

Local-scale habitat influences morphological diversity of species assemblages of cichlid fishes in a tropical floodplain river

Montaña CG, Winemiller KO. Local-scale habitat influences morphological diversity of species assemblages of cichlid fishes in a tropical floodplain river.

Ecology of Freshwater Fish 2010. © 2010 John Wiley & Sons A/S

Abstract – We examined the taxonomic and morphological diversity of cichlid fish assemblages in a floodplain river in Venezuela during the dry season at two spatial scales: macrohabitats (lagoons, main channels and creeks) and mesohabitats (leaf litter, sand banks, rocky shoals and woody debris). Nonmetric multidimensional scaling did not reveal differences for species assemblages among macro and mesohabitats. The first two axes from canonical correspondence analysis based on 19 species and six physical variables modelled >61% of the taxonomic variation in assemblages from rock shoals and woody debris, and 55% of variation in assemblages from sand banks and leaf litter. Principal components analysis based on 22 morphological variables yielded two dominant axes that explained >86% of variation in the cichlid assemblages. Morphological diversity was analysed to test the idea that assemblage structure is nonrandom, with structurally complex habitats supporting more species with more functional morphological diversity than simple habitats. Average and standard deviation (SD) of the morphological Euclidean distances of local assemblages among mesohabitats tended to decrease or be constant as the number of species increased. Regressions of the average nearest neighbour distance (NND) and SD of NND with species richness resulted in low and negative slopes of species assemblages among mesohabitats. These relationships suggest that when more species are added to a habitat patch, assemblage morphospace remains approximately constant, species average similarity increases and species dispersion in morphological space becomes more uniform. Results support that cichlids partition habitat at the local scale but not at the macrohabitat scale.

C. G. Montaña, K. O. Winemiller

Section of Ecology, Evolution and Systematic Biology, Department of Wildlife & Fisheries Sciences, Texas A&M University, College Station, TX, USA

Key words: Cichlidae; ecomorphology; habitat structure; Neotropics; Venezuela

C. G. Montaña, Section of Ecology, Evolution and Systematic Biology, Department of Wildlife & Fisheries Sciences, Texas A&M University, College Station, TX 77843 2258, USA; e-mail: car1607@tamu.edu

Accepted for publication January 4, 2010

Introduction

Species assemblage organisation is influenced by a large number of ecological factors that operate over multiple spatial scales and proximate to evolutionary time scales (Rosenzweig 1995; Thompson 2009). Multiple spatial scales have been used to interpret patterns of species diversity and assemblage structure (Levin 1992; Huston 1999; Holland et al. 2004). Many large-scale studies have examined patterns of species richness to changes along latitudinal gradients (e.g., Rosenzweig 1995) or analyse the manner in

which environmental conditions influence assemblage composition (e.g., Lowe et al. 2006). In fish assemblages, e.g., longitudinal fluvial gradients typically are associated with an increase in fish species richness with increasing stream sizes (Matthews 1986). Fish assemblage structure in Neotropical floodplain rivers has been interpreted as either random or nonrandom depending on the spatial scale and period of the annual hydrological cycle (Lowe-McConnell 1987; Goulding et al. 1988). In the Rio Negro-Amazon, Goulding et al. (1988) concluded that fish assemblages are essentially random collections of species among

various types of macrohabitats, whereas statistical analysis of fish assemblage structure in the Amazon River (Petry et al. 2003) and floodplain lakes in the Orinoco River (Rodríguez & Lewis 1997) revealed nonrandom associations in relation to physical environmental variables.

As a result of the logistic constraints associated with large spatial scales, most experimental studies have been at local scales. At local scales, assemblage structure is regulated by both abiotic filters (Zobel 1997) and biotic interactions (Jackson et al. 2001) acting simultaneously. Likewise, movements of individuals between habitats can contribute to spatial and temporal variability, and may inflate species richness by adding species that are essentially transient and incapable of permanent colonisation (Southwood 1988). Angermeier & Winston (1998) demonstrated that local fish species richness in temperate streams was better predicted by fish diversity within relatively small regions (e.g., physiographic units within river basins) than by fish diversity in larger regions (e.g., river basin), suggesting that local assemblages are affected by inter-stream connectivity and dispersal. Peres-Neto (2004) found that patterns of fish species co-occurrence in tropical rivers are principally driven by habitat conditions acting as environmental filters. Similarly, Willis et al. (2005) found that greater interspecific morphological diversity in local fish assemblages was associated with more structurally complex habitats in the littoral zone of a tropical floodplain river. Structurally complex habitats can facilitate coexistence of competitors (Janssen et al. 2007) and persistence of predators and their prey (Savino & Stein 1982).

Species coexistence via niche differentiation may be reflected by assemblage-wide patterns among certain morphological traits or trait combinations (MacArthur & Levin 1967; Ricklefs & Miles 1994; Wainwright & Reilly 1994). Niche partitioning among fishes has been inferred from patterns of species dispersion within total assemblage niche space (Winemiller 1991; Douglas & Matthews 1992). The strength of this inference depends on the strength of form-function-fitness relationships. Winemiller (1990) found that tropical fish assemblages exhibit higher levels of niche diversification than those in similar lotic habitats of temperate regions. He suggested that feeding specialisation and diverse patterns of locomotion for exploiting habitats were implicated in the observed patterns.

In this study, we studied fishes belonging to the family Cichlidae to examine spatial patterns of distribution based on two spatial scales in a tropical river: macrohabitats (main channel, lagoon and creek) and mesohabitats (habitats based on substrate types). The family Cichlidae is a species-rich and ecologically diverse group of freshwater fishes inhabiting the

tropical zone (Barlow 2000). This family reveals a particularly high degree of morphological and ecological diversification, with many species often coexisting in Neotropical habitats (Winemiller et al. 1995; López-Fernández et al. 2005). Most species in this family are diurnal and well adapted to transparent clear-water and black-water rivers, and many show habitat use patterns associated with seasonal water-level changes or reproduction (Hoeinghaus et al. 2003). The Cinaruco River in the Venezuelan Llanos contains 19 cichlid species ranging in size from invertivorous dwarf species to large predators. We were interested in identifying ecological patterns of cichlid species assemblages within different habitats of this river. Specifically, we ask: (i) if cichlid spatial distributions and species assemblage structure (fish composition, richness and abundance) are influenced by processes and environmental factors at macro or meso-scales and (ii) if functional diversity of species richness patterns based on morphological traits are correlated at local scales.

Materials and methods

This study was conducted in the Cinaruco River, a meandering low-gradient tributary of the Orinoco River that drains the llanos (savannas) of southern Apure State, Venezuela. The study area is centred at approximately 6°32'N and 67°24'W. The Cinaruco is a moderate blackwater (water colour ranging from 4 to 8 ftu), oligotrophic river, with sandy substrates, low pH (ranging from 4.5 to 6.5), high transparency (ranging from 1.5 to 3 m) and high fish diversity (over 280 fish species identified) (Winemiller et al. 1997; Montoya et al. 2006). The Cinaruco River has a strongly seasonal hydrology with pronounced annual rainy (May–October) and dry seasons (December–April) (Montoya et al. 2006). During the rainy season, the riparian forest and surrounding savannas are flooded, and aquatic organisms disperse widely throughout the river floodplain. The dry season is associated with a continuously falling water level that forces aquatic organisms off the floodplain and into the main river channel and lagoons (Winemiller & Jepsen 1998).

