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Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river

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Abstract High species richness and evenness in structurally complex habitats has been hypothesized to be associated with niche partitioning. To test this idea, relationships between habitat structural complexity in river littoral-zone habitats and morphological diversity of tropical fishes were examined in the Cinaruco River, Venezuela. Six habitat attributes were quantified in 45 sites spanning a range of structural complexity. Fishes were collected during day and night to estimate species density and relative abundances at each site. Twenty-two morphological variables were measured for each species. Principal components analysis (PCA) of physical habitat data yielded two axes that modeled >80% of variation across sites. The first two axes from PCA of fish morphological variables modeled >70% of variation. Species density during both day and night was negatively associated with flow velocity and positively associated with habitat complexity. Similarity of day and night samples from the same site was significantly greater for sites with high habitat complexity and low flow. In general, mean local assemblage morphological PC scores were not significantly associated with habitat PC scores. Average, maximum, and standard deviation of morphological Euclidean distances of local assemblages revealed positive associations with structural complexity and negative associations with flow. These relationships held even when the positive relationship of species density was statistically removed from assemblage mor-

phological patterns. Findings suggest that both species niche compression and assemblage niche space increase when habitat complexity is greater and flow velocity is lower in this tropical lowland river.

Keywords Ecomorphology · Littoral zone · Niche diversification · Orinoco river · Species density

Introduction

The influence of habitat heterogeneity on species richness is well appreciated (Huston 1994; Rosenzweig 1995), but the relationship between habitat structural complexity and density of species exhibiting different ecological characteristics has received comparatively little attention. In a classic study, MacArthur and MacArthur (1961) demonstrated that bird species richness and diversity were significantly correlated with foliage height diversity in North American forests. Habitat structural complexity influences many ecological interactions, including foraging efficiency and species coexistence (MacArthur and MacArthur 1961; Werner and Hall 1976; Vitt et al. 1997), predation rates (Huffaker 1958; Savino and Stein 1982; Flebbe and Dolloff 1995) and social interactions (Brown 1971; Anholt 1990; Petren and Case 1998). Thus, structural complexity of habitats has the ability to influence ecological interactions and community dynamics. For example, Menge and Sutherland's (1976) conceptual model of intertidal community dynamics assumed that total niche space increases with habitat complexity. Similarly, Schlosser's (1987) model of fish communities in streams predicted higher species density and niche diversity in habitats with greater structural complexity. Several aquatic studies, from coral reefs to temperate streams, have found significant associations of assemblage diversity with measures of habitat complexity or heterogeneity (Risk 1972; Gorman and Karr 1978; Luckhurst and Luckhurst 1978; Carpenter et al. 1981; Roberts and Ormond 1987; McCormick 1994).

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Because the ecological niche is composed of many dimensions, direct estimation of community niche relationships is a daunting challenge even for species-poor systems. Morphological traits that effect ecological performance can be employed as surrogates for niche attributes (Wainwright and Reilly 1994), and assemblage morphological traits have been used extensively to examine community structure (e.g., Findley 1976; Ricklefs and Travis 1980; Ricklefs et al. 1981; Miles and Ricklefs 1984). Keast and Webb (1966) described the association of morphological characters and ecological habits in fishes, and several studies have proposed that morphology is a good predictor of assemblage structure in both temperate (Gatz 1979a, 1979b; Page and Swofford 1984; Wood and Bain 1995) and tropical freshwater systems (Watson and Balon 1984; Winemiller 1991a). Following an approach first developed by Findley (1973, 1976), the relative size of the interspecific morphological space has been used to infer niche diversity in fish assemblages, and niche partitioning has been inferred from patterns of species dispersion within total niche space (Douglas 1987; Winemiller 1991a; Douglas and Matthews 1992; Winemiller et al. 1995). Of course, the strength of this inference depends on the strength of form/function and function/ecological performance relationships.

Here, we examine the relationship between habitat structural complexity and the taxonomic and morphological structure of fish assemblages in the littoral zone of a lowland tropical river. Recent studies of fish assemblages in the littoral zone of tropical rivers inferred random species associations (Jepsen 1997; Saint-Paul et al. 2000). In contrast, studies of piscivorous cichlids in South America (Jepsen et al. 1997) and Africa (Winemiller 1991b) revealed species-specific habitat associations and resource partitioning. Arrington (2002) reported predictable species associations among habitat classifications in the littoral zone of the Cinaruco River, Venezuela. D. A. Arrington et al. (unpublished) experimentally demonstrated that species density in littoral habitats of the Cinaruco River was determined by the structural complexity of constructed habitat patches and their distance from natural habitats with high complexity. To further investigate relationships between habitat structural complexity, species density and assemblage structure, the present study examines morphological patterns in fish assemblages of the littoral zone of the Cinaruco River, a tributary of the Orinoco River in southwestern Venezuela.

Materials and methods

The study was conducted in a section of the Cinaruco River in the llanos (plains) of Apure state, Venezuela, at approximately 6°33'N and 67°24'W. The Cinaruco is a low-gradient, nutrient-poor, species-rich (>280 fish species) river that is seasonally inundated due to rains in the associated catchment and impedance of discharge by floodwaters of the mainstem Orinoco River into which it flows. During the rainy season of May through Sep-

tember, the fringing gallery forest and extensive sections of the llanos are flooded, providing an important allochthonous source of nutrients for aquatic production (Jepsen et al. 1997).

Fieldwork was conducted during a 2-week interval of January 2002, which corresponds to the annual period of water recession. Forty-five survey sites located along the shoreline of the main channel or connected lagoons were chosen to represent a range of littoral habitats with variable degrees of structural complexity (e.g., open sandbanks, rocky outcroppings, woody debris, leaf litter). Aquatic macrophytes were essentially absent from the river system during the period fieldwork was conducted, but a few small emergent saplings were present at some sites.

Habitat complexity measurement

At each survey site, a 1-m² quadrat was outlined by driving four metal rods, each attached by 1 m of steel chain to two adjacent rods, into the substrate. Sites were located within 3 m of the shoreline at depths between 0.3 and 1.0 m. These shallow depths allowed visual estimation of structural density throughout the entire water column (see method below). Five variables were measured to quantify habitat complexity: current velocity, structural density, rugosity, porosity of the substrate, and substrate diversity. Water depth was measured and included in the analysis as an indicator of habitat volume (since area was constant). These variables were examined to account for different dimensions of complexity in the habitat. Previous studies have found that multiple variables were more strongly correlated with fish diversity than single variables (Gorman and Karr 1978) and stressed that each variable quantifies slightly different aspects of surface topography (McCormick 1994). Use of quantification rather than classification variables provides better precision and signal-to-noise ratios (Kaufman et al. 1999).

