

Habitat affinity, the seasonal flood pulse, and community assembly in the littoral zone of a Neotropical floodplain river

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Abstract. The annual flood pulse in tropical lowland rivers creates a continually moving land–water margin that forces aquatic organisms of the littoral zone to relocate to new habitats at intervals ranging from days to weeks. Thus, species assemblages in patchy littoral-zone habitats have large potential to be influenced by stochastic colonization dynamics, whereby organisms may exhibit weak selection for mesohabitat features and arrive on a patch in no particular sequence. We examined species assemblages of fishes and macroinvertebrates occupying habitats of varying structural complexity through an annual flood cycle of the Cinaruco River, a species-rich floodplain river in the southern llanos of Venezuela. We collected 268 standardized samples that contained 54,596 individual fishes representing 156 species (23 families) and 6973 macroinvertebrates representing 8 families. Analysis of species-specific patterns of habitat occupancy based on a randomization procedure indicated greater species selectivity during low water (92% of taxa) relative to rising- and falling-water periods (60% and 63% of taxa, respectively). Community-wide correspondence analysis (CA) revealed similar patterns. Assemblages from similar habitat types clustered together in the CA ordination, and these nonrandom patterns were most apparent during low water. Results from partial canonical correspondence analysis revealed that assemblage structure was strongly influenced by habitat type (patches of different composition located within the shallow littoral zone of either the river main channel or lagoons), which accounted for 56% of the total explainable variation in the species × sample matrix. Mesohabitat parameters (e.g., water velocity, depth), sampling period (month), and location on the landscape explained 30%, 23%, and 17% of variation, respectively. As water level changes and the aquatic–terrestrial interface moves across the landscape, species assemblages in patchy littoral habitats, while highly variable, reconstitute with significant determinism. At the same time, a large proportion of unexplained variation in assemblage structure probably is associated with unmeasured components of landscape variation as well as a stochastic element in colonization dynamics.

Key words: assemblage structure, beta diversity, habitat complexity, land–water interface, macroinvertebrates, Neotropical fishes, Orinoco Basin, variation partitioning, Venezuela.

Organisms are challenged to respond adaptively to ecological features and processes operating over variable time scales on landscapes consisting of habitat mosaics (Pianka 1966, Levin 1992). Identification of patterns of species occurrence and their relationships to habitat features provides a foundation for explicit, testable hypotheses of community structure and dynamics (Townsend 1989, Hubbell 2001). Local communities are assembled under the combined influence of stochastic and deterministic processes. Recently, Hubbell (2001) proposed that distributions of species relative abundances of many, and perhaps

most, local assemblages can be explained by a model of stochastic assembly from regional species pools. Yet most communities also display “environmentally mediated patterns” (Wilson 1999) in which patterns of species occurrence at the local scale correlate with characteristics of their abiotic environments. Biotic (deterministic) interactions, such as predation and competition (Levin and Paine 1974, Tilman 1982, 1994, Hurtt and Pacala 1995), may further constrain local communities such that assemblages exhibit persistent structure (Grossman et al. 1982) or non-random patterns of species relative abundance and distribution (Gotelli and Graves 1996).

The structure of fish and macroinvertebrate assemblages in streams frequently is associated with physical habitat features (Angermeier and Karr 1983, Schlosser

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1987, Gladden and Smock 1990, Grossman et al. 1998, Ramirez and Pringle 1998, March et al. 2001, Melo and Froehlich 2001). Decades of debate regarding stochastic vs deterministic fish assemblages in temperate streams has given way to the realization that both elements structure assemblages, and interpretations depend largely on the scale and resolution of observations (summarized by Matthews 1998). Thus, some studies have stressed high variability in stream fish assemblages (e.g., Grossman et al. 1990, Taylor and Warren 2001), and others emphasize nonrandom assemblage organization (e.g., Angermeier and Winston 1998, M rigoux et al. 1998, Jackson et al. 2001) in which habitat features seem to provide the basic template upon which communities are assembled (*sensu* Wilson 1999). The concept of habitat templates provides the basis for assessment tools for evaluating instream flow requirements for stream biota (Stalnaker 1993). However, the structure of stream faunas is not entirely determined by habitat availability because species vary in their responses to disturbance regimes (Orth 1987, Townsend and Hildrew 1994). Townsend (1989) proposed a patch-dynamics model for stream communities whereby local habitats experiencing frequent spate-driven hydrologic disturbances (e.g., intermittent and high-gradient streams) are dominated by proficient colonizers (*r*-strategists) that may experience only weak or occasional competition or predation. Species relative abundances in high-disturbance habitats would reflect colonization and recruitment dynamics. In contrast, local habitats subjected to infrequent or weak disturbances probably support communities structured by species interactions more than colonization (Menge and Sutherland 1987, Townsend 1989, Power 1995).

It is not known if the same mechanisms structure species assemblages in temperate streams and large tropical rivers. Early descriptive studies conducted in tropical lowland rivers suggested that fish assemblages are stochastically assembled in response to constant, gradual water-level fluctuations (Bonetto et al. 1969, Lowe-McConnell 1979), but this hypothesis has not been evaluated rigorously. Based on samples collected from a variety of habitats in the Rio Negro, Brazil, Goulding et al. (1988) concluded that species composition of local communities was not significantly different from random. Goulding et al. (1988) concluded that high α diversity, including many rare taxa, yielded low similarity among local communities in similar habitats. Dissimilar local assemblages in similar habitat types were presumed to be products of a random process of assembly (i.e., colonization dynamics) under a regime of constantly changing water level, a view consistent with Townsend's patch-dynamics model (Townsend 1989) and Hubbell's (2001) neutral model.

Lowe-McConnell (1964) and Junk et al. (1989) described floodplain–river ecosystem dynamics in which the seasonal flood pulse is the major driving variable for ecological processes. Among other effects, seasonal flooding allows aquatic organisms to redistribute themselves within the spatial mosaic of the river-floodplain (Rodr guez and Lewis 1994, 1997). Rising floodwaters make new aquatic habitats available, whereas floodwater subsidence and desiccation render shallow-water habitats inhospitable. Gradually changing water level forces aquatic organisms of the shallow littoral zone to colonize new habitats continually. Fishes and late instars of invertebrates move between habitat patches (Fernandes 1997, Smock 1999), whereas more ephemeral taxa may colonize new habitats largely via reproduction, dispersal of propagules, and establishment of new recruits (Lansac-T ha et al. 1993, Smock 1999). During the descending phase of a flood pulse, juvenile fishes migrate from ephemeral floodplain habitats into deeper main channel and lagoon habitats (Lowe-McConnell 1964, Bonetto et al. 1969, Winemiller 1996, Winemiller and Jepsen 1998, Agostinho et al. 2000).

A few studies of tropical river fish assemblages support Goulding et al.'s (1988) "random associations" hypothesis (Jepsen 1997, Saint-Paul et al. 2000), but other studies have shown assemblage patterns to be linked with environmental variation (Rodr guez and Lewis 1994, Winemiller 1996). During the dry season, lakes in the Orinoco River floodplain reveal regular patterns of fish-assemblage structure correlated with water transparency, and these patterns seem to be caused by an interaction between species sensory capabilities and feeding efficiencies relative to light penetration (Rodr guez and Lewis 1994, 1997, Lewis et al. 2000). These fish assemblages appear to be reshuffled in a random manner during the wet season when floodplain connectivity is high and water quality is more homogeneous. Analysis of a 10-y data set from a Venezuelan floodplain creek indicated that fish assemblage structure was associated with predictable seasonal variation in habitat quality and quantity (Winemiller 1996). Interannual variation in fish assemblage structure in residual floodplain pools of the Sokoto River, Nigeria, appeared to be influenced by habitat selection and stochastic factors, such as haphazard stranding during floodwater recession (Chapman and Chapman 1993). The greatest proportion of variation in species diversity of juvenile fish assemblages in floodplain creeks of French Guiana was explained by a statistical model that included both habitat variability (e.g., disturbance frequency) and habitat state (e.g., mean turbidity, depth) variables (M rigoux et al. 1999).

Here we examine species assemblage patterns in a large lowland river in the llanos (savanna) region of Venezuela (Orinoco Basin) that experiences a gradual but substantial (>5 m) annual flood pulse. Specifically, we evaluate associations between fish and macroinvertebrate assemblage structure and habitat within the shallow littoral zone. Aquatic macroinvertebrates appear relatively depauperate in this blackwater system (several species of shrimp and aquatic insects are locally abundant), but were included in our study because they respond to habitat dynamics by means comparable with fishes, and they interact with fishes in local food webs. Our objectives were to: 1) test for nonrandom occupation of habitat patches by individual taxa, 2) evaluate whether assemblage structure is consistent with the random association hypothesis of Goulding et al. (1988), and 3) examine seasonal/hydrological effects on assemblage–habitat relationships.