In this study, we identified floodplain lagoons, tributary creeks and the main river channel as the three major macrohabitats within the Cinaruco River. Many floodplain lagoons have permanent surface-water connections to the main channel during the dry season, but others become isolated. The main river channel contains long, broad sand banks that constitute a large portion of the river shoreline during the dry season. Small rocky shoals, leaf packs and submerged branches and tree trunks become important shoreline habitats in the main channel during the dry season when the water-level drops as much as 7 m. Creeks are fringed by

gallery forest and drain water from the floodplain into the main channel and lagoons. Littoral habitats of lagoons and creeks are patch mosaics of sand, leaf litter, submerged vegetation and submerged branches and trees falls (Arrington & Winemiller 2006).

Fieldwork was conducted during the dry season from 13 December 2005 to 8 May 2006. During the dry season, when water levels of the river floodplain descend, we expected to find more fish inhabiting different habitats in the littoral zone because of an overall reduction of habitat and food resource availability (Lowe-McConnell 1987). Cichlid fishes were collected from four lagoons, three creeks and an approximately 20-km stretch of the main channel. Fish samples were collected during the day (07:00–18:00) along the shoreline mesohabitats selected.

Habitat measurements

Within each macrohabitat, four mesohabitat categories were defined based on the substrate composition: sand banks (areas with >95% coarse-sand substrate), woody debris (areas with >95% snags or submerged-wood), rock shoals (areas with >90% covered by rocks) and leaf litter (areas with >90% covered by leaves). Mesohabitats within each of the three macrohabitats were surveyed monthly throughout the study period. At each mesohabitat, three environmental variables were measured: substrate type defined by bedrock, clay, silt, sand, leaf litter and woody debris; water depth; and water velocity. We estimated percent coverage of each substrate category to calculate a substrate diversity index according to Shannon's Diversity Index (H') (Krebs 1989). Water depth was measured with a graduated ruler in centimetres. Water current velocity was measured with the float method, whereby one measures the time it takes for a floating object (small plastic bottle) to travel a measured distance. Velocity was estimate as the linear distance travelled in metres divided by time in seconds ($m \cdot s^{-1}$). Because the water transparency is almost constant between macrohabitats, it was not included among the environmental variables affecting cichlid assemblages in the Cinaruco River.

Fish collections

On sand banks and leaf-litter substrates, fishes were sampled with a seine (6.4×1.8 m, 4-mm mesh). In these unstructured mesohabitats, seine hauls were initiated from a depth that usually was between 0.3 and 1.0 m, and terminated at the shoreline. At each collection site, samples consisted of three hauls that were nonoverlapping in the area covered (following method of Layman & Winemiller 2004). In locations with submerged woody debris and rocky patches, fishes were captured with small hooks (# 8) baited

with a small piece of fish flesh. Rocky patches were not observed in creeks. Fishes were captured using two techniques; therefore, catch-per-unit-effort (CPUE) data are not comparable between methods. Abundance was recorded as CPUE based on the method – the number of individuals collected with hooks per hour, or the number of individuals captured per metre of seine haul. We assumed that seining effectively captured all cichlid species present in sand bank and leaf-litter mesohabitats, whereas baited hooks probably did not effectively capture certain small species (e.g., *Apistogramma*, *Biotoecus* and *Crenicichla* aff. *wallacii*) or benthivorous geophagines (e.g., *Geophagus* and *Satanoperca*). The use of baited hook and seines in separate habitats also allowed the capture of those cichlids that segregate habitats due to their feeding habit; and in tropical rivers, the diversification of trophic niches and habitat affinities have already been demonstrated (Winemiller et al. 1995; Layman et al. 2009, Montaña & Winemiller 2009). Thus, during the low-water period, more fishes are encountered per unit area (Lowe-McConnell 1987).

Fishes were preserved in 15% formalin in the field, and specimens were later examined in the laboratory. Voucher specimens are archived in the Museo de Ciencias Naturales at UNELLEZ Guanare, Venezuela and The Royal Ontario Museum, Canada.

Morphological data

Morphological measurements were made using digital calipers or a plastic ruler. Following Winemiller's (1991) criteria, 23 characters were measured on adults for each specimen: (1) standard length (SL), (2) head length (HEAL), (3) head height (HEAH), (4) mouth or gape width (MOUW), (5) eye position (EYEP), (6) eye diameter (EYED), (7) mouth position (MOUP) as the angle formed by lines passing through the corner of the mouth and the tips of the upper and lower jaws, (8) snout length shut (SNTL), (9) snout length open (SNTO), (10) maximum Body depth (BODD), (11) maximum body width (BODW), (12) caudal peduncle length (PEDL), (13) body depth below mid-line (BDBM), (14) caudal peduncle depth (PEDD), (15) dorsal fin length (DORL), (16) dorsal fin height (DORH), (17) pectoral fin length (PECTL), (18) pectoral fin height (PECTH), (19) caudal fin length (CAUDL), (20) caudal fin height (CAUDH), (21) pelvic fin length (PELVL), (22) anal fin length (ANAL), (23) anal fin height (ANAH). Among the 23 variables, the values of 21 variables were converted to proportions following Winemiller (1991). In this manner, descriptors of body and fin shape can be analysed without the influence of body size. Ratios of body size 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 1991). Morphological measurements were made on five adult specimens of each species collected.

Statistical analysis

Data were analysed separately according to the field sampling method. A Spearman correlation matrix using SPSS was calculated to examine relationships among mesohabitat variables (substrate diversity, depth and current velocity). Specimens were grouped across all mesohabitat categories within each of the three macrohabitats for calculation of species relative abundance (RA), richness (S), evenness (E) and diversity using the H' (Krebs 1989).

Species assemblage structure was analysed using nonmetric multidimensional scaling (NMDS) and analysis of similarities (ANOSIM) performed with PRIMER 5 software (Primer-E Ltd. 2001. Primer 5 for Windows version 5. Plymouth Maine Laboratory, Plymouth, UK). NMDS was performed on species presence (1) and absence (0) data according to mesohabitats nested within macrohabitats. NMDS constructs two-dimensional ordination in a manner that best represents relationships among samples in a similarity matrix (Field et al. 1982). The robustness of the ordination in the plot is indicated by its stress value: <0.2 give a potentially useful two-dimensional picture, stress <0.1 corresponds to a good ordination and stress <0.05 is an excellent representation (Clarke & Warwick 1994). Similarity matrices were calculated using the Bray-Curtis Similarity Index (Bray & Curtis 1957). ANOSIM (Clarke & Warwick 1994), a nonparametric analogue of MANOVA, was used to test for differences in species composition among habitat categories. ANOSIM produces a statistic, R , that indicates the magnitude of difference among group of samples. An $R = 1$ indicates that assemblages completely differ among defined groups, and $R = 0$ indicates that the similarity between assemblages is very high (Clarke & Warwick 1994).