A single depth measurement was made in the center of the quadrat using a tape measure. The current velocity was measured using a General Oceanics mechanical flowmeter. Our estimate of structural density was similar to MacArthur and MacArthur's (1961) measure of foliage height diversity for terrestrial habitats. A white 1×1 m board marked with 10-cm² grids was placed along one side of the quadrat. The percent of the board blocked from sight by vertical structures (rocks, woody debris, stems of partially submerged saplings) was estimated from the opposite side of the quadrat. Estimates were made with the aid of a diving mask and snorkel. Only the submerged portion of the board was used to determine the percent of area blocked. Structural density measurements were taken in both horizontal dimensions of each quadrat, and the average of the two measurements was analyzed.

Rugosity (Risk 1972) was measured by first holding the end of a thin brass chain on one side of the quadrat, then allowing the chain to sink while released in a straight

line to the other side. As it was released, the chain was conformed by hand to the contour of the substrate and any structure present (i.e. rocks, woody debris). The distance between the two opposing sides of the quadrat was noted, and the length of chain conforming to the contour along this transect was measured using a tape measure. Two measures of rugosity were taken in each quadrat in both horizontal dimensions, each beginning at the middle of one side of the quadrat and ending at the middle on the other. For each quadrat, the two rugosity measures were averaged together for analysis.

Substrate porosity was measured by placing 2 l of substrate into a graduated container. The 2 l sample was collected from the top 5 cm of substrate. The container was then filled with water up to the 2 l mark, thereby filling the interstitial spaces in the substrate sample. The water and substrate were then emptied into a sieve, and the water was collected in a graduated cylinder. The amount of water collected in the cylinder provided an estimate of the volume of interstitial space in the substrate.

Substrate diversity was measured by estimating the percent cover of the number of substrate types in the quadrat. Substrate categories were defined as bedrock, clay, silt, sand, leaf litter, gravel (<0.5 cm diameter), pebble (0.5–3 cm), cobble (3–25 cm), large object [boulder (>25 cm) or log], fine roots or woody debris, and freshwater sponge. Percentage values were then used to calculate a diversity index according to the Shannon-Wiener formula, $-p_i (\log_{10} p_i)$ where p_i is the proportional abundance of substrate i , for each substrate category (Krebs 1989).

Collection of habitat occupants

Fishes were collected using a 2×1 m seine net with a 0.5-cm diameter mesh size. Daytime collections were made on 1 day, and nighttime collections were made on 2 days, following measurement of habitat complexity. For each collection, a single seine haul was made from approximately 4 m from the shore up to the shore and passing over the 1-m² quadrat. In a few instances, the seine leadline snagged on obstructions and a subsequent haul was made. During day collections, the seine haul was made slightly right of center of the quadrat, and during night collections hauls were slightly left of center. When present in the quadrat, woody debris was surrounded with the seine and kicked to capture hiding and sedentary fishes following the initial seine haul, and all material was restored afterwards. Fishes were preserved in 10% formalin and transferred to 70% ethanol for storage. In the laboratory, specimens were identified to species when possible, or otherwise cataloged by genus. Species abundances were recorded for each sample.

Morphological data

Morphological measurements were made using digital calipers and ocular micrometry, depending on the size of

the specimen. Following the criteria described by Winemiller (1991a), the following 21 features were measured: (1) maximum standard length (max-sl), (2) maximum body depth (body-d), (3) maximum body width (body-w), (4) caudal peduncle length (ped-l), (5) caudal peduncle depth (ped-d), (6) caudal peduncle width (ped-w), (7) body depth below midline (bdbm), (8) head length (head-l), (9) head depth (head-d), (10) eye position (eye-p), (11) eye diameter (eye-d), (12) mouth gape in the vertical dimension (gape), (13) snout length (snt-l), (14) dorsal fin height (dor-h), (15) dorsal fin length (dor-l), (16) pectoral fin length (pec-l), (17) caudal fin length (cau-l), (18) caudal fin height (cau-h), (19) pelvic fin length (pel-l), (20) anal fin height (ana-h), (21) and anal fin length (ana-l). Additionally, the variable mouth position (mou-p) was measured by quantifying the angle between an imaginary line connecting the tips of the open jaws and an imaginary line running between the center of the pupil and the posterior-most vertebra (e.g., 90° representing a terminal mouth). Among the 22 measured variables, the measured values of 20 variables were converted to proportions of standard length, body depth, body width, or head length following Winemiller (1991a). In this manner, variables were descriptors of body and fin shape without the influence of body size. Use of proportions can introduce allometric bias into shape analysis, but allometric influences should be negligible in interspecific comparisons in which a single size class is chosen to represent a given species (Winemiller 1991a). In addition to the 21 shape elements, max-sl was included in multivariate analyses as a descriptor of body size that was independent of our shape variables. Morphological measurements were made on between one and three specimens of each species collected, depending on availability [Appendix A (Electronic Supplementary Material)]. Without exception, each species was represented by a fairly uniform size distribution (conspecifics collected from shallow littoral habitats were either all adults or all juveniles).

Statistical analyses

Habitat data distributions were examined with a one-sample Kolmogorov-Smirnov (K-S) test of normality using the statistics software package SPSS 11.0 for Windows. A correlation matrix was calculated for the six habitat variables using SPSS to examine interrelationships. Principal components analysis (PCA) using the correlation matrix was conducted on the habitat variables using CANOCO for Windows version 4.0 (ter Braak and Smilauer 1998) to create several composite habitat complexity variables. Data were log transformed to improve normality. PC axes were interpreted as gradients of overall habitat complexity (Meffe and Sheldon 1988). PCA provided a score for each survey site on each multivariate habitat complexity axis. Multi-metric composite indices are desirable because they have greater precision and explanatory power compared to their individual component metrics (Kaufman et al. 1999).

Log-transformed morphological data were also analyzed with PCA (correlation matrix) using CANOCO to create several composite morphological gradients and values for each species on these multivariate axes. The average and standard deviation (SD) of the morphological values (scores on the first two PC axes) were calculated for the assemblage of species at each site. The average value for the assemblage was interpreted as an indicator of the relative position of the assemblage along the morphological gradients, whereas the standard deviation was interpreted as an indicator of morphological variation within the assemblage (i.e. morphological space occupied). Additionally, a matrix of Euclidean morphological distances for all species pairs was calculated from the first four morphological PC axes. For each site, a submatrix of species pairs occupying that site was compiled, and the average, SD, and maximum Euclidean morphological distances in each local assemblage were recorded. Following previous studies (i.e. Findley 1973; Ricklefs et al. 1981; Winemiller 1991a) average Euclidean distance is interpreted as an index of the degree of morphological separation within the assemblage, SD of Euclidean distances indicates the relative evenness of species packing or dispersion (lower SD indicating greater evenness), and maximum Euclidean distance indicates the degree of morphological separation between the two most disparate members of the local assemblage.