Methods

Study system

Field sampling was conducted in the Cinaruco River, Apure State, Venezuela (between lat 6°32'N, long 67°25'W and lat 6°34'N, long 67°13'W). The Cinaruco River is a blackwater (low pH, low conductivity, low suspended solids) tributary of the whitewater (neutral pH, high conductivity, high suspended solids) Orinoco River. This meandering lowland river has an extensive floodplain, 1 to 4 km wide in the study region, which is seasonally inundated. During the low-water period (typically January to March), aquatic habitats are reduced to a spatial mosaic consisting of the main channel (average width = 150 m, depth = 2–3 m), side channels, and lagoons (i.e., floodplain lakes with a permanent surface-water connection to the main channel). Beginning in April or May, rising water floods the gallery forest and flanking savanna, greatly increasing the area of aquatic habitat. The flood crest occurs typically in September, and falls continuously from October through December. The timing and range of water-level fluctuation during the year of our study were characteristic for this system (Fig. 1).

The Cinaruco River supports a diverse fish fauna (>260 species) dominated by species characteristic of Amazonian blackwater rivers (Jepsen 1997, Arrington and Winemiller 2003, Hoeinghaus et al. 2003, Layman and Winemiller 2004). Trophic specializations (e.g., lepidophagy, fin-eating, seed-eating) and morphological diversification contribute to the ecological diversity observed in this system (Jepsen 1997, Jepsen and Winemiller 2002, Layman et al. 2005). Earlier work on this system speculated that near-shore fish assemb-

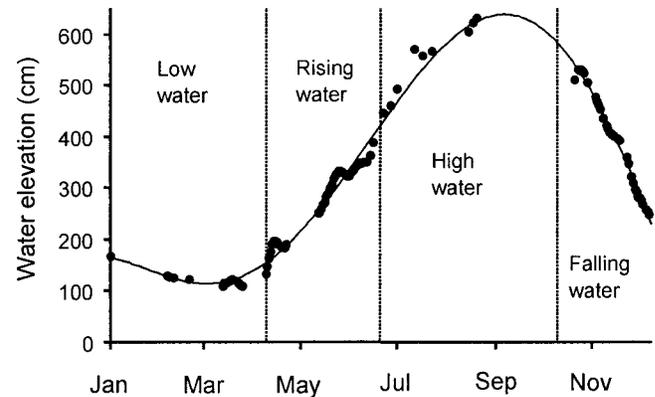


FIG. 1. Pattern of the annual flood-pulse in the Cinaruco River at Laguna Larga during 1999. Four hydrological periods were defined for sampling: low-water = January to March, rising-water = April to June, high-water = July to September, and falling-water = October to December. The y-axis scale is intended to show magnitude of water-level fluctuation, not elevation above sea level.

lages were randomly structured (Jepsen 1997), but a separate study found that piscivorous peacock cichlids (*Cichla* spp.) occurred nonrandomly among habitat types (Jepsen et al. 1997).

Field sampling

Our monthly surveys were divided among 3 hydrologic periods: low-water (January–March), rising-water (April–June), and falling-water (October–December) (Fig. 1). No samples were collected during the high-water (July–September) period. Sampling targeted fishes and macroinvertebrates (e.g., palaemonid shrimp, polymitarcyid mayflies, dragonfly larvae), the dominant macrofaunal (>5 mm length) elements of shallow habitats in this system. Quantitative surveys were conducted in near-shore habitats (water depth = 20–130 cm) in both the river main channel and continuously connected backwater lagoons during 1999. Each month (except for the high-water period), 7 broad sandbanks (0.1–0.5 km in length) in the river main channel and 7 sandbanks in 7 different lagoons were sampled. In our study, sandbanks were defined as areas with >95% coarse-sand substrate. These areas often corresponded to pointbars located on the inside of meanders. On each sandbank, samples were collected from 3 different habitat types (categories defined a priori) that varied in structural complexity. Areas of open sand and patches of submerged wood (snags) were sampled in both river main channel and lagoon areas (total of 14 open-sand areas and 14 submerged-wood patches/mo). In addition, patches of simulated-rock habitat (see below) were sampled in

the river main channel (total of 7/mo), and natural patches of leaf litter (areas with >80% coverage by dead leaves) were sampled in lagoons (total of 7/mo).

Patches of submerged wood and simulated rock were created to allow effective sampling of these hard, structurally complex substrates. Each month, a single submerged-wood habitat was constructed on each of the river main channel and lagoon sandbanks (14 submerged-wood patches/mo). Submerged-wood patches (1 m²) were constructed with similarly composed collections of branches (diameter = 3–25 cm, length = 75–100 cm) gathered from the river. Natural rock patches, the least common of our 4 habitat types, occur in discrete patches along the shoreline of the river main channel (rock patches are less common in lagoons). Each month a single simulated-rock patch (1 m²) was placed on each of the 7 main-channel sandbanks. These patches consisted of 8 unglazed ceramic building blocks (10 × 20 × 30 cm), each with 8 square internal compartments open on each end of the block. Fishes and macroinvertebrates commonly take refuge in the many interstices of naturally occurring rock habitats, and piles of ceramic blocks simulated this key feature of natural rock patches, yet allowed us to sample inhabitants efficiently by encircling the patch with a seine and systematically removing each block to collect occupants. Furthermore, fish species that colonized our submerged-wood and simulated-rock patches were nearly all the same ones collected from natural submerged-wood and rock habitats, respectively (Willis et al. 2004).

Seven days after samples were collected for a given month, patches of submerged wood and simulated rock were randomly relocated among sandbanks. Thus, for each month, each constructed habitat remained in place for 21 to 24 d prior to sampling. Naturally occurring habitat patches frequently become available (during the rising-water period) or inhospitable (during the falling-water period) over a similar time interval (Fig. 1). Moreover, we have demonstrated experimentally that simulated-rock patches reach asymptotic species density in ~24 d (Arrington et al. 2005).

All samples were collected during daylight hours using the same seine (6.4 m × 1.8 m with 4-mm mesh). The method of deployment in each habitat type was designed to maximize capture of relatively small (1.5–8 cm) benthic fishes, and macroinvertebrates and relatively sedentary fishes of any size. Fast-swimming midwater fishes occupying positions above substrates probably eluded capture in many instances (Arrington and Winemiller 2003), but this potential source of bias should not have varied systematically among habitat types, locations, or seasons. We sampled open-sand

habitats at randomly selected sites within a given stretch of sandbank using 3 nonoverlapping hauls in which the seine was oriented perpendicular to shore and dragged 10 m parallel to the shoreline before exiting on the shore (total area sampled = 120 m²). Each leaf-litter sample was obtained from 3 nonoverlapping 5-m hauls of the seine parallel to shore (total area sampled = 60 m²). Simulated-rock and submerged-wood habitats were sampled by completely encircling constructed habitats with the seine (total area sampled = 1 m²), then removing the blocks or wood (taking care to dislodge all macrofauna) before pulling the seine and its contents onto shore. For every sample, care was taken to ensure the collection of all fishes and macroinvertebrates retained in the seine net. Abundance data for samples were standardized as number of individuals/m² before analysis.

The following environmental variables were measured at each sampled habitat patch: water velocity, water depth, leaf-litter % cover, and vegetation (including macroalgae) % cover. Water depth and velocity were measured at 3 locations within each habitat patch (shallow edge, center, deep edge). The % of the substrate covered by vegetation and leaf litter was estimated visually. During the falling-water period (October–December), we were unable to sample lagoon sandbank habitats because almost all unforested littoral areas were too deep. During this period, some main-channel sandbanks were colonized by macrophytes (*Eleocharis* sp., *Zanichellia* cf. *palustris*) and filamentous algae, and both vegetated and non-vegetated sandbank habitats were sampled in the river main channel.

Fishes and macroinvertebrates in each sample were preserved in 10% formalin. Preserved specimens were identified and counted in the laboratory; fish were identified to species, and invertebrates generally were identified to family. Trophic classifications were based on Merritt and Cummins (1984), Taphorn (1992), and Arrington et al. (2002). Specimens are archived in the Museo Ciencias Naturales, Guanare, Venezuela, and the Texas Cooperative Wildlife Collection, College Station, Texas, USA. Removal of nearly 55,000 individual fish from the study region over a 12-mo interval did not impact populations because samples were collected over a large area and most fishes removed were small species with life histories conferring high population resilience (Winemiller 1989).

Data analysis

The fauna from each habitat patch was treated as a separate sample. Spatial and temporal variation in patterns of relative abundance and habitat occupancy

by constituent species were analyzed using randomization and ordination techniques.

Weighted preference index.—Species' seasonal distributions in relation to habitat types were analyzed using the weighted preference index (WPI), a randomization technique that does not require knowledge of the availability of the various habitats in the environment (Clark et al. 1999). WPI for species j is calculated as

$$\text{WPI}_j = \sqrt{\left[\sum_{i=1}^S p_i \left(\frac{n_{ij}}{p_i} - \frac{N_j}{P} \right)^2 / P \right]} \quad (1)$$

where i = habitat types 1 to S , S is the number of habitat types, p_i is the number of samples of habitat type i , P is the total number of samples, n_{ij} is the number of samples containing species j in habitat type i , and N_j is the total number of samples in which species j occurred. A separate WPI value was calculated for each species during each hydrologic period in which the species occurred in >4 samples. Perfect generalists have WPI scores = 0; species with nonrandom habitat use have significant positive scores. To test for significance, observed WPI values were compared with those obtained for each frequency of occurrence, within the range of observed values, by randomizing our species \times sample matrix. Significance was indicated when an observed WPI value exceeded the 95th percentile of simulated values ($\alpha = 0.05$). EcoSim (version 7, Acquired Intelligence, Inc. and Kesey-Bear, Jericho, Vermont) was used to produce randomized matrices. Total species occurrences were held constant (e.g., common species remain common in randomized matrices), species occurrences among samples were allowed to vary in an equally probable manner (species were equally likely to occur in any sample), and random matrices produced with missing species or empty sites were discarded. When >1 species had the same frequency of occurrence value, we randomly selected a single species' 95th percentile of simulated values to represent that position along the abscissa.