Relationships between fish assemblage composition (NMDS axis scores) and physical variables (e.g., substrate composition, water depth and water velocity) were examined using PC-ORD version 5 (McCune & Mefford 2006). Before running NMDS, fish abundance datasets were grouped according to the field sampling method and then values were log transformed. We used Bray-Curtis dissimilarities as the distance measure, a coefficient that has been repeatedly demonstrated to be robust for ecological community data (Faith & Norris 1989). A two-dimensional solution was used for all analyses in deriving stress values. A Monte Carlo test of stress of randomised data was done with 50 runs and 100 iterations (McCune & Mefford 2006).

To ordinate specimens in morphological space, principal components analysis (PCA) based on the correlation matrix of morphological variables was performed; species loadings on the dominant axes provided the basis for inter-assemblage comparisons of species distribution in morphological space. Morphological data of 95 specimens (five individuals \times 19 species) were log-transformed and analysed with PC-ORD version 5. Because the measurements of morphological traits made on five individuals were highly consistent, we calculated the species mean values for the 23 morphological attributes, and these mean values were used to calculate Euclidean distance between species based on species loadings on the first two PC axes. Sub-matrices containing species comprising individual mesohabitat samples were compiled. Following Winemiller (1991), we calculated the average of nearest neighbour distance (NND) which is an index of species packing in morphological space; the standard deviation (SD) of NND which is an index of evenness of species dispersion or packing in morphological space (a lower SD indicates a more regular dispersion pattern); and the average distance to the assemblage centroid (CD) which provides an estimate of the relative size of the morphological hypervolume defined by an assemblage. Assemblage average morphological NND, SD of NND and average CD were regressed (using linear regressions) against species richness using SPSS 15.0. Correlations were explained based on the correlation coefficient (R^2) and slopes. Abbreviations of cichlid names and trophic categories appear in Table 1.

Results

Physical habitat characteristics

Substrates in areas with woody debris and leaf litter were more heterogeneous than substrates of sand banks and rocky shoals (Table 2). Water velocity was low and varied little among mesohabitats (0.00–0.22 $\text{m}\cdot\text{s}^{-1}$), and water depth ranged from 0.12 to 1.35 m (Table 2). Lower averages were recorded for velocity and depth in mesohabitats containing leaf litter and woody debris. Spearman's correlation analysis showed significant correlations between water substrate diversity with depth ($P < 0.01$) and velocity ($P < 0.05$). Compared with the littoral zone of the main channel, lagoons experience lower water velocities and thus accumulate more organic matter, leaf litter and woody debris.

Fish assemblages in relation to two habitat scales

Among 268 mesohabitat samples (669 total seine hauls and 340.8 total hours fishing with hooks), 8620

Table 1. Cichlid species from the Cinaruco River, name abbreviations, trophic classifications, and subfamily groups (following Smith *et al.* (2008) classification).

Species	Name Abbrev.	Trophic class	Tribes
<i>Acaronia vultuosa</i>	A.v	I/P	Cichlasomatini
<i>Aequidens diadema</i>	A.d	I	Cichlasomatini
<i>Apistogramma hoignei</i>	A.h	I	Geophagini
<i>Apistogramma</i> sp.	A.sp.	I	Geophagini
<i>Biotodoma wavrini</i>	B.w	I	Geophagini
<i>Biotoecus dicentrarchus</i>	B.d	I	Geophagini
<i>Crenicichla lugubris</i>	C.l	I/P	Geophagine
<i>Crenicichla</i> aff. <i>wallacii</i>	C.af.w	I/P	Geophagini
<i>Geophagus abalios</i>	G.a	I	Geophagini
<i>Geophagus dicrozoster</i>	G.d	I	Geophagini
<i>Heros</i> sp.	H.sp.	I	Heroini
<i>Hoplarchus psittacus</i>	H.ps	I	Heroini
<i>Hypselecara coryphaenoides</i>	H.co	I	Heroini
<i>Mesonauta insignis</i>	M.in	I	Heroini
<i>Satanoperca daemon</i>	S.d	I	Geophagine
<i>Satanoperca mapiiritensis</i>	S.m	I	Geophagine
<i>Cichla intermedia</i>	C.in	P	Cichlini
<i>Cichla orinocensis</i>	Cor	P	Cichlini
<i>Cichla temensis</i>	C.te	P	Cichlini

P = piscivore (consume the whole prey), I = invertivore, I/P = invertivore/piscivore

Table 2. Ranges (minimum and maximum) of mesohabitats variables recorded in lagoon, channel and creek littoral habitats.

Habitat	Mesohabitat	No. patches sampled	Substrate diversity	Depth (m)	Velocity (m·s ⁻¹)
Lagoon	WD	38	0.55	0.32–1.30	0.01–0.02
	LL	40	0.60	0.36–1.12	0.01–0.02
	SB	42	0.42	0.12–1.35	0.01–0.04
	R	10	0.35	0.21–1.00	0.01–0.08
Channel	WD	20	0.51	0.37–1.20	0.01–0.08
	LL	20	0.65	0.29–0.93	0.01–0.04
	SB	30	0.30	0.35–1.00	0.02–0.22
	R	12	0.31	0.35–0.96	0.01–0.20
Creek	WD	20	0.37	0.28–1.09	0–0.01
	LL	16	0.52	0.12–0.78	0–0.01
	SB	20	0.23	0.45–1.13	–0.02

Substrate diversity index values ranged from 0 to 1.0. Mesohabitats: woody debris (WD), leaf litter (LL), sand banks (SB) and rock shoals (R).

individuals belonging to 19 species were collected. Overall, macrohabitats yielded between nine and fifteen cichlid species. Within macrohabitats, the total number of species and RA of individual species (Table 3) depended on the mesohabitat type and associated fishing method. In sand bank and leaf-litter habitats, the most commonly collected species were *Apistogramma* sp. and *Crenicichla* aff. *wallacii* followed by *Biotodoma* and *Geophagus* species. In submerged woody debris and rock shoals, the most common species were *Crenicichla lugubris*, *Heros* and *Hypselecara* (Table 3). Neither dwarf cichlids (e.g., *Apistogramma*, *C.* aff. *wallacii*) nor large geophagines (e.g., *Geophagus*, *Satanoperca* and *Biotodoma*) were

captured from woody debris and rock shoals. However, we observed individuals of these species near both mesohabitat types on several occasions. Thus, clearly the absence in the samples is because of the fishing method (hook and line) used in these mesohabitat types. We did not find significant variation in species richness among months ($P > 0.50$). Likewise, when comparing species diversity and evenness by mesohabitat categories, little variation was found among habitats sampled with the same method (Table 4).

The ANOVA revealed significant differences between macrohabitats for samples collected with the seine for both species diversity, H ($F_{2,19} = 4.0$; $P < 0.05$) and evenness, E ($F_{2,19} = 5.2$; $P < 0.03$). Seine samples also had significant differences between mesohabitat types for both species diversity ($F_{1,20} = 6.2$; $P < 0.02$) and evenness ($F_{1,20} = 3.5$; $P < 0.07$). When using baited hooks, no significant differences were found in species richness among macro and mesohabitat types when compared using ANOVA (most of the cases, $P > 0.50$). Based on ANOSIM, there were no significant differences in species composition among macrohabitats (R -statistic = 0.06; Fig. 1) and mesohabitat types (R -statistic = 0.07; Fig. 1).