Associations among habitat values and assemblage variables were examined via standard linear regression using Microsoft Excel XP Professional. Because morphological variation (SD of assemblage mean morphological Euclidean distances) was positively correlated with species density, we also examined the linear relationship between habitat complexity and residual values from the regression of morphology SD against species density (thus factoring out the influence of species density). Similarity of the relative abundances of species in day and night assemblages was examined using Sorensen's index of similarity, also calculated using Microsoft Excel. Comparisons between day versus night and lagoon versus channel assemblage morphologies were analyzed via paired non-parametric multivariate tests (Multi-response permutation procedures, MRPP) using PC-ORD version 4 (McCune and Mefford 1997).

Results

Sites sampled spanned a range of values for each habitat variable (Table 1). The K-S test revealed that the distribution of habitat data, with the exception of depth and substrate diversity ($p > 0.2$), was significantly different from normal ($p < 0.03$). Consequently, Spearman's correlation analysis was conducted on these data. Several structural variables were significantly correlated, with moderate to strong correlations occurring between depth and rugosity, structural density and rugosity, structural density and substrate diversity, and rugosity and substrate diversity (Table 2).

The first and second axes from PCA of habitat data modeled 60% and 21% of variation, respectively (eigenvalues 0.604 and 0.207). The first axis was negatively associated with water velocity, and positively associated with structural variables (Table 3). The second PC axis described a gradient of sites with lower values of all variables versus sites with higher values (Table 3). Thus, the first axis described a habitat gradient in which structural complexity is negatively associated with water velocity, and the second axis described a gradient in which structural complexity is positively associated with water velocity.

Day and night samples from the 45 sites yielded 19,255 fish specimens, representing six orders, 22 families, 65 genera, and 99 species. These data conformed to a standard species abundance curve with few abundant species and many rare species [Appendix A (Electronic Supplementary Material)]. Individual sites yielded between 1 and 31 species. One channel site could not be sampled during the night because the water depth at that location had fallen to < 15 cm during the preceding 48 h. Overall, day and night samples from the same habitat had high taxonomic similarity, with 50% of Sorensen's similarity values > 0.50 (Fig. 1a). Assemblage day/night similarity was significantly positively corre-

Table 1 Averages and ranges of habitat complexity variables recorded in channel and lagoon littoral-zone habitats (substrate diversity values range from 0 to 1.0)

	Depth (cm)	Velocity (m/s)	Density (%)	Rugosity (cm)	Porosity (ml)	Substrate diversity
Channel						
Average	37.1	0.078	11.9	123.8	227.4	0.2
Range	17–74	0–0.24	0–65	101–318	2–1,100	0–0.6
Lagoon						
Average	53.1	0.008	20.0	150.7	567.9	0.3
Range	22–80	0–0.03	0–75	102–322	25–1750	0–0.7

Table 2 Matrix of Spearman's correlation coefficients for habitat variables. Correlations > 0.4 were considered moderate to strong

	Depth	Velocity	Density	Rugosity	Porosity
Depth					
Current velocity	–0.35*				
Structural density	0.38**	–0.38*			
Rugosity	0.45**	–0.37*	0.87**		
Porosity	0.03	–0.39**	0.28	0.30*	
Substrate diversity	0.32*	–0.29	0.53**	0.47**	0.35*

* $p < 0.05$; ** $p < 0.01$

Table 3 Habitat-complexity PCA axis 1 (modeling 60% variation) and axis 2 (21% variation) eigenvectors

	Axis 1	Axis 2
Depth	0.382	–0.150
Current velocity	–0.930	–0.367
Structural density	0.656	–0.617
Rugosity	0.451	–0.404
Porosity	0.564	–0.423
Substrate diversity	0.389	–0.177

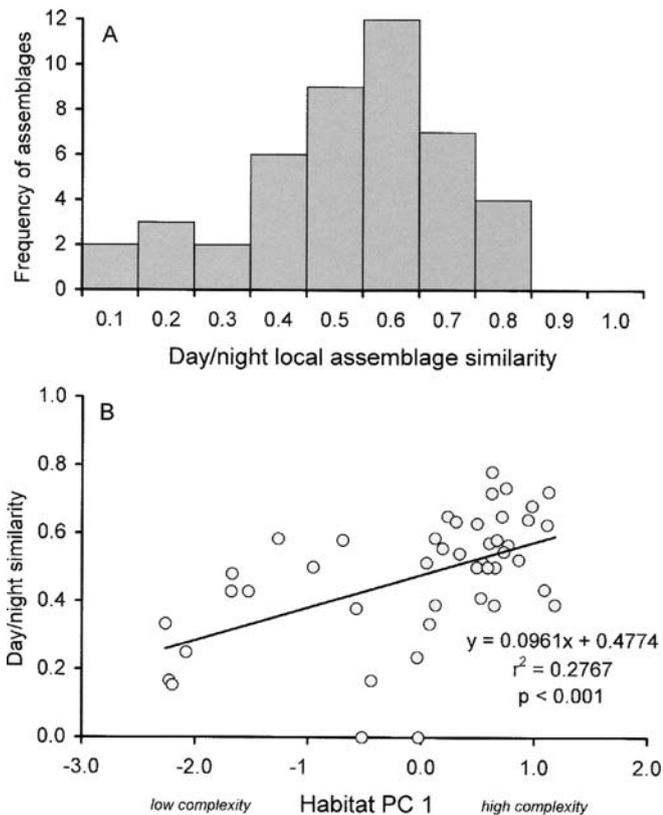


Fig. 1 a Frequency histogram of Sorensen's similarity index values for samples collected at the same site during day and night; b *Biplot* showing positive association between habitat structural complexity (higher scores on PC1 indicate higher complexity) and day/night similarity of fish assemblages

lated with habitat structural complexity as indexed by habitat PC axis 1 (Fig. 1b). Based on linear regression, species density was positively associated with high complexity habitats (higher PCA axis-1 scores) and inversely with flow velocity during both day ($R^2=0.35$, $p < 0.0001$) and night ($R^2=0.17$, $p < 0.005$).