Community ordination.—Unconstrained ordination (correspondence analysis [CA]) orders samples and species along axes optimized to model variation in species composition. Our species \times sample matrix, including samples from each season, location, and habitat type was analyzed to determine whether there was nonrandom organization of fish and macroinvertebrate assemblages. CA was done using CANOCO (version 4.5, Microcomputer Power, Ithaca, New York; ter Braak and Šmilauer 1998). Species (fishes) and family (invertebrates) abundances in samples were transformed [$y' = \log(y + 1)$] to minimize the range and skew of distributions. Taxa that did not occur in $>5\%$ of samples (i.e., 15 of 268 samples) were

eliminated from the multivariate dataset. By selecting Hill's scaling and focusing on sample scores, species turnover is expressed as standard deviation (SD) units, in which species turnover is $\sim 50\%$ between samples separated by 1 SD, and nearly complete turnover in species composition occurs at 4 SD units (Hill and Gauch 1980). CA produced an arch effect (Hill and Gauch 1980), but detrending was not done because of criticisms of detrended correspondence analysis (DCA) (Wartenberg et al. 1987, Oksanen and Minchin 1997). Mean similarity of samples within and among habitat types during different periods was estimated by comparing mean pairwise Euclidean distances based on sample CA axis 1 and 2 scores.

Multivariate relationships between community structure and environmental variables were evaluated with constrained ordination (canonical correspondence analysis [CCA]; ter Braak and Šmilauer 1998) using CANOCO. CCA entails an additional step during which sample and species scores are optimized relative to a set of explanatory variables, in this case environmental variables. Partial canonical correspondence analysis (pCCA) was used to partition variation in local community composition among 4 sets of environmental variables (Borcard et al. 1992, Økland 1999, 2003, Økland et al. 2003), which resulted in 15 components of variation. Briefly, variation partitioning permits evaluation of the relative importance of each set of environmental variables both separately and jointly. Variation caused solely by a single set of environmental variables is termed the unique component, whereas variation shared by ≥ 2 sets of constraining variables is termed partial intersection (e.g., the partial intersection of habitat and location [habitat \cap location]). Partial intersections may be large because of nonindependence between sets of variables. To avoid inflating the amount of variation explained, each set of explanatory variables was reduced to those variables that were significant ($\alpha = 0.01$) using the forward selection procedure in CANOCO (Borcard et al. 1992, Økland 2003). Based on this forward selection procedure, the following variables were included in the partial CCA: mesohabitat (maximum water velocity, maximum water depth, leaf litter % cover, and vegetation % cover), habitat (river sand, river submerged-wood, river rock, lagoon sand, lagoon submerged-wood, lagoon leaf-litter), location (3 main-channel sandbanks and 2 lagoon sandbanks), and month (January, February, March, April, June, November, and December). Categorical variables were transformed into dummy binary variables (ter Braak and Šmilauer 1998). Monte Carlo permutation tests ($n = 1000$ permutations) were used to evaluate the significance of species–environment relationships.

The amount of variation explained is reported in inertia units (IU) \times 1000. See Økland (2003) for a detailed description and justification of the variation partitioning methodology; a recent application of the technique is found in Økland et al. (2003).

Results

We collected 268 standardized seine samples from 6 habitat types distributed over 14 sandbanks. Sampling yielded 54,596 fish specimens representing 155 species and 1 family and 6973 individual macroinvertebrates representing 5 families and 2 other taxa (Appendix). A small shrimp species (*Macrobrachium* cf. *dierythrum*) had the greatest frequency of occurrence in samples (59%) and was the 2nd-most abundant species overall (11%). The fish species that occurred in the greatest number of samples (40%) was a small invertivorous pike cichlid, *Crenicichla* af. *wallacei*, but this species made up <1% of individuals sampled. *Aphyocharax alburnus*, a small invertivorous characid, was the 2nd-most frequently collected fish species, occurring in 37% of samples and making up 7% of individuals. The most abundant species was *Hemigrammus analis*, another small invertivorous characid that accounted for 13% of individuals, occurring in 30% of samples. Twenty-two of 164 total taxa (13%) were represented by a single individual.

WPI

Most commonly sampled taxa were nonrandomly distributed among habitats. Based on comparisons with null distributions generated from randomizations of the species \times sample matrix, nonrandom ($\alpha = 0.05$) habitat use was greatest during the low-water season. For example, the benthic invertivore *Creagrutus phasma* (Characidae) occurred in 67% of main-channel open-sand samples, the algivorous catfish *Parotocinclus eppleyi* (Loricariidae) occurred in 24% of river main channel submerged-wood samples, the invertivorous driftwood catfish *Centromochlus concolor* (Auchenipteridae) occurred in 50% of lagoon submerged-wood samples, and the invertivorous *Pyrrhulina lugubris* (Lebiasinidae) occurred in 29% of lagoon leaf-litter samples. None of these species was ever collected in other habitat types during the low-water season. Across all seasons, 5 (5%) of the 92 species (those that occurred in >4 samples) revealed extreme habitat specialization, i.e., they occurred in only a single habitat type. Most species occurred in multiple habitat types (Appendix), but their distributions were skewed among habitat types, especially during the low-water period when 97% of species were distributed among habitat types in a statistically nonrandom pattern (Fig. 2). During the rising- and falling-water periods, a

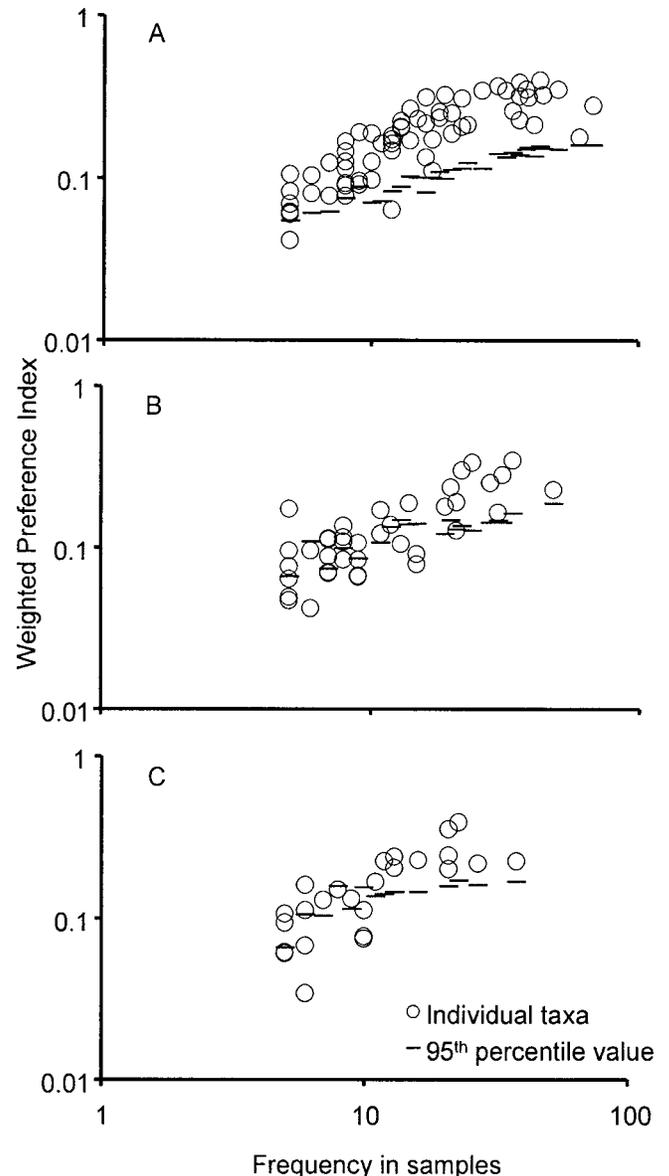


FIG. 2. Distribution of fish and macroinvertebrate taxa with $n > 4$ individuals in terms of the weighted preference index for habitat type during low-water ($n = 74$ taxa) (A), rising-water ($n = 43$ taxa) (B), and falling-water ($n = 32$ taxa) (C) hydrologic periods. The dash indicates the 95th percentile value from randomization calculations (see text for details). Taxa above the dash showed a statistically significantly ($p < 0.05$) nonrandom distribution in relation to habitat type. Taxa below the dash were randomly distributed ($p > 0.05$).

smaller % of species exhibited nonrandom patterns of habitat occupancy (60% and 63%, respectively). When consideration of WPI scores was restricted to only those species that occurred in >15 samples (per hydrologic period), a greater % of species demonstrated a nonrandom pattern of occupancy of available

habitats (low water: 100% of species, rising water: 91% of species, falling water: 71% of species).