The NMDS ordination of fish abundance data for mesohabitat types containing woody debris and rock shoals resulted in two axes that explained 79.4% of variation (Axis 1: 72.5% and Axis 2: 6.9%; Fig. 2a). The solution was considered statistically useful compared with randomisation results ($P < 0.03$, Fig. 2a). Species such as *Cichla intermedia*, *Cichla temensis* and *Hypselecara coryphaenoides* were positively correlated with Axis 1 which indicated that these species were associated with greater rock coverage and velocity. A second NMDS ordination performed on fish abundance data for sand bank and leaf litter resulted in two axes that explained 81.0% of total variation (Axis 1: 63.7% and Axis 2: 17.3%; Fig. 2b). The solution for the second NMDS ordination was also considered statistically useful compared with randomisation results ($P < 0.02$, Fig. 2b). *Geophagus abalios*, *Geophagus dicrozoster*, *Satanoperca*, *Biotodoma wavrini* and *Biotoecus dicentrarchus* were negatively correlated with Axis 1 and 2, indicating that they were more abundant in sites dominated by sandy substrates. Other species such as *Apistogramma hoignei*, *Acaronia vultuosa* and *H. coryphaenoides* had low positive scores on Axis 2, indicating their association with leaf-litter substrates.

Morphological patterns

The first two axes of the PCA performed on the morphological data modelled approximately 86% of the total variation (PC1 = 82.8 and PC2 = 2.9;

Table 3. Per cent relative abundance of cichlid species collected with a seine (in sand banks and leaf litter) and baited hook (in woody debris and rock shoals) in the Cinaruco River.

Species	Sand banks			Leaf litter			Woody debris			Rock shoals	
	LG	CH	C	LG	CH	C	LG	CH	C	LG	CH
A.v	†	†	†	0.4	0.8	†	1.8	†	0.7	1.1	†
A.h	0.5	†	†	0.9	5.4	†	†	†	†	†	†
A.d	†	†	†	†	†	†	5.7	3.4	4.4	4.1	3.1
A.sp.	51.3	26.4	36.8	57.8	55.2	64.2	†	†	†	†	†
B.w	7.1	11.9	10.5	2.7	3.9	3.4	†	†	†	†	†
B.d	10.8	12.3	16.9	4.9	5.1	10.4	†	†	†	†	†
C.l	0.6	3.1	0.5	0.6	3.9	†	43.5	35.8	25.9	22.7	25.3
C.aff.w	11.3	12.1	10.9	15.5	16.3	17.5	2.9	†	2.9	†	†
G.a	5.3	13.9	5.6	4.6	3.1	0.6	†	†	†	†	†
G.d	6.4	11.1	5.7	3.1	2.3	0.6	†	†	†	†	†
H.sp.	0.5	0.8	1.8	2.3	1.3	0.6	11.4	10.1	12.9	23.5	20.4
H.ps	0.9	†	†	0.2	†	†	4.3	9.5	1.5	5.7	9.9
H.co	0.4	0.2	†	0.3	1.7	0.6	15.5	9.4	28.8	26.2	15.4
M.in	0.3	0.2	†	3.4	1.2	0.8	5.6	8.1	7.9	6.8	9.3
S.d	5.2	4.6	2.6	2.5	3.3	0.9	†	†	†	†	†
S.m	0.4	†	†	0.2	†	†	†	†	†	†	†
C.in	†	†	†	†	†	†	†	5.1	†	†	6.8
C.or	0.5	1.8	0.5	0.9	1.3	0.4	5.5	9.4	8.9	6.2	3.6
C.te	0.4	1.5	0.6	0.5	0.4	†	3.8	9.2	6.1	3.7	6.2

†Species absent are represented by asterisks.
 LG, Lagoon; CH, channel, C, creek.

Table 4. Cichlid assemblage attributes according to two spatial scales, macro and mesohabitat: *S*, species richness (total no. species), *H'*, species diversity (Shannon Index) and *E*, species evenness.

Habitat	Mesohabitat	<i>S</i>	<i>H'</i>	<i>E</i>
Lagoon (18 spp.)	WD	11	0.81	0.77
	LL	17	0.60	0.48
	S	15	0.67	0.57
	R	9	0.80	0.84
Channel (19 spp.)	WD	11	0.91	0.87
	LL	16	0.71	0.59
	SB	16	1.06	0.88
	R	12	0.89	0.81
Creek (15 spp.)	WD	10	0.82	0.82
	LL	13	0.73	0.66
	S	11	0.76	0.73

Fig. 3). The first axis described a gradient influenced most strongly by mouth position, mouth width, snout length, dorsal and anal fin length, and caudal peduncle depth, (Table 5; Fig. 3). Large positive scores on PC1 were associated with species having moderately elongate bodies, short snouts and low jaw protrusibility (e.g., *Apistogramma* and *Biotodoma*) and species with highly elongate bodies (e.g., *Crenicichla* aff. *wallacii*). Large negative scores on the same axis were associated with individuals having relatively tall and laterally compressed bodies and short snouts (e.g., *Mesonauta*, *Aequidens*, *Hypselecara*, *Heros* and *Hoplarchus*). The second axis showed a morphological gradient strongly influenced by body depth, mouth position, caudal peduncle depth, dorsal fin height, anal fin length and pelvic fin length. Large

positive scores were represented by large species with large mouths and fusiform bodies (e.g., *Cichla*) and species with an elongate body with a caudal peduncle almost as deep as long (e.g., *Crenicichla lugubris*). Negative scores on the same axis were associated with species having laterally compressed bodies and long pelvic and anal fins (e.g., *Biotodoma*, *Geophagus* and *Satanoperca*).

Morphological similarity

Total assemblage morphological space measured by average Euclidean distance to the assemblage CD did not vary significantly in relation to species richness for any of the macro or mesohabitats (Fig. 4; Table 6). Mean values and SD for the NND tended to decrease with increasing species richness (Fig. 4; Table 6). In woody debris and rock patches, the mean values of NND ranged from 0.34 to 0.54, and SD ranged from 0.30 to 0.41, respectively. In sand banks and leaf-litter patches, mean of NND and SD of NND ranged from 0.46 to 0.58 and from 0.30 to 0.37, respectively.

Mean values for the distance to the CD ranged from 0.41 to 0.48 for assemblages from woody debris and rock shoals, and 0.53 and 0.65 for assemblages from sand banks and leaf-litter habitats. Regression slopes of the mean and SD of NND in relation to species richness were low and negative in most cases, and slopes for the CD were low but positive (Table 6). This result indicates a pattern of limiting similarity in relation to local-scale species richness (low slopes for regressions of mean NND), and an even pattern of

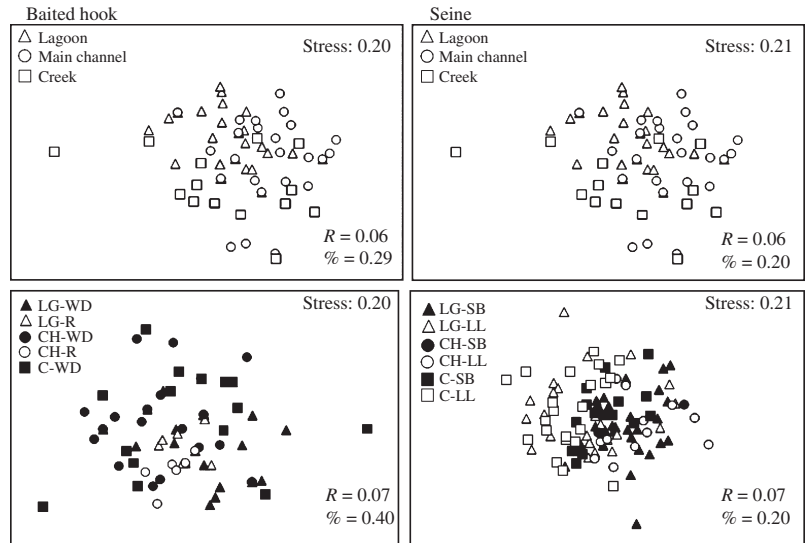


Fig. 1. Non-metric multidimensional ordination of cichlid species based on seine and baited hook samples at two spatial scales: macrohabitat (represented by lagoon, main channel, and creek) and mesohabitat (represented by woody debris (WD), rock shoals (R), sandbanks (SB), and leaf litter (LL)).

dispersion of species within assemblage morphospace (low slopes for regressions of SD of NND).