The first two axes from PCA performed on morphological data with the entire fauna modeled 53% and 38% of variation (eigenvalues 0.520 and 0.379), respectively. The first axis ordered species along a gradient strongly influenced by snout and caudal peduncle length, mouth orientation, and body depth. The second axis indicated a morphological gradient strongly influenced by body length, dorsal and anal fin height, eye diameter, and caudal peduncle and mouth depth. A plot of species scores on these two PC axes (Fig. 2a) revealed that this analysis was dominated by three loricariid catfish species, with all other species grouped tightly near the axes origins. The three loricariid species were extreme outliers with highly elongate bodies and ventral mouths.

Because loricariids were uncommon in the dataset (total individuals = 6), a second PCA was performed on the morphological dataset without the three loricariid species. The goal of this analysis also was to expand the separation of species in assemblage morphological space. The second PCA of morphological data yielded a dom-

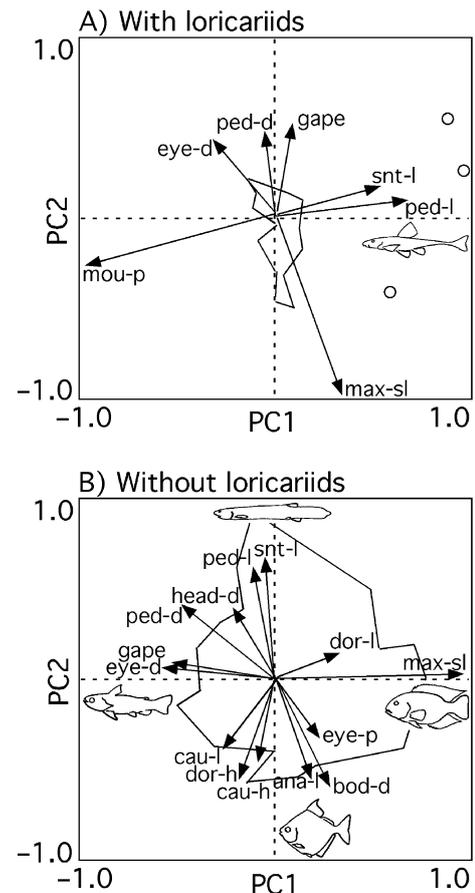


Fig. 2 Eigenvector loadings on the first two PCA axes based on species values for 22 morphological variables based on analysis a with and b without three uncommon loricariid species. Full variable names are listed in Materials and methods. Vector directions/lengths represent eigenvectors of morphological variables for each axis. Species representing morphological extremes in each dimension are illustrated (a: *Rineloricaria* sp.; b: top = *Ochmacanthus alternus*, right = *Hoplarchus psittacus*, bottom = *Metynnys argenteus*, left = *Tatia concolor*)

inant axis that modeled 71% (eigenvalue 0.718) of the total variation, and a second axis that modeled 9% (eigenvalue 0.093) of total morphological variation (Table 4). The analysis without loricariids yielded a broader and more even distribution of species scores on the first two axes, and the two gradients described by these axes were largely switched (Fig. 2b). Maximum body length was strongly associated with PC axis 1 (Table 4, Fig. 2b). Because shape elements were ratios (except for mou-p which was an angle) and therefore independent of body sizes of individual specimens, this body-size gradient was derived solely from interspecific differences. Thus, high scores on axis 1 were associated with large cichlids with relatively deep bodies, large eyes, etc., and low scores were associated with small characids and catfishes with relatively elongate bodies, small eyes, etc. (Table 4 and Fig. 2b). Because it achieved a greater dispersion of species based on a more even influence by a greater number of morphological variables, results from the second PCA of morphological data that excluded the

three rare loricariid species were used for all subsequent tests of association with habitat complexity.

For day and night data separately, linear regressions were performed on the average morphology of local assemblages (centroids based on morphology PCA axis 1 or 2 scores) versus corresponding habitat features (as indicated by habitat PCA axis 1 or 2 scores). Only one of eight relationships (average morphology axis 2 vs habitat axis 2 at night) was statistically significant ($R^2=0.23$, $p<0.001$). These regressions indicate that, overall, assemblage morphological centroids did not vary systematically with level of habitat complexity and current velocity.

Average morphological Euclidean distance between species in local assemblages was significantly correlated with habitat complexity and flow (as indicated by habitat PCA axis 1) for both the day and night datasets (Fig. 3). The positive slopes of these regressions indicate greater between-species morphological separation in habitats with less flow and greater complexity. Average between-species morphological distance was not significantly correlated with the second habitat PCA axis for either day ($R^2=0.01$, $p=0.60$) or night ($R^2=0.03$, $p=0.25$). The SD of the morphological Euclidean distances of local assemblages was weakly but significantly and positively correlated with habitat PCA axis 1 for both the day and night datasets (Fig. 3). Again, this indicates more variable (skewed) spacing of species in assemblage morphological space in habitats with less flow and greater complexity. SD of morphological distance was weakly and significantly correlated with the second habitat PCA axis for night ($R^2=0.14$, $p<0.025$), but not significantly correlated for day samples ($R^2=0.001$, $p=0.89$). The maximum morphological Euclidean dis-

tance of local assemblages was weakly but significantly correlated with habitat PCA axis 1 for both the day and night datasets (Fig. 3), which suggests more extreme morphologies are present in habitats with less flow and greater complexity. Maximum morphological distance was significantly correlated with the second habitat PCA axis for night ($R^2=0.165$, $p<0.01$), but not for day samples ($R^2=0.001$, $p=0.96$).

Regressions of the average, SD, and maximum morphological Euclidean distances versus species density yielded statistically significant weak (average distance) or moderate (SD, maximum) positive relationships (Fig. 4). Thus, relationships between assemblage morphological patterns and habitat features could be biased by a positive relationship between species density and habitat complexity, because more complex habitats with lower flow apparently support more species. To eliminate the potential influence of species density on morphological attributes, the residuals were computed from regressions between the average, SD, and maximum morphological Euclidean distances for day and night datasets. These residuals for local assemblages were regressed against habitat PCA axis 1 scores for corresponding sites. Linear relationships between morphology and habitat PC1 were positive (indicating greater average, SD and maximum morphological distance with increasing habitat complexity and decreasing flow) and statistically significant (except for average distance for day samples), but weaker than the relationships revealed using untransformed data. (Fig. 5).