Community ordination

CA of our complete sample \times species matrix resulted in nonrandom clustering of samples (Fig. 3A, B, C). (Species scores resulting from the CA of the complete sample \times species matrix are available from: http://wfsc.tamu.edu/winemiller/data/Arrington_Winemiller_JNABS_appendix-B.htm). The 1st CA axis (eigenvalue = 0.62, 8.3% of variation) separated samples and species along an axis that approximated a gradient of habitat structural complexity. Samples were distributed along axis 1 in ascending order: lagoon submerged-wood, river submerged-wood, lagoon open-sand, river open-sand. The 2nd CA axis (eigenvalue = 0.53, 7.0% of variation) tended to separate lagoon leaf-litter samples from other samples because of a unique and diverse assemblage of small characids. Total among-habitat β diversities for the first 2 CA axes (measured as gradient lengths) were 6.5 SD and 5.0 SD, respectively (Fig. 3A, B, C), indicating complete dissimilarity among samples located at opposite ends of these gradients.

CA revealed differences in assemblage composition among habitat types and between main-channel and lagoon samples. For example, submerged-wood habitat in the river main channel supported a different local community than submerged-wood habitat in lagoons (Fig. 4). Polymitarciid mayflies (collector-gatherer; not shown), *Dekeyseria scaphyrhyncha* (loricariid catfish, algivore/detritivore), and *Platydoras costatus* (doradid catfish, invertivore) were collected regularly from submerged-wood habitat in lagoons (Fig. 4). Of these taxa, only *D. scaphyrhyncha* was collected from submerged-wood habitat in the river main channel during low water. *Pimelodella* sp. (pimelodid catfish, invertivore) was collected consistently in main-channel simulated-rock habitat, less consistently in main-channel submerged-wood habitat, and infrequently in main-channel open-sand habitat; this species was never collected from lagoon habitats. Two small invertivorous characids (*Rhinobrycon negrensis* and *Bryconamericus* sp.) both occurred frequently in main-channel open-sand samples, but rarely in lagoon open-sand samples, whereas other small invertivorous characids (e.g., *Moenkhausia copei*, *Hemigrammus vorderwinkleri*) and small invertivorous cichlids (e.g., *Apistogramma* sp., *Biotodoma wavrini*) dominated lagoon samples. Dragonfly larvae (Gomphidae) were collected from both main-channel and lagoon habitats, but they were much more commonly sampled from lagoon leaf-litter habitats (Appendix).

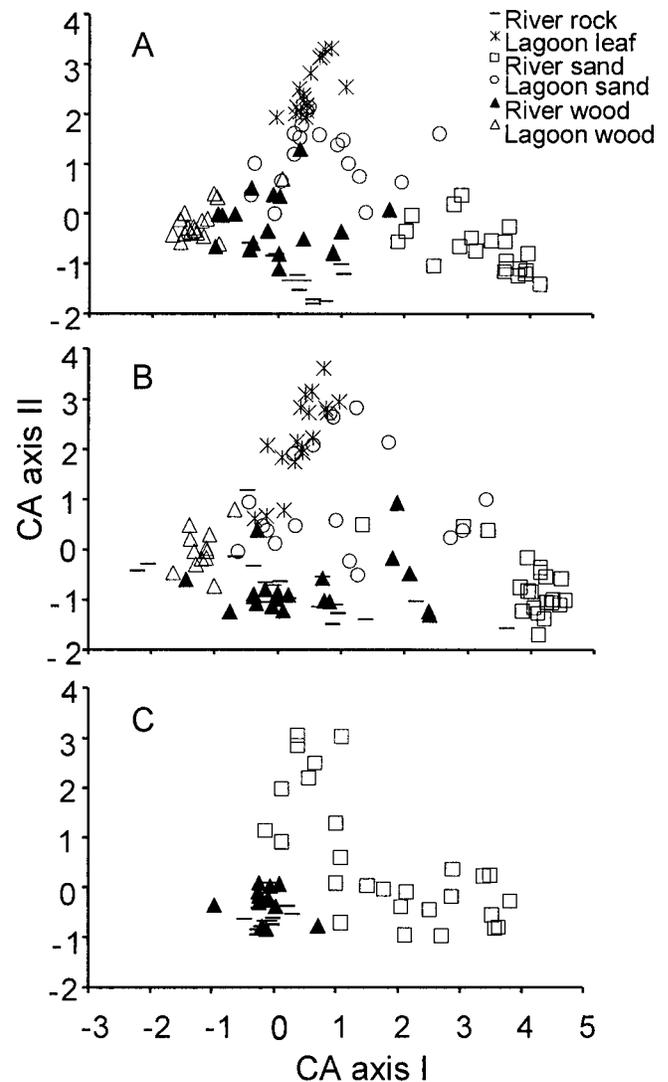


FIG. 3. Sample scores from correspondence analysis (CA) of the complete sample \times species matrix during low-water (A), rising-water (B), and falling-water (C) hydrologic periods. To facilitate interpretation, the 3 water periods are graphed separately. Axes are scaled in standard deviation (SD) units. Approximately 50% change in species composition occurs in 1 SD and a complete turnover in species composition of samples occurs in 4 SD units. Rock = simulated rock, wood = submerged wood.

On average, community composition was most distinct among habitats during the low-water period (Fig. 3A). During this period, sample scores from river sand, river simulated rock, lagoon leaf litter, and lagoon submerged wood did not overlap, though some common species (e.g., *Macrobrachium* cf. *dierythrum*) occurred in all sampled habitats. During the rising-water period, higher within-habitat variability in sample CA scores yielded greater overlap among main-channel samples from different habitat types (Fig. 3B),

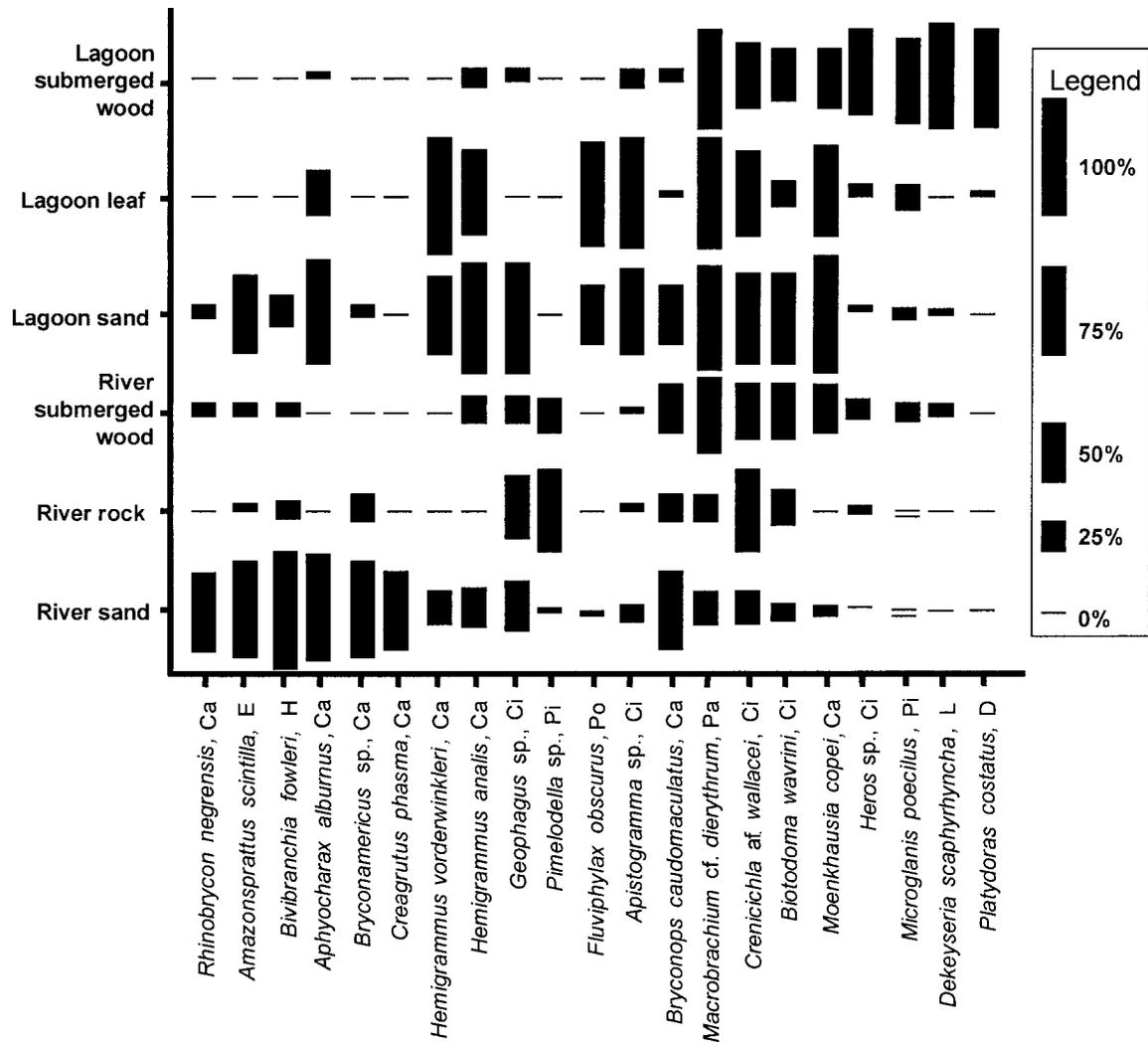


FIG. 4. Habitat occupancy by 21 dominant taxa (i.e., 5 most commonly sampled taxa/habitat type) during the low-water hydrologic period. Taxa are sorted along the abscissa using correspondence analysis (CA) axis-1 scores. Scaled frequency of occurrence (%) is plotted for each species for each habitat type. Letters following species names indicate family-level taxonomy: Ca = Characidae, Ci = Cichlidae, D = Doradidae, E = Engraulidae, H = Hemiodontidae, L = Loricariidae, Pa = Palaemonidae, Pi = Pimelodidae, Po = Poeciliidae. Rock = simulated rock, wood = submerged wood.