Combining all local mesohabitat assemblages in linear regressions of mean values and SD of NND versus species richness yielded significant patterns (Table 6). For example, for habitats sampled with hook and line, mean of NND versus species richness, $R^2 = 0.54$ ($P < 0.0001$); and for habitats sampled with the seine, mean of NND versus species richness, $R^2 = 0.30$ ($P < 0.005$). Linear regressions of the mean of CD versus species richness were weak but significant for fish assemblages in woody debris and rock shoals ($R^2 = 0.38$, $P < 0.0001$), but not statistically significant for those in sand bank and leaf-litter mesohabitats ($R^2 = 0.16$, $P > 0.10$). Regressions of the average NND and SD of NND with species richness resulted in low and negative slopes of species assemblages in all mesohabitats. These relationships suggest that when more species are added to a habitat assemblage, morphospace remains approximately constant, species

average similarity increases and species dispersion in morphological space becomes more uniform.

Discussion

Assemblage structure and habitat-spatial scale

Cichlid assemblages in the Cinaruco River did not show significant structural variation among macrohabitats during the dry season, a conclusion supported by high overlap in NMDS plots. Cichlid species richness hardly differed among the three macrohabitats. One species, *Cichla intermedia*, was only found in the main channel, and one, *Satanoperca mapiritensis*, was only found in lagoons. The Cinaruco River is a floodplain river that undergoes gradual and predictable seasonal water-level fluctuations (Montoya et al. 2006), and this dynamic forces littoral-zone fishes to move frequently to new patches. Arrington & Winemiller (2006) found that fish assemblage com-

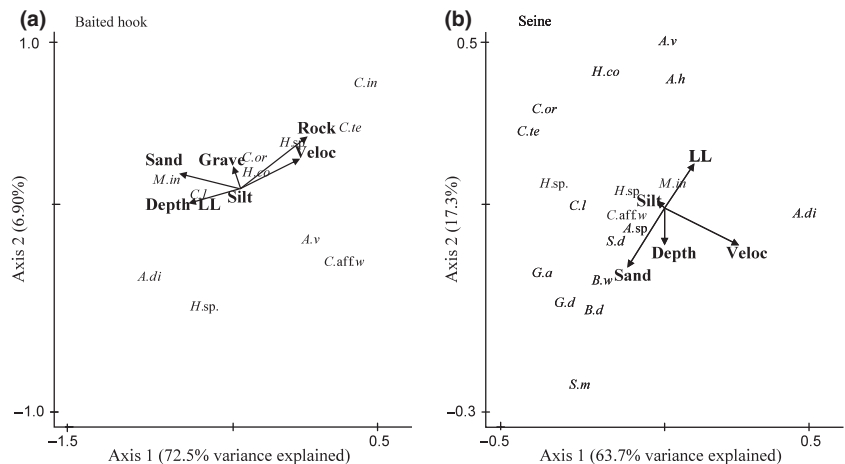


Fig. 2. Non-metric multidimensional scaling (NMS) ordination of cichlid assemblages and habitat parameters according to two sampling methods and four mesohabitat types: a) Baited hook samples from woody debris and rock shoals, b) Seine samples from sandbanks and leaf litter mesohabitats. Physical vectors show the direction and magnitude of correlations within the ordination space between physical variables and fish assemblages.

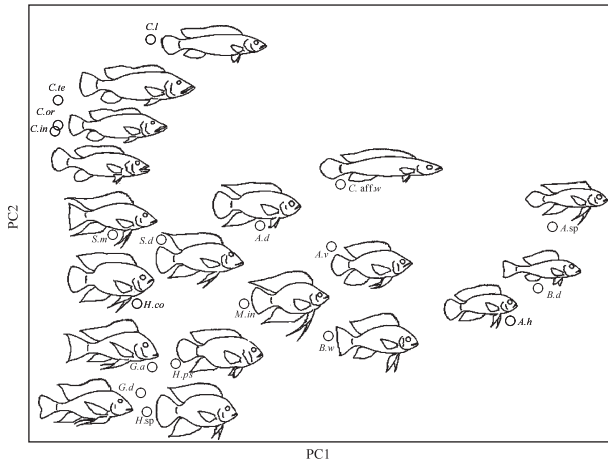


Fig. 3. Principal components analysis ordination of Cinaruco River cichlid species based on 22 morphological variables. Each point represents the average of five individuals.

position was more regular during the dry season, the period when the present study was conducted. During the dry season, creeks and lagoons become lentic systems, as do many littoral habitats within the main channel. Fish habitat occupancy in tropical floodplain rivers can be strongly influenced by physical factors operating at both the reach scale (Rodriguez & Lewis 1997) and local patch scale (Willis et al. 2005; Arrington & Winemiller 2006).

At the local scale of mesohabitat patches, there was high overlap in cichlid assemblage structure. But assemblage composition differed when comparing species RA based on samples obtained from the two different collecting methods. Based on seine samples, *Apistogramma* and *Crenicichla* aff. *wallacii* were more abundant in leaf-litter habitats, whereas *Geophagus* species and *Satanoperca* species were more abundant on sand banks. Based on hook and line samples, *Crenicichla lugubris* was more abundant in woody debris, whereas *Heros*, *Hoplarchus* and *Hypselecara* were more abundant in rock patches. It should be noted that the hook-and-line method employed in rock shoals and woody debris patches was inefficient for capturing microphagous cichlids, thus conclusions regarding use of these structurally complex habitats by these species are not possible.

Substrate heterogeneity and composition was consistently influential in the multivariate models. Experimentally, Arrington & Winemiller (2006) demonstrated that fish species density in littoral habitats of the Cinaruco River was influenced by the structural complexity of the habitats, e.g., more structurally complex habitats patches supported more diverse and unique assemblages than habitats containing homogeneous substrates, such as sand banks. Likewise, Willis

Table 5. Axis eigenvalues, percentage variation modeled, cumulative variation and variable loadings from PCA 1 and PCA 2 of 19 cichlid species based on morphological characters.