Multi-response permutation procedures paired-sample tests were performed to investigate significant differences between average morphological characteristics of fish assemblages (assemblage morphological centroids and occupied morphological space) in day versus night collections, and channel versus lagoon mesohabitats. In general, MRPP tests revealed no differences in assemblage morphologies of habitats between day and night collections. One exception was a diel change in the morphological centroid of lagoon habitats ($A=0.02$, $p=0.02$). In contrast, a change between the morphological centroid and morphological space occupied between channel and lagoon habitats was observed to be marginally significant ($A=0.04$, $p=0.05$) and highly significant ($A=0.0009$, $p<0.00001$), respectively. These correlations were more significant when day and night collections were considered together than when considered separately (e.g. $A=0.097$ and $p=0.0001$ for SD of night collections in lagoon habitats).

Habitat structural complexity and flow velocity are inversely correlated (Tables 2 and 3). High flow areas in the main river channel have shifting sand substrates and relatively little deposition of organic materials. Woody debris and leaf litter accumulate in low flow areas, especially lagoons. Thus, the analysis of habitat structural complexity is constrained by the strong association between complexity and flow when viewed across the entire spectrum of river-floodplain habitats. To control for the effect of flow, analyses were repeated with only

Table 4 Morphology PCA axis 1 (modeling 71% variation), axis 2 (9%), axis 3 (6%) and axis 4 (4.5%) eigenvectors based on the dataset that excluded three rare loricariid species

	Axis 1	Axis 2	Axis 3	Axis 4
Maximum standard length	0.999	0.013	0.031	-0.007
Mouth position	-0.001	-0.898	0.388	-0.162
Body depth	0.219	-0.546	-0.683	-0.209
Body width	-0.124	-0.022	-0.369	-0.250
Caudal peduncle length	-0.075	0.509	0.237	0.152
Head length	-0.001	-0.229	-0.476	-0.634
Eye position	0.252	-0.289	-0.746	-0.389
Dorsal fin height	-0.073	-0.453	-0.192	-0.162
Dorsal fin length	0.286	0.108	-0.601	-0.639
Pectoral fin length	-0.117	-0.013	-0.568	-0.417
Caudal fin length	-0.221	-0.382	-0.336	-0.457
Caudal fin height	-0.151	-0.529	-0.176	-0.121
Pelvic fin length	0.135	-0.057	-0.486	-0.654
Anal fin height	-0.047	-0.310	-0.491	-0.346
Anal fin length	0.166	-0.516	-0.363	0.385
Caudal peduncle depth	-0.376	0.354	0.480	-0.566
Body depth below midline	-0.205	0.039	-0.054	0.099
Head depth	-0.144	0.292	0.020	-0.408
Mouth gape	-0.426	0.110	0.178	-0.085
Caudal peduncle width	-0.139	0.064	0.241	-0.359
Eye diameter	-0.456	0.107	0.488	0.004
Snout length	-0.045	0.570	0.531	-0.185

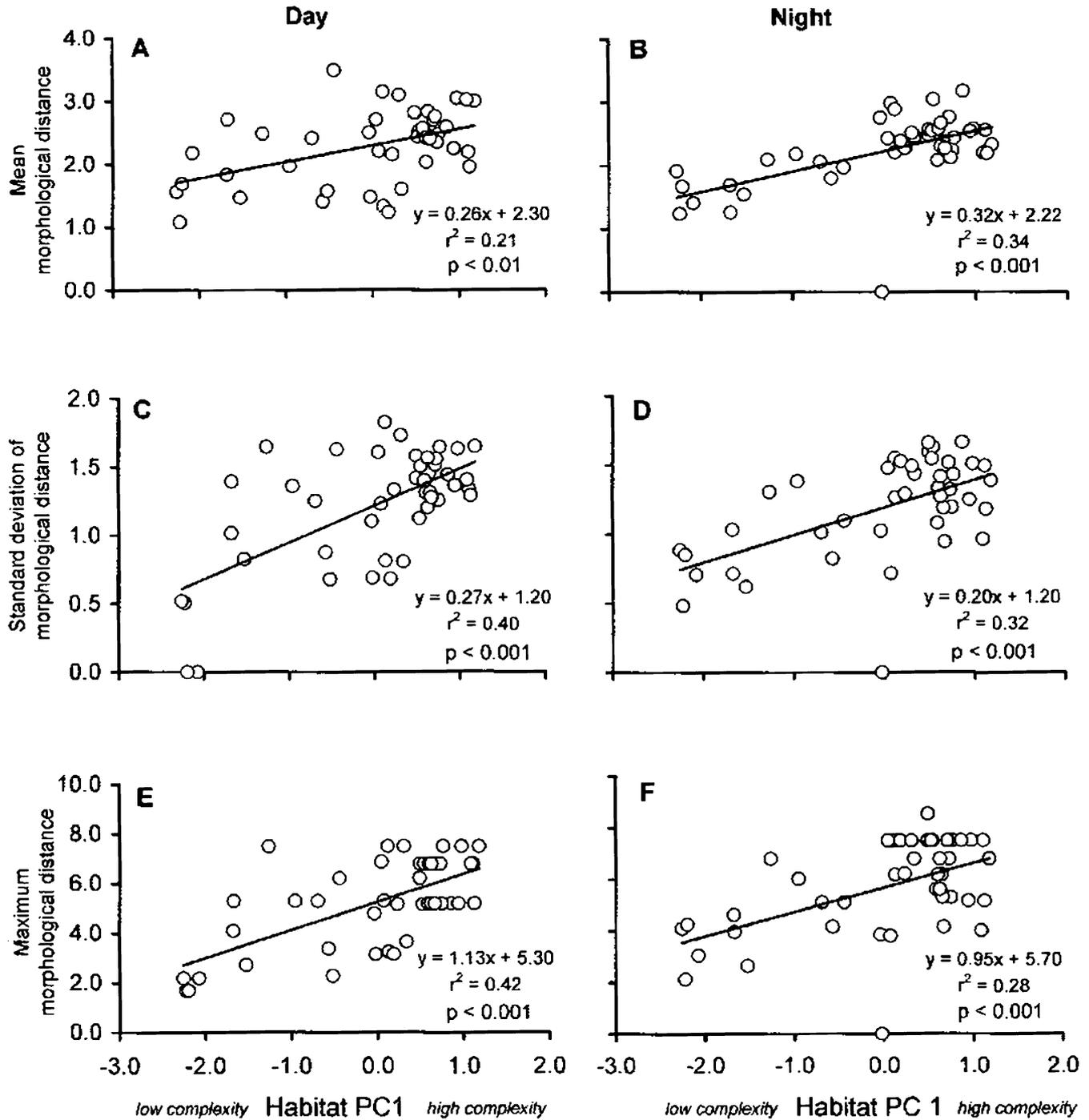


Fig. 3 Biplots showing the positive relationship between habitat complexity (higher scores on habitat PC1 indicate greater complexity) and mean pair-wise morphological Euclidean distance based on **a, b** morphology PCA 1–4 scores, **c, d** SD of pair-wise morphological distance, and **e, f** maximum pair-wise morphological distance

the lagoon sites in which there was no flow during the dry season ($n=28$). With flow eliminated as a variable, the correlations (for both day and night samples) between mean morphological distance, SD of morphological distance, and maximum morphological distance with habitat PCA axis 1 were not statistically significant ($p=0.18$ – 0.82) and extremely weak ($R^2=0.002$ – 0.07). When assemblage morphological values were transformed as residuals from regressions with species density