and the same pattern was true for main-channel samples collected during the falling-water period (Fig. 3C). Within-habitat similarity, measured as the inverse of mean within-habitat pairwise Euclidean distance (1/mean ED), was greatest (1.12) during the low-water period when habitat availability was lowest and densities of aquatic organisms were highest. Within-habitat similarity was 0.95 during the falling-water period and 0.77 during the rising-water phase. Among-habitat similarity was greatest (0.52) during falling water relative to low- and rising-water periods (0.37 and 0.34, respectively). Dispersion of within-habitat sample differences (SD of mean within-habitat ED) was lowest during the low-water period (0.29) followed by the rising (0.48) and falling-water (0.95) periods.

Lagoon habitats were not sampled during the falling-water period, but main-channel samples indicated that variation in community structure was greater during this period than during the low-water period, and variation was highest for river open-sand samples. During the falling-water period, main-channel open-sand habitats included sites with aquatic macrophytes and filamentous algae. The presence or absence of aquatic plants appeared to account for divergence among main-channel open-sand CA axis scores during the falling-water period. Species density of main-channel open-sand samples lacking aquatic plants (10.2 ± 1.4 [mean \pm SE]; $n = 18$) was lower than species density for main-channel open-sand samples with aquatic plants (20.2 ± 3.6 ; $n = 9$).

TABLE 1. Partial canonical correspondence analysis (pCCA) showing the % of variation in the species \times sample matrix explained by sets of significant environmental variables ($p < 0.01$). Variation explained (VE) is given in inertia units (IU \times 1000) and represents the amount of variation explained by the constraining variables that is not shared with the covariables. Components of variation shared by ≥ 2 sets of constraining variables are termed partial intersections (e.g., Habitat \cap Location). Fraction of total variation explained (TVE) is the relative amount of variation explained by the different sets of constraining variables and equals VE/TVE. Total inertia = 7554, sum of all canonical eigenvalues = 2468, and TVE = 32.7. \cap = intersection of components of variation, \cup = union of components of variation.

Constraining Variables	Covariables	VE (IU \times 1000)	Fraction of TVE
Habitat	Month \cup Location \cup Mesohabitat	960	38.9
Month	Location \cup Habitat \cup Mesohabitat	445	18.0
Mesohabitat	Month \cup Location \cup Habitat	283	11.5
Habitat \cap Mesohabitat	Month \cup Location	272	11.0
Location	Month \cup Habitat \cup Mesohabitat	236	9.6
Month \cap Mesohabitat	Habitat \cup Location	84	3.4
Habitat \cap Location	Month \cup Mesohabitat	53	2.1
Location \cap Habitat \cap Mesohabitat	Month	45	1.8
Location \cap Mesohabitat	Month \cup Habitat	45	1.8
Habitat \cap Month	Location \cup Mesohabitat	20	0.8
Month \cap Location \cap Habitat \cap Mesohabitat		39	1.6
Month \cap Location \cap Habitat	Mesohabitat	3	0.1
Month \cap Location	Habitat \cup Mesohabitat	0	0.0
Month \cap Location \cap Mesohabitat	Habitat	-4	-0.2
Month \cap Habitat \cap Mesohabitat	Location	-13	-0.5

Variation partitioning using pCCA explained 33% of the total variation in the species \times sample matrix (i.e., total variance explained [TVE] = 33% of total inertia [TI]). Among the 4 sets of explanatory variables, habitat explained the largest unique portion of TVE (38.9%) in the species \times sample data matrix (Table 1). In total, habitat (including the unique component and all partial intersections) explained $\sim 56\%$ of TVE in the species \times sample matrix, whereas mesohabitat parameters, month, and location variables explained only $\sim 30\%$, $\sim 23\%$, and $\sim 17\%$ of TVE, respectively (Table 1). Two of the 3rd-order partial intersections explained a small negative component of TVE.

Discussion

Patch dynamics

The seasonally dynamic aquatic–terrestrial interface in low-gradient Neotropical floodplain rivers results in gradual but continuous alteration of local habitats between suitable and inhospitable states. Patches of woody debris, leaf litter, or rock habitat located above the water line are completely inhospitable to aquatic organisms until submerged by floodwaters. Similarly, as low-elevation substrates are submerged at greater depths during the rising-water phase, they represent poor habitat for most of the small fish genera surveyed in the present study. Thus, we suggest that the patch-dynamics concept of stream community ecology (Townsend 1989) applies to the littoral zone of the

Cinaruco River. This idea does not imply that community assembly in large tropical rivers is regulated by spate-driven hydrologic disturbances; rather, it proposes that it is regulated by gradual and continuous change in water depth that results in sufficient temporal variation in spatially heterogeneous littoral zones that local communities are strongly influenced by colonization dynamics. Therefore, Townsend's (1989) "mobility controlled" concept of community dynamics appears to apply to tropical lowland rivers given the rate of water-level change and the mobility of constituent taxa, particularly fishes and relatively long-lived, motile invertebrates such as shrimp.

Frequent spatial reshuffling, i.e., both active and passive repositioning, of organisms creates large potential for stochastic effects on assemblage structure. Predictable patterns of community assembly may occur in mobility-controlled environments if species preferentially colonize or differentially survive in particular habitats; however, under mobility control, competitive exclusion should rarely, if ever, occur (Tilman 1994, Hurtt and Pacala 1995). Our results indicate that most sampled taxa inhabited littoral habitats in a nonrandom manner throughout seasonal water-level changes, although we were able to evaluate habitat occupancy for only a subset ($n = 92$) of the fishes in this river ($n > 260$). However, nonrandom habitat occupancy is not necessarily a product of deterministic interactions, but rather may result from species-specific evolutionary constraints (Grossman et al. 1998, Peres-Neto 2004). With the

exception of open-sand substrate, which is the dominant substrate of the river landscape, benthic habitats are patchily distributed across main-channel and floodplain elevations. Changing water levels induce a shift in patch occupancy, which is probably a result of colonization dynamics, species-specific evolutionary constraints, and biotic interactions (Grossman et al. 1998, Layman and Winemiller 2004, Arrington et al. 2005).

Habitat affinities

Evidence of habitat affinity was particularly compelling for species never collected from open-sand habitats ($n = 56$ of 164 species collected in our study). These species were repeatedly forced to traverse extensive stretches of open-sand habitat to colonize structured habitat patches, yet they never occurred in samples from open-sand habitats. In general, each habitat was dominated by invertivorous taxa, though habitats with firm substrates (i.e., submerged wood and simulated rock) supported a disproportionate number of algae grazers (e.g., loricariid catfishes). Submerged-wood habitats also supported a unique fauna (e.g., driftwood catfishes of the family Auchenipteridae) that is thought to use these complex habitats diurnally as a refuge from predation (Lowe-McConnell 1964, Arrington and Winemiller 2003). Similarly, we have shown that a significant number of fish species and at least one additional shrimp species (*Acetes paraguayensis*) are exclusively collected from river main-channel sand banks during nocturnal samples; these species presumably occupy very shallow littoral waters at night as a refuge from predation (Arrington and Winemiller 2003).

Among-habitat β diversity, i.e., species turnover, indicated complete dissimilarity between samples at the extremes of assemblage gradients. Such clear among-habitat differences in species composition indicate that local communities are not random associations of species drawn from a common pool (sensu Goulding et al. 1988, Hubbell 2001), but rather local community assembly appears, at a minimum, to be constrained by the underlying habitat upon which the community is assembled. Nonetheless, assemblage structure varied considerably within many habitat categories, and more so during the rising- and falling-water periods. This within-habitat variation in assemblage structure is analogous to nonpersistent assemblage structure through time and suggests a significant stochastic influence on local community assembly (Grossman et al. 1982). In addition, unaccounted environmental factors may have influenced assemblage structure.