	Axis 1	Axis 2
Eigenvalues	20.58	0.60
% variation	93.54	2.74
Cumulative variation	93.54	96.29
HEAL	-0.21	0.18
HEAH	-0.11	-0.05
BODD	-0.14	-0.42
BODW	-0.25	0.16
PEDD	-0.12	0.08
PEDL	0.22	0.40
BDBM	-0.21	-0.09
EYEP	-0.18	-0.01
EYED	0.21	-0.32
MOUP	-0.69	-0.58
MOUW	-0.17	0.25
SNTL	-0.35	-0.16
SNTO	0.08	-0.06
DORL	-0.43	-0.07
DORH	-0.43	-0.65
ANAL	-0.03	-0.51
AN AH	-0.40	-0.72
CAUDD	-0.45	-0.27
CAUDL	-0.20	-0.21
PECTL	-0.12	-0.31
PECTH	-0.22	-0.33
PELVL	-0.25	-0.11

et al. (2005) found high correlations between fish species density and structurally complex habitats associated with low current velocity. Structurally complex, littoral habitats support greater primary and secondary production, including food resources that many fishes exploit (Winemiller et al. 2006). Likewise, these habitats potentially provide suitable refuge sites for fishes with a diversity of shapes and sizes, and are important in maintaining high beta diversity (Arrington et al. 2005). Structurally complex habitats also can reduce predation (Crook & Robertson 1999); e.g., small cichlids can move in and around leaf litter or enter into holes in woody debris or rocks.

Taxonomic, morphological and functional diversity

Taxonomically, we did not find much variation in fish assemblages among major macrohabitat types. Within mesohabitats, one species, *Acaronia vultuosa*, differed between sand banks and leaf litter and one species, *Cichla intermedia*, between rock shoals and woody debris. As a consequence, morphological diversity did not differ significantly between macro and mesohabitat categories. When ordering cichlid species by major environmental variables, species were separated based on substrate composition, suggesting that ecological factors interacting with the mechanics of feeding may drive niche partitioning and coexistence of species with similar morphologies.

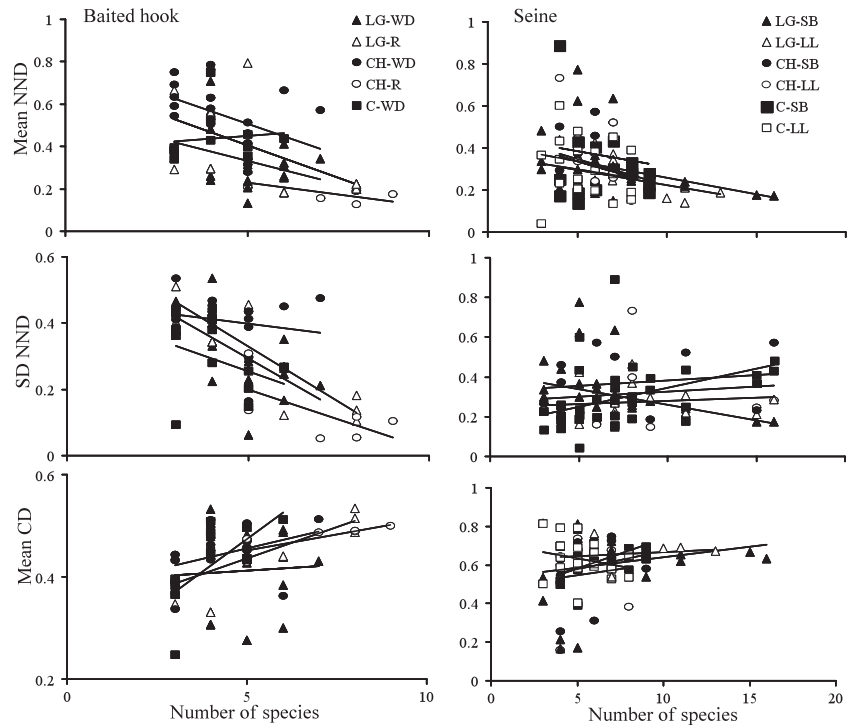


Fig. 4. Three measures of distances between species in the morphospace plotted as a function of number of species in four mesohabitat types in the littoral zone of the Cinaruco River. All linear regressions were statistically significant ($p < 0.05$) with the exception of regressions for CD based on seine samples.

Ecomorphological and behavioural specialisation for feeding and habitat use may facilitate niche partitioning in species-rich Neotropical communities (López-Fernández et al. 2005). Jepsen et al. (1997) found that each of the three sympatric species of *Cichla* from the Cinaruco River consumed a wide range of prey fishes, yet these piscivores subdivided their consumption of the prey assemblage based on habitat, prey type and hydrological season. *Cichla temensis* occupied a wide range of lotic (main channel) and lentic (lagoons and creeks) habitats, *Cichla orinocensis* was more abundant in shallow areas with submerged structures in lagoons, and *Cichla intermedia* is a specialist restricted to flowing channel habitats. During the low-water period, *C. intermedia* and *C. orinocensis* had greater dietary overlap and consumed small characids and invertebrates, whereas *C. temensis* tended to forage on larger cichlids and characiforms from deeper littoral areas (Jepsen et al. 1997). In the present study, invertivorous species were separated primarily based on substrate categories; e.g., *Apistogramma*, *Crenicichla* aff. *wallacii*, *Acaronia*, *Mesonauta* and *Hypselocara* were primarily associated with patches having high content of leaf litter and organic matter, whereas *Geophagus* species and *Satanoperca* occurred in patches with sandy bottoms. Piscivorous species, such as *Cichla* species and *Crenicichla lugubris*, revealed a degree of segregation from the other species and affinity with physically complex substrates.

Morphological attributes of fishes reflect important features of ecology, including feeding behaviour and adaptations to use various habitats (Gatz 1979). Species occupying the same habitats may have similar morphology in response to adaptations to physical environments (Grant 1972), or they may have divergent morphology as response to interspecific competition (Brown 1971). Thus, high taxonomic and morphological similarity among coexisting species may reflect a lack of niche specialisation (Winemiller 1991). In our study, six morphological features (mouth position, eye diameter, mouth width, anal and dorsal fin height, and caudal peduncle depth) were strongly associated with a few key environmental variables suggesting that use of habitat patches by these species is influenced by functional morphology. Yet in the case of *Cichla* species, all of which are morphologically similar, the three species in the Cinaruco River revealed habitat partitioning (Jepsen et al. 1997). The two sympatric species of *Crenicichla*, *C. lugubris* and *C. aff. wallacii*, both have elongate bodies but differ greatly in size (average 198.4 and 44.6 mm respectively; Montaña & Winemiller 2009). *Crenicichla lugubris* feeds mainly on small fishes, whereas *Crenicichla* aff. *wallacii* prefers invertebrates. Differences in body size and, to a lesser degree, habitat use seem to be the main factors that cause dietary segregation between these congeners during the dry season. Other species grouped by their laterally compressed bodies and short snouts (e.g., *Biotodoma*, *Aequidens*, *Heros*, *Hoplarchus*, *Hypselecara* and

Table 6. Coefficient of determination (R^2), slope values and p-values for three measures of morphological dispersion of cichlid species in littoral-zone mesohabitat patches in relation to species richness: mean nearest neighbour distance (NND), standard deviation NND and mean distance to the centroid (CD).