(to control for the influence of species density), the six correlations with habitat PCA axis 1 were slightly stronger but not statistically significant at $\alpha=0.05$ (day samples: mean distance $R^2=0.12$, SD distance $R^2=0.09$, maximum distance $R^2=0.09$; night samples: mean distance $R^2=0.14$, SD distance $R^2=0.02$, maximum distance $R^2=0.01$). Regression slopes were negative in every case, mostly under the influence of a single outlier (a site with very low habitat complexity).

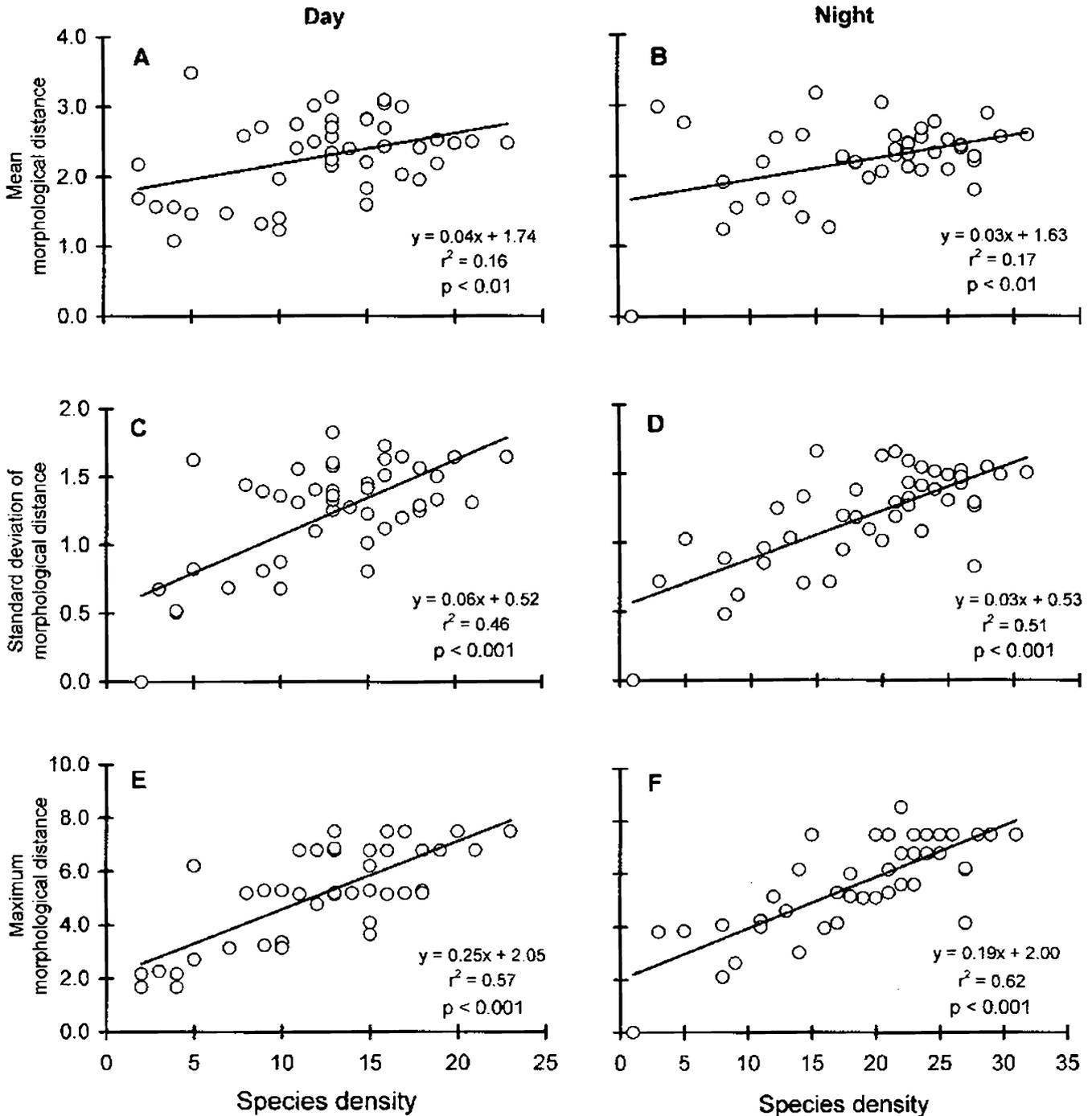


Fig. 4 Biplots showing the positive relationship between species density and mean pair-wise morphological Euclidean distance based on a, b morphology PCA 1–4 scores, c, d SD of pair-wise morphological distance, and e, f maximum pair-wise morphological distance

Discussion

Flow and structural complexity

Morphological variation and spacing of species within the morphology space of local fish assemblages were greater in habitats of the Cinaruco River with greater structural complexity and lower flow, physical features that strongly co-varied. Most structured sites in the main

channel were located where the current slows and woody debris and leaf litter accumulate. Submerged structures in fluvial habitats also block water flow and promote accumulation of debris that further increases habitat complexity. Flow reduction also promotes particle sorting during sedimentation and greater substrate diversity. Studies that have examined fish-habitat associations in temperate floodplain rivers (e.g., Meffe and Sheldon 1988) have found patterns of water velocity and struc-

