more strongly structured during the low-water period and less structured during the periods of rising and falling water levels. Other studies in the tropics have shown that seasonal hydrology (Cox Fernandes 1999) and diel periodicity (Arrington and Winemiller 2003) can influence fish assemblage structure at the local scale.

Conclusions

Adaptive diversification over evolutionary time and environmental filtering in the short term both appear to influence the structure of perciform assemblages in rivers when comparisons are across regional scales. For example, Alfermann and Miranda (2013) found that land cover, water depth, and primary productivity influenced centrarchid assemblages of 53 lakes in

floodplains of the lower Mississippi River. Patterns of morphological trait dispersion suggest that biotic interactions are more influential in tropical cichlid assemblages with high species richness than temperate centrarchid assemblages. This conclusion is in general agreement with findings from other studies of fish assemblages in lowland rivers in tropical (Rodriguez and Lewis 1997, Willis et al. 2005, Arrington and Winemiller 2006) and temperate (Tonn et al. 1990, Winemiller et al. 2000) regions. At the local scale of the mesohabitat patch, strong patterns of species over-dispersion within morphospace support the hypothesis that biotic interactions influence community assembly during low-water periods when fish densities are highest. Our results contrast with those from recent morphological analyses of estuarine fish assemblages that inferred a dominant role for environmental filtering with little evidence of limiting similarity at the local scale (Mouchet et al. 2012). Morphological trends in relation to species richness within mesohabitat patches were not consistent, with some cases inferring greater species packing in morphospace, some indicating less species packing, and some indicating neither. This result, together with the significant overdispersion of species within assemblage morphospace observed overall at the patch scale, suggests that mesohabitats in lowland rivers tend to be saturated with these perciform fishes during low-water phases of the hydrological cycle.

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Supplemental Material

Appendix A

Cichlid and centrarchid species used in this study (*Ecological Archives* M084-005-A1).

Appendix B

Morphological variable loadings for PC axes 1–4 from analysis of 19 cichlids from the Cinaruco River, 7 cichlids from the Tambopata floodplain lake, 12 centrarchids from the Neches River, and 11 centrarchids from the Brazos River (*Ecological Archives* M084-005-A2).

Appendix C

Ranges of species richness for perciform fish assemblages within mesohabitats in two macrohabitats of four floodplain rivers (*Ecological Archives* M084-005-A3).

Appendix D

Slopes of regressions and coefficient of determination of observed and randomized data for three indices of morphological dispersion in relation to number of species in local species assemblages across all mesohabitat types (*Ecological Archives* M084-005-A4).

Appendix E

Simple linear regressions, coefficient of determination for observed and random data, slope values for observed and random data, and P values resulting from t test analysis between observed and random analysis in the regression slopes of the three measures of morphological dispersion of cichlids and centrarchids in relation to species richness (*Ecological Archives* M084-005-A5).

Supplement

Sampler, a program for computing geometric properties of random samples (*Ecological Archives* M084-005-S1).