Habitat	Dependent variable	R^2	Slope (γ)	P-value
Lagoon-WD	Mean NND	0.10	-0.04	0.247
Channel-WD	Mean NND	0.18	-0.06	0.523
Creek-WD	Mean NND	0.02	-0.01	0.872
Lagoon-R	Mean NND	0.32	-0.06	0.040*
Channel-R	Mean NND	0.48	-0.02	0.038*
Lagoon-SB	Mean NND	0.32	-0.03	0.040*
Channel-SB	Mean NND	0.20	-0.06	0.446
Creek-SB	Mean NND	0.08	-0.01	0.644
Lagoon-LL	Mean NND	0.52	-0.05	0.001*
Channel-LL	Mean NND	0.22	-0.06	0.401
Creek-LL	Mean NND	0.02	-0.01	0.606
Lagoon-WD	SDNND	0.35	-0.06	0.033*
Channel-WD	SDNND	0.04	-0.01	1.163
Creek-WD	SDNND	0.13	-0.04	0.679
Lagoon-R	SDNND	0.77	-0.07	0.001*
Channel-R	SDNND	0.42	-0.04	0.022*
Lagoon-SB	SDNND	0.11	-0.02	0.274
Channel-SB	SDNND	0.02	-0.01	0.756
Creek-SB	SDNND	0.06	-0.02	0.769
Lagoon-LL	SDNND	0.20	-0.01	0.147
Channel-LL	SDNND	0.04	-0.02	0.748
Creek-LL	SDNND	0.02	-0.01	0.578
Lagoon-WD	Mean CD	0.02	0.01	0.822
Channel-WD	Mean CD	0.13	0.02	0.347
Creek-WD	Mean CD	0.47	0.05	0.053*
Lagoon-R	Mean CD	0.57	0.02	0.001*
Channel-R	Mean CD	0.66	0.01	0.001*
Lagoon-SB	Mean CD	0.04	0.01	1.677
Channel-SB	Mean CD	0.07	0.03	0.891
Creek-SB	Mean CD	0.18	0.02	0.285
Lagoon-LL	Mean CD	0.03	0.01	0.564
Channel-LL	Mean CD	0.01	0.01	1.008
Creek-LL	Mean CD	0.06	-0.02	0.570

*Significant P-values.

Mesonauta) seem to segregate among habitats based on feeding behaviour (C.G. Montaña & K.O. Winemiller unpublished dietary data). *Biotodoma* was mostly associated with sandy substrates, whereas the other five were associated with more structurally complex habitats. Large geophagine species such as *Satanoperca* and *Geophagus* with moderately elongate bodies and long snouts also showed high affinity for sandy substrates. *Satanoperca daemon* was more abundant and present in all three macrohabitats, whereas its congener, *Satanoperca mapiritensis*, was only found in lagoons. Some fishes of the Cinaruco River are strongly associated with structurally complex rock shoals and woody debris (Arrington & Winemiller 2006). Willis et al. (2005) found high correlations between morphological diversity of littoral-zone fish assemblages of the Cinaruco River and habitat structural complexity. Stream habitat heterogeneity can mediate coexistence when fish species exploit

resources in different ways (Schlosser 1987; Wood & Bain 1995).

Morphological volume within local assemblages

In this study, we found that the total assemblage morphological space measured by average Euclidean distance to the assemblage CD did not vary significantly in relation to species richness for any of the macro- or mesohabitat categories. This result implies that assemblage niche space does not increase as a function of species richness at either the scale of local patches or broad habitat units. As species are added to local assemblages, the mean NND tended to decrease slightly suggesting that species are packing closer together in morphological space (Mouillot et al. 2007). The SD of the NND declined with increasing species richness in mesohabitat patches indicating that even spacing is maintained within the morphological space.

In the Cinaruco River, water recession during the dry season may result in stronger interspecific interactions within littoral-zone patches, and this may account for nonrandom patterns of community structure (Arrington et al. 2005). In the tropics, habitat and food availability are reduced during the low-water season (Lowe-McConnell 1987; Winemiller & Jepsen 1998), and predation becomes more intense (Jepsen et al. 1997). Thus, fish faunas from the tropics are more taxonomically, morphologically and ecologically diverse than temperate faunas, and niche diversification appears to be influenced by biotic interactions as well as habitat volume and heterogeneity (Winemiller 1991).

Our findings are consistent with the hypothesis that cichlid species of the Cinaruco River are fairly uniformly distributed among macro- and mesohabitats during the dry season, and species assemblages at local scales are mainly influenced by fine-scale environmental factors such as substrate composition. In this regard, our conclusions agree with interpretations from previous studies of fish assemblage structure in littoral habitats on the same river (Willis et al. 2005; Arrington & Winemiller 2006). During the dry season, the water level is relatively stable and low, and fish assemblage structure appears to be more nonrandom in relation to the habitat features (Arrington & Winemiller 2006; Layman et al. 2009). As a group, cichlids tend to be invertivorous or piscivorous and also have relatively deep bodies and broad fins that enhance maneuverability but at the expense of the speed. Maintenance of an even pattern of cichlid species dispersion within the morphospace in more species-rich local assemblages suggests that ecological interactions influence patterns of habitat occupancy at the mesohabitat scale during the dry season in the Cinaruco River.

Acknowledgements

We are grateful to the members of Cinaruco Fishing Club, especially Carol Marzuola and Guillermo Belloso, and Jose Garcia and family for crucial logistic support during our work on Cinaruco River. Donald Taphorn at UNELLEZ provided additional logistical assistance and helped with identification of fishes. Pablo Medina and Wilson Garcia are given special thanks for their help in the field. Donald Taphorn, Hernán López-Fernández, and Katie Roach helped improve previous drafts. Fish collections were made under scientific permit #000074 issued by the Instituto Nacional de Acuicultura y Pesca (INAPESCA) of the República Bolivariana de Venezuela. Funding to study cichlid assemblages in Cinaruco River was provided by National Science Foundation grant to Kirk Winemiller, Hernan López-Fernández and Rodney Honeycutt (DEB 0516831), and American Cichlids Association-Paul V. Loisel Conservation award to Carmen Montaña.