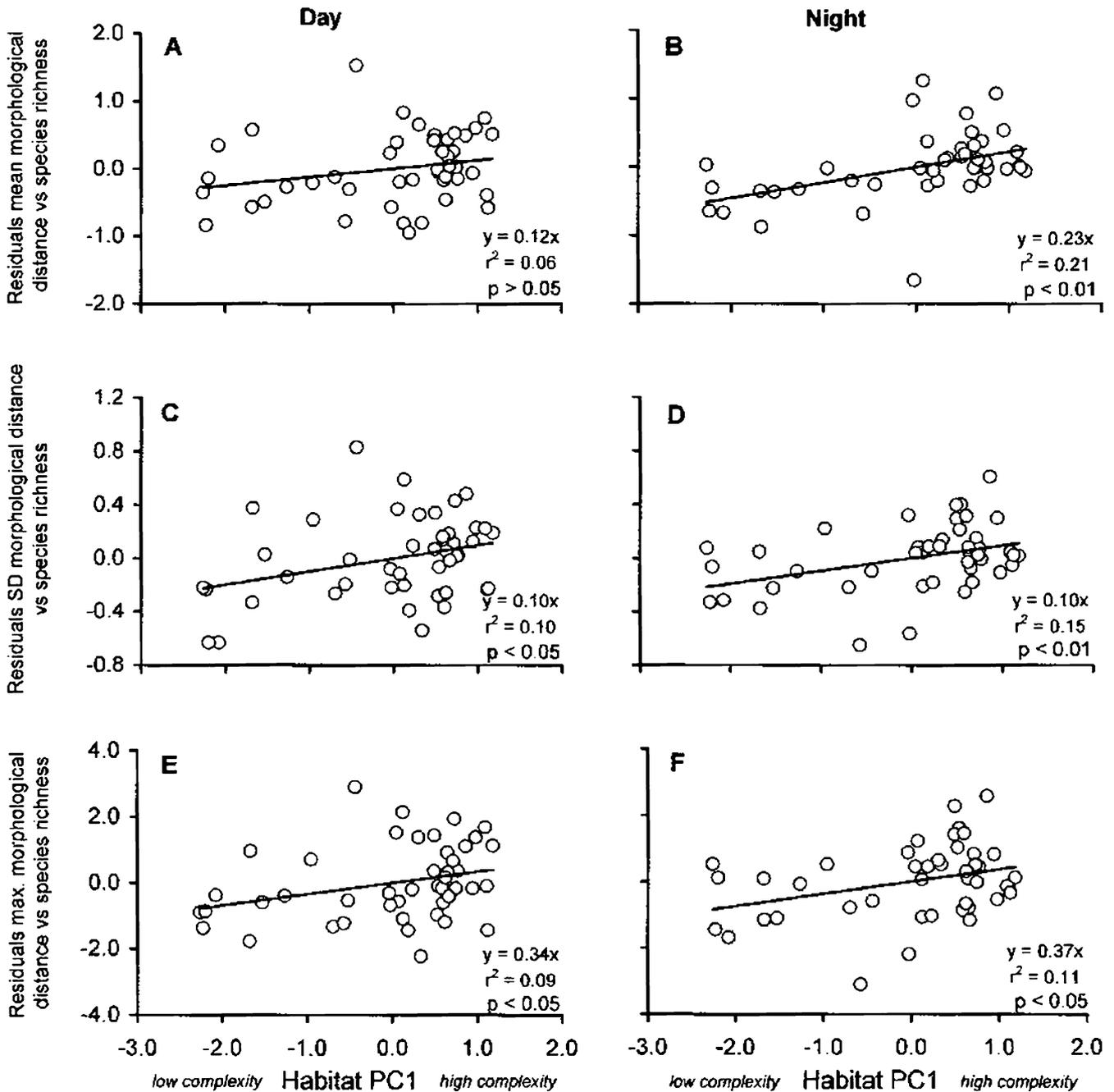


Fig. 5 Biplots showing the positive relationship between habitat complexity (higher scores on habitat PC1 indicate greater com-

plexity) and average morphological distance corrected for species richness (i.e. residual of mean pair-wise morphological Euclidean distance based on **a, b** morphology PCA 1–4 scores regressed against species richness), **c, d** SD of pair-wise morphological

tural complexity similar to those described here for the Cinaruco River. Flow velocity was relatively low at all of the channel littoral sites we surveyed (Table 1). Lagoon habitats lack flow during the low-water season when our study was conducted. During the peak of the annual flood season, water often flows through lagoons where littoral areas accumulate woody debris and leaf litter from densely forested riparian areas.

Habitat structural complexity is difficult to estimate, and biological correlates of complexity depend heavily

on identification of biologically relevant scales of measurement (McCormick 1994). In fast-flowing streams, current velocity introduces an element of physical complexity that influences fishes' use of aquatic habitats both horizontally and vertically (Wood and Bain 1995). Most stream researchers have assumed current velocity to be a form of "structure", and have incorporated velocity as a contributing variable in habitat complexity indices (e.g., Gorman and Karr 1978). In contrast to high-gradient streams for which structural complexity has often been

based on discrete meso-habitat categories (e.g., pools, riffles, runs), floodplain river habitats span a broad three-dimensional continuum (Meffe and Sheldon 1988). Thus, it may not be appropriate to view flow as an element of habitat complexity in all, or even most, habitats of lowland floodplain rivers. Again, our findings reveal an inverse relationship between flow and structural complexity to which fishes respond based, in part, on their morphology.

The only means to eliminate flow as a confounding variable was to examine fish morphology–habitat relationships based on the 28 lagoon sites that lacked flow. This analysis resulted in weak and statistically non-significant relationships, suggesting that water velocity may be a key variable driving patterns of morphological variation in local fish assemblages. For two reasons, this conclusion is not necessarily correct. First, the lagoon sites almost all had relatively high structural complexity so that a narrow range of complexity levels was available for analysis. Low-complexity open sandbank sites are relatively uncommon in lagoons. Second, a single low-complexity lagoon site was associated with a low mean, SD, and maximum morphological distance between species, which was consistent with the trend in the full dataset that included both channel and lagoon sites.

Another line of evidence suggests that complexity, not flow, was the primary habitat feature influencing the morphological structure of fish assemblages. If low current velocity was the principal factor influencing high assemblage morphological diversity, then areas with high flow should have been dominated by streamlined body forms. However, habitat PCA axis 1 (flow having the highest loading) was not significantly correlated with average species scores on morphology PCA axis 1 or 2 for either day or night samples (p values from 0.31 to 0.90). Thus, there was no general tendency toward a particular morphology in habitats with faster flow and lower structural complexity. Yet, there was a strong tendency for assemblages to be more morphologically diverse, with species spaced further apart, when flow was low and habitat complexity was high. Since, low-flow, high-complexity habitats also contained more species ($R^2_{\text{day}} = 0.36$, $p < 0.0001$; $R^2_{\text{day}} = 0.17$, $p < 0.01$), it seems likely that morphological diversity in structurally complex habitats is associated with ecological factors not directly related to current velocity.