Factors affecting assemblages

Variation partitioning using pCCA explained only 33% of total variation in the species \times sample matrix. This statistic can be misleading because interpretation of unexplained variation as random noise is inappropriate (Økland 1999). In other studies, TVE values have ranged between 20 and 50%, with smaller TVE values observed when β diversity is large (Økland 1999), as in our study. Therefore, we follow Økland (1999) and focus on the contribution of sets of explanatory variables relative to TVE (i.e., % of TVE).

Variation partitioning (pCCA) indicated that local communities were primarily assembled under the influence of habitat type. Nonetheless, all 4 variable sets contributed to the explanation of variation in assemblage composition. Habitat had the greatest unique and cumulative influence on community structure. Mesohabitat characteristics (e.g., water depth and velocity) were 2nd-most important, explaining 30% of TVE. The influence of mesohabitat appeared to be greatest when taken in combination with the other sets of variables (e.g., shared variation), a finding similar to that of MÉRIGOUX et al. (1999) in a study of fish communities in floodplain creeks of French Guiana. Occurrence patterns of several species provide clear examples of the interaction of these mesohabitat variables with habitat categories. *Centromochlus concolor*, a small auchenipterid catfish, and *Parotocinclus eppleyi*, a small loricariid catfish, were associated with main-channel submerged-wood in higher water velocities, whereas the cichlids *Hoplarichus psittacus* and *Mesonauta insignis* were associated with submerged wood in still waters along the edge of the river main channel. Juveniles of *Heros* sp., another cichlid, were common in shallow submerged wood that provided invertebrate prey and cover, whereas *Bryconops alburnoides*, a rapid midwater characid, was associated with submerged wood in deeper main-channel areas. Unlike other species occupying submerged-wood habitats, *B. alburnoides* does not occupy the interstitial spaces in woody debris, but instead swims above and around submerged wood. We were unable to determine if community structure was influenced predominantly by the stochastic effects of colonization dynamics and species-specific evolutionary constraints or the deterministic effects of biotic interactions. However, an independent study in this same system demonstrated that species-specific responses to environmental variation were caused, in part, by species interactions (Arrington et al. 2005). Arrington et al. (2005) also demonstrated significantly nonrandom species co-occurrence patterns in created rock habitat patches after ~24 d of colonization (i.e.,

the colonization period used in our study). Therefore, we conclude that nonrandom habitat occupancy was not caused solely by stochastic factors associated with colonization dynamics, but also was influenced by species interactions.

Patterns of habitat occupancy for some species seem to reflect availability of food resources and suitable refuge from predation. Nonrandom patterns of habitat use were most prevalent during the low-water season when the total volume of aquatic habitat was reduced, most fishes and macroinvertebrates presumably experienced greatest resource limitation (Lowe-McConnell 1964, Winemiller and Pianka 1990), and piscivory was probably most intense (Winemiller 1990, Jepsen et al. 1997, Rodríguez and Lewis 1997, Wantzen et al. 2002, Layman and Winemiller 2004).

In conclusion, our findings reject a pure random associations hypothesis and reveal that local assemblages of fishes and macroinvertebrates in shallow habitats of tropical floodplain rivers possess significant elements of nonrandom structure. As the aquatic-terrestrial interface moves across the landscape's lateral elevation gradient in accordance with the annual flood pulse, local communities of substrate-associated organisms are continuously disassembled and reassembled in shallow-water habitats, most of which are patchily distributed. Relatively distinct communities occur among different substrate types, and variation in community structure within habitats is a product of stochastic colonization events as well as a response to fine-scale variation in local environmental factors, seasonal water-level fluctuations, location of the habitat, and, perhaps, by abiotic and biotic factors that we did not examine. For example, Layman and Winemiller (2004) demonstrated experimentally that the presence of large piscivores affects the abundance and size distribution of small fishes in the littoral zone of the Cinaruco River main channel. The disturbance dynamics of littoral-zone habitats in tropical lowland rivers appears to be sufficiently predictable and gradual that community assembly is influenced, albeit to a small degree, by deterministic ecological processes, particularly during the low-water period. As predicted by the patch-dynamics model of community dynamics (Townsend 1989), local community assembly also revealed apparent stochastic influences associated with colonization dynamics, especially during the annual period of rising water.

Acknowledgements

We thank Servicio Autonomo de Los Recursos Pesqueros y Acuicolas (SARPA) of Venezuela for providing scientific collecting permit #0192. D. Tap-

horn provided invaluable taxonomic and logistical assistance throughout this study. We thank the Stergios family for their generous hospitality. G. Webb and C. Lofgren of Tour Apure and E. Pelaez and J. Marzuola of the Cinaruco River Fishing Club provided housing and logistical assistance, and J. Arrington, C. Garcia, J. Garcia, C. Layman, and C. Marzuola assisted with field collections. The Museo de Ciencias Naturales staff in Guanare also helped count and curate specimens, and J. V. Montoya identified the shrimp. A. Benke, C. Layman, C. Taylor, and R. Økland provided valuable comments on an earlier draft of this manuscript. This research was funded through grants from National Geographic Society (KOW), the L. T. Jordan Institute (DAA), and the International Sportfish Fund (KOW and DAA). DAA was supported as a Tom Slick Senior Graduate Fellow during the writing of this manuscript. Specimens were collected under authority of Animal Use Protocol #8-414 Texas A&M University.

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Received: 16 September 2004

Accepted: 18 August 2005

APPENDIX. Species (or other taxa) collected in sandbank seine samples from the Cinaruco River, Venezuela. Values in parentheses are the number of samples collected per habitat type. Species are sorted by rank (taken from overall rank-abundance plot). Total abundance is the number of individuals collected. Other values shown are the % of samples in which the species occurred. (Occurrence of species [$n = 164$] collected in littoral-zone habitat samples [$n = 268$] is available from: http://wfsc.tamu.edu/winemiller/data/Arrington_Winemiller_JNABS_appendix-A.htm)