References

- Angermeier, P.L. & Winston, R. 1998. Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology* 79: 911–927.
- Arrington, D.A. & Winemiller, K.O. 2006. Habitat affinity, the seasonal flood pulse, and community assembly in the littoral zone of a Neotropical floodplain river. *Journal of North America Benthological Society* 25: 126–141.
- Arrington, D.A., Winemiller, K.O. & Layman, C.A. 2005. Community assembly at the patch scale in a species-rich tropical river. *Oecologia* 144: 157–167.
- Barlow, G.W. 2000. The cichlid fishes: nature's grand experiment in evolution. Perseus Publishing, Cambridge.
- Bray, J.R. & Curtis, J.C. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monograph* 27: 325–349.
- Brown, J.H. 1971. Mechanisms of competitive exclusion between two species of chipmunks. *Ecology* 52: 305–311.
- Clarke, K.R. & Warwick, W.M. 1994. Similarity-based testing for community pattern: the 2-way layout with no replication. *Marine Biology* 118: 167–176.
- Crook, D.A. & Robertson, A.I. 1999. Relationships between riverine fish and woody debris: implications for lowland rivers. *Marine Freshwater Research* 50: 941–953.
- Douglas, M.E. & Matthews, W.J. 1992. Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. *Oikos* 65: 213–224.
- Faith, D.P. & Norris, R.H. 1989. Correlation of environmental variables with patterns of distribution and abundance of common and rare freshwater macroinvertebrates. *Biological Conservation* 50: 77–98.
- Field, J.G., Clarke, K.R. & Warwick, M. 1982. A practical strategy for analyzing multi-species distribution patterns. *Marine Ecology Progress Series* 8: 37–53.
- Gatz A.J. Jr 1979. Ecological morphology of freshwater stream fishes. *Tulane Studies in Zoology and Botanic* 21: 91–124.
- Goulding, M., Carvalho, M.L. & Ferreira, E.G. 1988. Rio Negro: rich life in poor water. SBP Publishing Company, The Hague.
- Grant, P.R. 1972. Convergent and divergent character displacement. *Biological Journal of the Linnean Society* 4: 39–68.
- Hoeinghaus, D., Layman, C.A., Arrington, D.A. & Winemiller, K.O. 2003. Spatiotemporal variation in fish assemblage structure in tropical floodplain creeks. *Environmental Biology of Fishes* 67: 379–387.
- Holland, J.D., Bert, D.G. & Fahring, L. 2004. Determining the spatial scale of species' response to habitat. *BioScience* 54: 227–233.
- Huston, M.A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86: 393–401.
- Jackson, D.A., Peres-Neto, P.R. & Olden, J.D. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic and spatial factors? *Canadian Journal of Fisheries and Aquatic Sciences* 58: 157–170.
- Janssen, A., Sabelis, M.W., Magalhaes, S., Montserrat, M. & van der Hammen, T. 2007. Habitat structure affects intraguild predation. *Ecology* 88: 2713–2719.
- Jepsen, D.B., Winemiller, K.O. & Taphorn, D.C. 1997. Temporal patterns of resource partitioning among *Cichla* species in a Venezuelan blackwater river. *Journal of Fish Biology* 51: 1085–1108.
- Krebs, C.J. 1989. *Ecological methodology*. Harper and Row, New York.
- Layman, C.A. & Winemiller, K.O. 2004. Size-based responses of prey to piscivore exclusion in a neotropical river. *Ecology* 85: 1311–1320.
- Layman, C.A., Montaña, C.G. & Allgeier, J.E. 2009. Linking community assembly and rates of water level change in river littoral habitats. *Aquatic Ecology*. doi: 10.1007/s10452-009-9256-5.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943–1967.
- Lowe, W.H., Likens, G.E. & Power, M.E. 2006. Linking scales in stream ecology. *BioScience* 56: 591–597.
- Lowe-McConnell, R.H. 1987. *Ecological studies in tropical fish communities*. Cambridge University Press, Cambridge.
- López-Fernández, H., Honeycutt, R.L. & Winemiller, K.O. 2005. Molecular phylogeny and evidence for adaptive radiation in geophagine cichlids from South America (Perciformes: Labroidae). *Molecular Phylogeny and Evolution* 34: 227–244.
- MacArthur, R.H. & Levin, R. 1967. Limiting similarity convergence and divergence of coexisting species. *American Naturalist* 101: 377–387.
- Matthews, W.J. 1986. Fish faunal “breaks” and stream order in the eastern and central United States. *Environmental Biology of Fishes* 17: 81–92.
- McCune, B. & Mefford, M.J. 2009. PC-ORD. Multivariate analysis of ecological data, Version 5. MjM Software, Glendon Beach, OR.
- Montaña, C.G. & Winemiller, K.O. 2009. Comparative feeding ecology and habitats use of *Crenicichla* species (Perciformes: Cichlidae) in a Venezuelan floodplain river. *Neotropical Ichthyology* 7: 267–274.
- Montoya, J.V., Roelke, D., Winemiller, K.O., Cotner, J.B. & Snider, J. 2006. Hydrological seasonality and benthic algal biomass in a Neotropical floodplain river. *Journal of North American Benthological Society* 25: 157–170.

- Mouillot, D., Dumay, O. & Tomasini, J.A. 2007. Limiting similarity, niche filtering and functional diversity in coastal lagoon fish communities. *Estuarine Coastal and Shelf Science* 71: 443–456.
- Peres-Neto, P.R. 2004. Patterns in the occurrence of fish species in streams: the role of site suitability, morphology and phylogeny versus species interactions. *Oecologia* 140: 352–360.
- Petry, P., Bayley, P.B. & Markle, D.F. 2003. Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon river floodplain. *Journal of Fish Biology* 63: 547–579.
- Ricklefs, R.E. & Miles, D.B. 1994. Ecological and evolutionary inferences from morphology: an ecological perspective. In: Wainwright, P.C. & Reilly, S.M. eds. *Ecological morphology*. Chicago: University of Chicago Press, pp. 13–41.
- Rodriguez, M. & Lewis M. Jr 1997. Structure of fish assemblages along environmental gradient in floodplain lakes in the Orinoco River. *Ecological Monograph* 67: 109–123.
- Rosenzweig, M.L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Savino, J.F. & Stein, R.A. 1982. Predatory-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Transaction of American Fisheries Society* 111: 225–226.
- Schlosser, J.I. 1987. A conceptual framework for fish communities in small warmwater streams. In: Matthews, W.J. & Heins, D.C., eds. *Community and evolutionary ecology of North American stream fishes*. Norman: University of Oklahoma Press, pp. 17–24.
- Smith, W.L., Chakraborty, P. & Sparks, J.S. 2008. Phylogeny, Taxonomy, and evolution of Neotropical cichlids (Teleostei: Cichlidae:Cichlinae). *Cladistics* 24: 1–17.
- Southwood, T.R. 1988. Tactis, strategies and templets. *Oikos* 52: 2–18.
- Thompson, J.N. 2009. The coevolving web of life. *The American Naturalist* 173: 125–150.
- Wainwright, P.C. & Reilly, S.M. 1994. *Ecological morphology: integrative organismal biology*. University of Chicago Press, Chicago.
- Willis, S.C., Winemiller, K.O. & López-Fernández, H. 2005. Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. *Oecologia* 142: 284–295.
- Winemiller, K.O. 1990. Spatial and temporal variation in tropical fish networks. *Ecological Monograph* 60: 331–367.
- Winemiller, K.O. 1991. Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecological Monographs* 61: 343–365.
- Winemiller, K.O. & Jepsen, D.B. 1998. Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology* 53: 267–296.
- Winemiller, K.O., Kelso-Winemiller, L.C. & Brenkert, A.L. 1995. Ecological and morphological diversification in fluvial cichlid fishes. *Environmental Biology of Fishes* 44: 235–261.
- Winemiller, K.O., Taphorn, D.C. & Barbarino-Duque, A. 1997. Ecology of *Cichla* (Cichlidae) in two blackwater rivers of southern Venezuela. *Copeia* 4: 690–969.
- Winemiller, K.O., Montoya, J.V., Roelke, D.L., Layman, C.A. & Cotner, J.B. 2006. Seasonal varying impact of detritivorous fishes on the benthic ecology of a tropical floodplain river. *Journal of North American Benthological Society* 25: 250–262.
- Wood, B.M. & Bain, M.B. 1995. Morphology and microhabitat use in stream fish. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 1487–1498.
- Zobel, M. 1997. The relative role of the species pools in determining plant species richness. An alternative explanation of species coexistence?. *Trends in Ecology and Evolution* 12: 266–269.