Habitat complexity and ecological interactions

Several ecological phenomena could promote greater morphological diversity. Littoral habitats containing woody debris and leaf litter might support higher primary and secondary productivity, thereby affording fishes greater foraging opportunities on more varied substrates. The dominant substrate in the river channel is open sand substrate. In areas with water current, sand substrates are unstable and support relatively sparse biomass of algae and invertebrates (K.O. Winemiller, D.L. Roelke, J.V.

Montoya, unpublished data). In contrast, submerged woody debris and leaves often support visible periphyton growth and moderate populations of mayflies and prawns (Arrington 2002). Structurally complex habitats also have more surface area to support benthic production. Angermeier and Karr (1984) manipulated woody debris in a temperate stream and found that treatments with woody debris contained more aquatic invertebrates and fishes with greater fish species density than areas without woody debris. They concluded that woody debris mainly benefits fishes in terms of cover/camouflage rather than enhancement of food supply or protection from strong currents. Yet abundant and diverse resources on diverse substrates would also allow fishes to exploit food resources in a variety of ways. For example, small invertivorous doradid and auchenipterid catfishes enter holes and cracks in wood both for protection and for feeding on invertebrates. Omnivorous anostomids are long and slender with supraterritorial mouths that allow them to feed on the underside of sticks. Cichlids and characids of different sizes and body shapes move with agility in and around snags and leaf litter.

Under conditions of resource limitation, habitats with high structural complexity could facilitate species coexistence via niche partitioning (Hugueny 1990). In this scenario, each individual should exploit those food resources and microhabitats for which its morphology and physiology confer a competitive advantage (e.g. Werner and Hall 1976). Thus, greater species packing would be possible in habitats with greater structural complexity. Regressions of habitat PCA axis-1 scores with the average, SD, and maximum morphological distances within sites suggest that both niche compression and segregation could be associated with greater habitat complexity. Numerous morphological characters of fishes have known functions that influence ecological performance, such as swimming speed and maneuverability (e.g., relative body depth, fin aspect ratios, caudal peduncle depth), or feeding from different regions of the water column (e.g., mouth and eye position, body depth above midline) (Keast and Webb 1966; Gatz 1979b; Webb 1984; Wood and Bain 1995). Thus, ecological diversity in species assemblages in a habitat can be coarsely inferred from the size of the morphological space (Douglas 1987; Winemiller 1991a; Douglas and Matthews 1992). In the Cinarucu River, correlations were observed between species density, the diversity of morphological traits, and habitat structural complexity. This agrees with findings from studies of fish assemblage structure in streams of West Africa (Hugueny 1990) and French Guiana (Mérigoux et al. 1998), and is generally consistent with Schlosser's (1987) conceptual model for streams. Microhabitat or resources are likely used in a greater number and variety of ways in sites with higher complexity and lower flow. Of course this hypothesis is based on patterns derived from analysis of 22 morphological traits, and many unexamined traits (e.g., dentition, pharyngeal apparatus, gut anatomy) would be directly associated with resource exploitation (e.g., foraging). Assemblage morphological

centroids were not significantly correlated with habitat complexity and flow, which suggests that local assemblages of fishes do not systematically shift toward different means of using space, locomotion, and/or resources in relation to habitat complexity and flow (as observed, for example, in high elevation, hill stream fishes that tend to be benthic and fusiform or elongate).

Structural complexity also can reduce predation mortality (Huffaker 1958). Prey should have more options for hiding and escaping predators in habitats containing more substrates with more variable shapes and sizes. In the Cinaruco River, several small fish species reside inside holes and cracks in submerged logs and sticks (e.g. *Tatia concolor*, *Microglanis poecilus*), and several others move through leaf litter (e.g. *Elacocharax pulcher*, *Brachyhypopomus* sp.). More complex habitats could also reduce visual contact, encounter rates, and aggressive interactions between interference competitors (Petren and Case 1998; Jones et al. 2001).

Complexity and within-site diurnal variation

Similarity of day and night samples was greater in more complex habitats. Arrington and Winemiller (2003) documented the diel assemblage changeover in shallow sandbank habitats of the Cinaruco River. In that study, nocturnal samples contained significantly more individuals (68%) and species (54%) than paired diurnal samples. They found consistent differences in assemblage structure between diurnal and nocturnal samples that were attributed to species-specific habitat use and activity patterns. In the current study, the average number of individuals (273) and species (18.5) collected in night samples were higher than values in day samples (individuals = 155, species = 12.6). Thus, diel changeover with higher species density and abundance at night is corroborated, yet the degree of species replacement was lower in more structurally complex habitats with low flow. Several factors could account for this pattern. At night, many small fishes move into shallow shoreline areas to escape large nocturnal predators (pimelodid catfishes). Copp and Jurajda (1993) found that small fishes in the Morava River, Czech Republic, moved inshore to a much greater extent on shallow banks than steep banks, and they concluded that shallow banks provided a refuge from large nocturnal piscivores. Fishes may have less need to move inshore at night in areas of the Cinaruco River containing more structurally complex habitats. In addition, habitats with high structural complexity may have greater resource stability that results in less frequent movement among these habitats in general. Small fishes in structurally complex habitats may have less need to move offshore for foraging during the daytime.

Conclusion

Arrington (2002) reported predictable associations of species groups among major habitat categories in the

Cinaruco River (sand beaches, rocky shoals, lagoon snags, etc.), and the present study found significant trends in the distribution of morphological features of fishes in habitats with variable levels of structural complexity. Arrington (2002) also reported more regular assemblage patterns in relation to habitat categories during the low-water period than the high-water period of the annual flood cycle of the Cinaruco River. This finding suggests that ecological interactions (with resources, competitors, or predators) drive species patterns of habitat occupancy during the dry season. If true, then associations between fish assemblage structure and habitat complexity should be strongest during the annual low-water season, the period during which the present study was conducted. Fish densities achieve their highest levels within contracted aquatic habitats during the dry season, and non-piscivorous fishes should experience resource limitation, including availability of food and preferred habitats (Lowe-McConnell 1979; Winemiller 1990; Agostinho and Zalewski 1994). Zaret and Rand (1971) reported greater niche compression and habitat segregation among fishes in a Panamanian stream during the dry season. In the Cinaruco River, higher fish species richness in structurally complex habitats with low current velocity is associated with greater morphological diversity, lower average interspecific similarity, and more variable spacing of species in assemblage morphological space. The most likely explanation for these patterns is greater species packing and refuge from predation in more structurally complex habitats.

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