Rank	Order	Species (or other taxa)	Total abundance	River sand (69)	River submerged wood (49)	River simulated rock (45)	Lagoon sand (36)	Lagoon submerged wood (32)	Lagoon leaf litter (37)
1	Characiformes	<i>Hemigrammus analis</i>	8036	26.1	10.2	2.2	69.4	12.5	73.0
2	Decapoda	<i>Macrobrachium cf. dierythrum</i>	6768	30.4	69.4	62.2	63.9	68.8	81.1
3	Characiformes	<i>Hemigrammus vorderwinkleri</i>	6633	29.0	0.0	0.0	41.7	0.0	75.7
4	Characiformes	<i>Aphyocharax alburnus</i>	4596	88.4	6.1	2.2	63.9	3.1	29.7
5	Clupeiformes	<i>Amazonsprattus scintilla</i>	3782	42.0	8.2	2.2	52.8	0.0	5.4
6	Characiformes	<i>Bivibranchia fowleri</i>	3383	72.5	10.2	11.1	16.7	0.0	0.0
7	Characiformes	<i>Microschemobrycon casiquiare</i>	3094	39.1	12.2	2.2	52.8	25.0	21.6
8	Characiformes	<i>Moenkhausia copei</i>	3015	15.9	16.3	0.0	61.1	34.4	73.0
9	Perciformes	<i>Apistogramma</i> sp. A	2363	15.9	12.2	2.2	66.7	15.6	83.8
10	Characiformes	<i>Characidium</i> sp. A	2243	36.2	4.1	0.0	58.3	6.3	29.7
11	Characiformes	<i>Hemigrammus</i> sp. A	2175	15.9	2.0	2.2	8.3	0.0	54.1
12	Characiformes	<i>Rhinobrycon negrensis</i>	1892	65.2	8.2	6.7	11.1	0.0	0.0
13	Characiformes	<i>Bryconamericus</i> sp. A	1537	53.6	10.2	17.8	8.3	0.0	0.0
14	Characiformes	<i>Hemigrammus micropterus</i>	1323	18.8	2.0	2.2	30.6	15.6	35.1
15	Characiformes	<i>Hemigrammus microstomus</i>	875	2.9	0.0	0.0	0.0	0.0	0.0
16	Perciformes	<i>Geophagus</i> sp.	866	37.7	24.5	33.3	66.7	15.6	0.0
17	Characiformes	<i>Parapristella georgiae</i>	636	8.7	0.0	0.0	11.1	0.0	32.4
18	Characiformes	<i>Bryconops caudomaculatus</i>	610	56.5	22.4	22.2	36.1	9.4	2.7
19	Characiformes	<i>Hemigrammus</i> sp. B	539	7.2	0.0	0.0	16.7	0.0	27.0
20	Characiformes	<i>Knodus cf. heterestes</i>	509	26.1	6.1	4.4	33.3	3.1	2.7
21	Characiformes	<i>Hemigrammus schmardae</i>	453	14.5	6.1	2.2	0.0	0.0	0.0
22	Characiformes	<i>Hemigrammus elegans</i>	399	5.8	4.1	0.0	11.1	12.5	13.5
23	Perciformes	<i>Biotodoma wavrini</i>	357	10.1	18.4	11.1	58.3	25.0	21.6
24	Perciformes	<i>Crenicichla af. wallacei</i>	350	17.4	40.8	53.3	47.2	53.1	43.2
25	Characiformes	<i>Microschemobrycon callops</i>	298	23.2	6.1	0.0	5.6	0.0	0.0
26	Characiformes	<i>Imparfinis</i> sp.	247	50.7	2.0	6.7	8.3	0.0	0.0
27	Characiformes	<i>Moenkhausia</i> sp. B	207	4.3	4.1	0.0	16.7	0.0	0.0
28	Characiformes	<i>Hemigrammus</i> sp. C	192	0.0	0.0	0.0	36.1	18.8	2.7
29	Cyprinodontiformes	<i>Fluviphylax obscuris</i>	174	4.3	0.0	0.0	27.8	0.0	56.8
30	Characiformes	<i>Cyphocharax spilurus</i>	173	5.8	0.0	0.0	8.3	6.3	10.8
31	Siluriformes	<i>Parotocinclus eppleyi</i>	172	1.4	24.5	0.0	0.0	0.0	0.0
32	Characiformes	<i>Hemiodus gracilis</i>	152	2.9	2.0	0.0	30.6	25.0	10.8
33	Characiformes	<i>Serrasalmus</i> sp.	150	8.7	0.0	0.0	0.0	0.0	0.0
34	Characiformes	<i>Cyphocharax oenas</i>	145	7.2	0.0	0.0	5.6	3.1	8.1
35	Characiformes	<i>Moenkhausia cf. ceros</i>	143	8.7	10.2	2.2	16.7	3.1	8.1
36	Perciformes	<i>Satanoperca daemon</i>	137	7.2	12.2	2.2	19.4	15.6	8.1
37	Characiformes	<i>Hyphessobrycon bentosi</i>	134	4.3	0.0	0.0	2.8	3.1	10.8
38	Perciformes	<i>Heros</i> sp. A	132	2.9	18.4	6.7	8.3	46.9	13.5
39	Siluriformes	<i>Platydoras costatus</i>	125	0.0	0.0	6.7	0.0	68.8	2.7
40	Characiformes	<i>Creagrutus phasma</i>	123	39.1	2.0	4.4	0.0	0.0	0.0
41	Perciformes	<i>Cichla</i> sp.	110	2.9	0.0	0.0	5.6	0.0	0.0
42	Siluriformes	<i>Pimelodella</i> sp. A	109	1.4	12.2	51.1	0.0	0.0	0.0
43	Ephemeroptera	Polymitarcyidae	104	1.4	2.0	0.0	0.0	53.1	2.7
44	Siluriformes	<i>Microglanis poecilus</i>	94	0.0	10.2	4.4	5.6	53.1	10.8
45	Characiformes	<i>Hemiodus unimaculatus</i>	88	4.3	4.1	0.0	22.2	12.5	0.0
46	Siluriformes	<i>Pseudocetopsis</i> sp.	86	0.0	18.4	13.3	0.0	15.6	0.0
47	Siluriformes	<i>Dekeyseria scaphyrhyncha</i>	84	0.0	10.2	2.2	2.8	62.5	0.0
48	Characiformes	<i>Hyphessobrycon metae</i>	80	0.0	0.0	0.0	5.6	3.1	27.0
49	Characiformes	<i>Serrabrycon magoi</i>	77	5.8	0.0	0.0	11.1	0.0	16.2
50	Odonata	Gomphidae	75	13.0	2.0	13.3	2.8	6.3	32.4
51	Perciformes	<i>Biotococcus dicentrarchus</i>	71	4.3	2.0	0.0	25.0	12.5	8.1
52	Characiformes	<i>Argonectes longiceps</i>	70	7.2	2.0	2.2	30.6	3.1	0.0
53	Characiformes	<i>Hemigrammus stictus</i>	66	5.8	0.0	0.0	0.0	0.0	2.7
54	Characiformes	<i>Characidium</i> sp. B	64	21.7	2.0	0.0	13.9	0.0	0.0

APPENDIX. Continued.

Rank	Order	Species (or other taxa)	Total abundance	River sand (69)	River submerged wood (49)	River simulated rock (45)	Lagoon sand (36)	Lagoon submerged wood (32)	Lagoon leaf litter (37)
55	Characiformes	<i>Characidium</i> sp. C	57	2.9	0.0	0.0	0.0	0.0	0.0
56	Siluriformes	<i>Centromochlus concolor</i>	52	0.0	2.0	0.0	0.0	37.5	0.0
57	Characiformes	<i>Nannostomus unifasciatus</i>	51	0.0	0.0	0.0	8.3	0.0	27.0
58	Siluriformes	<i>Scorpiodoras</i> sp. B	51	0.0	0.0	2.2	0.0	3.1	5.4
59	Perciformes	<i>Pyrrhulina lugubris</i>	48	1.4	2.0	4.4	5.6	53.1	5.4
60	Characiformes	<i>Pyrrhulina lugubris</i>	46	4.3	0.0	0.0	2.8	0.0	21.6
61	Perciformes	<i>Mesonauta insignis</i>	45	2.9	14.3	2.2	5.6	15.6	2.7
62	Siluriformes	<i>Acanthodoras</i> sp.	39	0.0	0.0	0.0	0.0	25.0	0.0
63	Characiformes	<i>Melanocharacidium dispilomma</i>	36	0.0	14.3	4.4	0.0	12.5	0.0
64	Characiformes	<i>Curimatella dorsalis</i>	34	0.0	0.0	0.0	11.1	3.1	2.7
65	Characiformes	<i>Hemigrammus rhodostomus</i>	33	1.4	0.0	2.2	0.0	0.0	13.5
66	Characiformes	<i>Curimatopsis evelynae</i>	30	2.9	0.0	0.0	2.8	3.1	13.5
67	Characiformes	<i>Pseudanos gracilis</i>	29	0.0	2.0	4.4	0.0	43.8	0.0
68	Siluriformes	<i>Centromochlus</i> sp.	27	0.0	2.0	4.4	0.0	15.6	2.7
69	Characiformes	<i>Acestrorhynchus minimus</i>	26	0.0	4.1	2.2	16.7	0.0	8.1
70	Perciformes	<i>Crenicichla</i> sp. B	26	0.0	0.0	2.2	0.0	43.8	2.7
71	Siluriformes	<i>Ochmacanthus alternus</i>	26	7.2	2.0	2.2	25.0	0.0	5.4
72	Siluriformes	<i>Ochmacanthus orinoco</i>	23	4.3	0.0	0.0	13.9	0.0	2.7
73	Characiformes	<i>Hoplias malabaricus</i>	20	5.8	6.1	0.0	0.0	15.6	10.8
74	Characiformes	<i>Nannostomus eques</i>	20	0.0	0.0	0.0	2.8	0.0	18.9
75	Characiformes	<i>Bryconops alburnoides</i>	19	5.8	6.1	0.0	8.3	0.0	0.0
76	Characiformes	<i>Moenkhausia colletti</i>	19	1.4	0.0	0.0	0.0	0.0	0.0
77	Characiformes	<i>Hemigrammus</i> cf. <i>tridens</i>	18	2.9	0.0	0.0	2.8	0.0	0.0
78	Perciformes	<i>Hypseleacara coryphaenoides</i>	18	0.0	0.0	0.0	2.8	18.8	10.8
79	Characiformes	<i>Moenkhausia</i> sp. A	18	1.4	0.0	0.0	0.0	3.1	0.0
80	Siluriformes	<i>Scorpiodoras</i> sp. A	18	5.8	2.0	4.4	2.8	9.4	2.7
81	Characiformes	<i>Bryconamericus</i> sp. B	17	2.9	2.0	0.0	0.0	0.0	0.0
82	Characiformes	<i>Moenkhausia lepidura</i>	16	0.0	0.0	0.0	8.3	0.0	5.4
83	Characiformes	<i>Copella metae</i>	15	4.3	0.0	0.0	0.0	0.0	10.8
84	Characiformes	<i>Hemiodus microlepis</i>	15	0.0	0.0	0.0	5.6	0.0	0.0
85	Siluriformes	<i>Rineloricaria</i> sp.	15	1.4	6.1	2.2	11.1	0.0	2.7
86	Characiformes	<i>Moenkhausia</i> sp. C	14	0.0	0.0	0.0	0.0	0.0	8.1
87	Characiformes	<i>Iguanodectes spilurus</i>	13	0.0	0.0	0.0	8.3	0.0	8.1
88	Perciformes	<i>Mikrogeophagus ramirezi</i>	13	2.9	0.0	0.0	0.0	0.0	0.0
89	Characiformes	<i>Acestrorhynchus microlepis</i>	11	0.0	0.0	0.0	8.3	6.3	5.4
90	Siluriformes	<i>Auchenipterichthys longimanus</i>	11	0.0	0.0	0.0	0.0	21.9	0.0
91	Characiformes	<i>Hemiodus immaculatus</i>	11	1.4	2.0	0.0	13.9	6.3	0.0
92	Heteroptera	Naucoridae	11	2.9	2.0	2.2	0.0	6.3	8.1
93	Siluriformes	<i>Pseudopimelodus apurensis</i>	11	0.0	4.1	2.2	0.0	18.8	0.0
94	Perciformes	<i>Acaronia vultuosa</i>	10	1.4	0.0	0.0	0.0	3.1	13.5
95	Characiformes	<i>Brycon pesu</i>	10	7.2	2.0	0.0	2.8	0.0	0.0
96	Perciformes	<i>Cichla temensis</i>	10	0.0	8.2	0.0	2.8	3.1	0.0
97	Siluriformes	<i>Glyptoperichthys gibbiceps</i>	10	0.0	0.0	0.0	0.0	21.9	0.0
98	Characiformes	<i>Brycon falcatus</i>	9	0.0	0.0	0.0	13.9	0.0	2.7
99	Characiformes	<i>Bryconops humeralis</i>	9	0.0	0.0	0.0	0.0	0.0	5.4
100	Characiformes	<i>Hemigrammus belotti</i>	9	2.9	0.0	0.0	0.0	0.0	0.0
101	Siluriformes	<i>Otocinclus</i> sp.	9	4.3	8.2	2.2	0.0	0.0	0.0
102	Perciformes	<i>Cichla orinocensis</i>	8	0.0	4.1	0.0	2.8	12.5	0.0
103	Siluriformes	<i>Pimelodus blochi</i>	8	0.0	0.0	6.7	0.0	0.0	0.0
104	Synbranchiiformes	<i>Synbranchus marmoratus</i>	8	0.0	0.0	0.0	0.0	18.8	0.0
105	Siluriformes	<i>Peckoltia</i> sp. A	6	0.0	6.1	0.0	0.0	0.0	0.0
106	Characiformes	<i>Boulengerella cuvieri</i>	5	0.0	4.1	0.0	0.0	0.0	2.7
107	Siluriformes	<i>Goeldiella eques</i>	5	0.0	0.0	2.2	0.0	9.4	2.7
108	Megaloptera	Corydalidae	5	0.0	4.1	0.0	0.0	0.0	0.0
109	Characiformes	<i>Leporinus melanopleura</i>	5	0.0	2.0	6.7	0.0	0.0	0.0
110	Characiformes	<i>Myleus</i> sp.	5	1.4	4.1	0.0	2.8	0.0	0.0
111	Characiformes	<i>Oxyropsis acustirostris</i>	5	0.0	2.0	0.0	0.0	0.0	0.0
112	Siluriformes	<i>Rhamdia quelen</i>	5	0.0	0.0	8.9	0.0	3.1	0.0

APPENDIX. Continued.

Rank	Order	Species (or other taxa)	Total abundance	River sand (69)	River submerged wood (49)	River simulated rock (45)	Lagoon sand (36)	Lagoon submerged wood (32)	Lagoon leaf litter (37)
113	Hemiptera	Nepidae	5	0.0	0.0	0.0	0.0	0.0	8.1
114	Siluriformes	<i>Trachycorystes trachycorestes</i>	5	0.0	0.0	0.0	0.0	12.5	0.0
115	Perciformes	<i>Aequidens diadema</i>	4	0.0	0.0	0.0	2.8	0.0	2.7
116	Odonata	Zygoptera	4	2.9	2.0	2.2	0.0	0.0	0.0
117	Characiformes	<i>Chalceus macrolepidotus</i>	4	0.0	0.0	0.0	2.8	3.1	5.4
118	Characiformes	<i>Leporinus fasciatus</i>	4	0.0	2.0	4.4	0.0	0.0	0.0
119	Characiformes	<i>Metynnis hypsauchen</i>	4	1.4	0.0	0.0	2.8	0.0	0.0
120	Siluriformes	<i>Orinocodoras eigenmanni</i>	4	0.0	0.0	0.0	0.0	12.5	0.0
121	Siluriformes	<i>Acanthodoras spinosissimus</i>	3	0.0	0.0	0.0	0.0	3.1	2.7
122	Perciformes	<i>Apistogramma</i> sp. B	3	1.4	2.0	0.0	0.0	0.0	0.0
123	Perciformes	<i>Cichla intermedia</i>	3	0.0	6.1	0.0	0.0	0.0	0.0
124	Characiformes	<i>Curimatopsis</i> sp.	3	2.9	0.0	0.0	0.0	0.0	2.7
125	Siluriformes	<i>Farlowella vittata</i>	3	0.0	2.0	0.0	0.0	0.0	0.0
126	Characiformes	<i>Hemiodus semitaeniatus</i>	3	0.0	0.0	0.0	8.3	0.0	0.0
127	Characiformes	<i>Leporinus</i> sp.	3	0.0	0.0	0.0	0.0	6.3	0.0
128	Siluriformes	Loricariidae	3	0.0	2.0	0.0	2.8	3.1	0.0
129	Siluriformes	<i>Pimelodella</i> sp. B	3	0.0	2.0	2.2	0.0	0.0	0.0
130	Perciformes	<i>Satanoperca mapiritensis</i>	3	0.0	0.0	0.0	2.8	0.0	5.4
131	Siluriformes	<i>Ancistrus</i> sp.	2	0.0	2.0	0.0	0.0	3.1	0.0
132	Characiformes	<i>Asiphonichthys condei</i>	2	0.0	0.0	0.0	0.0	0.0	2.7
133	Characiformes	<i>Boulengerella lucius</i>	2	0.0	0.0	0.0	0.0	3.1	0.0
134	Characiformes	<i>Boulengerella</i> sp.	2	0.0	0.0	0.0	0.0	0.0	5.4
135	Characiformes	<i>Characidium</i> sp. D	2	1.4	0.0	0.0	0.0	0.0	0.0
136	Siluriformes	<i>Heptapterus</i> sp.	2	0.0	0.0	0.0	0.0	0.0	5.4
137	Characiformes	<i>Hyphessobrycon</i> sp. A	2	1.4	0.0	0.0	0.0	0.0	2.7
138	Characiformes	<i>Hyphessobrycon</i> sp. B	2	0.0	0.0	0.0	0.0	0.0	5.4
139	Perciformes	<i>Hypoclinemus mentalis</i>	2	2.9	0.0	0.0	0.0	0.0	0.0
140	Characiformes	<i>Leporinus</i> cf. <i>latofasciatus</i>	2	0.0	0.0	0.0	0.0	0.0	2.7
141	Characiformes	<i>Oxybrycon parvulus</i>	2	1.4	0.0	0.0	0.0	0.0	0.0
142	Rajiformes	<i>Potamotrygon orbignyi</i>	2	0.0	0.0	0.0	2.8	0.0	2.7
143	Characiformes	<i>Anostomus ternetzi</i>	1	0.0	2.0	0.0	0.0	0.0	0.0
144	Coleoptera	Coleoptera larvae	1	0.0	0.0	0.0	0.0	3.1	0.0
145	Siluriformes	<i>Corymbophanes</i> sp.	1	0.0	2.0	0.0	0.0	0.0	0.0
146	Perciformes	<i>Crenicichla</i> sp. C	1	0.0	0.0	2.2	0.0	0.0	0.0
147	Siluriformes	<i>Doras</i> ("Stenodoras") cf. <i>microstomus</i>	1	1.4	0.0	0.0	0.0	0.0	0.0
148	Siluriformes	<i>Farlowella</i> sp.	1	0.0	2.0	0.0	0.0	0.0	0.0
149	Siluriformes	<i>Haemomaster venezuelae</i>	1	1.4	0.0	0.0	0.0	0.0	0.0
150	Gymnotiformes	<i>Hypopygus lepturus</i>	1	0.0	0.0	0.0	0.0	0.0	2.7
151	Siluriformes	<i>Hypostomus</i> sp.	1	0.0	0.0	2.2	0.0	0.0	0.0
152	Characiformes	<i>Laemolyta taeniatus</i>	1	0.0	2.0	0.0	0.0	0.0	0.0
153	Characiformes	<i>Leporinus brunneus</i>	1	0.0	0.0	2.2	0.0	0.0	0.0
154	Characiformes	<i>Leporinus maculatus</i>	1	0.0	0.0	2.2	0.0	0.0	0.0
155	Characiformes	<i>Moenkhausia oligolepis</i>	1	0.0	0.0	0.0	0.0	0.0	2.7
156	Characiformes	<i>Myleus rubripinnis</i>	1	0.0	0.0	0.0	2.8	0.0	0.0
157	Characiformes	<i>Parauchenipterus</i> sp.	1	0.0	0.0	0.0	0.0	3.1	0.0
158	Siluriformes	<i>Peckoltia</i> sp. B	1	0.0	0.0	2.2	0.0	0.0	0.0
159	Characiformes	<i>Phenacogaster megalostictus</i>	1	0.0	0.0	0.0	0.0	0.0	2.7
160	Characiformes	<i>Potamorhina</i> sp.	1	1.4	0.0	0.0	0.0	0.0	0.0
161	Rajiformes	<i>Potamotrygon motoro</i>	1	0.0	0.0	0.0	0.0	0.0	2.7
162	Cyprinodontiformes	<i>Rachovia maculipinnis</i>	1	0.0	0.0	0.0	2.8	0.0	0.0
163	Characiformes	<i>Semaprochilodus kneri</i>	1	0.0	0.0	0.0	0.0	3.1	0.0
164	Siluriformes	<i>Trichomycterus</i> sp.	1	0.0	0.0	2.2	0.0	0.0	0.0