Oecologia (2005)
DOI 10.1007/s00442-005-0014-7

COMMUNITY ECOLOGY

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Community assembly at the patch scale in a species rich tropical river

Received: 23 March 2004 / Accepted: 13 January 2005

Abstract In tropical floodplain rivers, communities associated with structurally complex habitats are disassembled and reassembled as aquatic organisms repeatedly colonize new areas in response to gradual but continuous changes in water level. Thus, a neutral model reflecting random colonization and extinction dynamics may be sufficient to predict assemblage patterns at the scale of local habitat patches. If water level fluctuations and associated patch dynamics are sufficiently predictable, however, community assembly on habitat patches also may be influenced by species-specific responses to habitat features and/or species interactions. We experimentally manipulated structural complexity and proximity to source habitat (which influences colonization rate) of simulated rocky patches in the littoral zone of a tropical lowland river and demonstrate significant effects of both factors on species density of fishes and macroinvertebrates. Interspecific variation in vagility significantly affected assemblage response to habitat complexity. In a second experiment, created habitat patches were sampled over time intervals ranging from 1 day to 36 days to examine temporal dynamics of community assembly. A null-model test revealed that assemblage structure became increasingly non-random, concomitant with increasing species density, over time. Community dynamics in newly formed habitat patches appeared to be dominated by dispersal, whereas in older patches, abundances of individual species increasingly were influenced by habitat characteristics. These data suggest that species-specific responses to environmental variation resulted, in part, because of species interactions. We conclude that community assembly in shallow habitats of this tropical lowland river is influenced by physical habitat characteristics, the spatial distribution of habitat patches, and species interactions as habitats are saturated with individuals.

Keywords Assembly rules · Neotropical fishes · Null model · Patch dynamics · Species density

Communicated by Dan Simberloff

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Introduction

One of the most fundamental challenges in ecology and conservation biology is to understand the factors that determine patterns of species abundance, distribution, and co-occurrence. Neutral models of community drift have received much attention recently because they can predict certain features of natural communities, such as patterns of species relative abundance (e.g. Bell et al. 2001; Hubbell 2001). The neutral view is controversial, because community ecology has long assumed that deterministic ecological interactions, as well as random factors associated with disturbance, influence the process of community assembly (Clements 1949; Whittaker 1954; Menge and Sutherland 1987; Jackson et al. 2001). Hubbell (2001) recently created a neutral model that assumes ecological drift, i.e. community assembly via random dispersal. This model reasonably predicts the structure of several forests, coral reefs and bird assemblages, as well as the distribution of species-relative abundances for at least one fish assemblage in a Neotropical stream (Hubbell 2001). Yet, an analysis of the long-term dynamics of the same tropical fish assemblage (Winemiller 1996) revealed concordant assemblage structure among years for dry-season samples, but high

among-year variation for wet-season samples. Citing prior research on food web interactions in this system, Winemiller (1996) stressed the role of biotic interactions during the annual period of water recession that causes marked increases in densities of aquatic organisms (Lowe-McConnell 1964, 1987).

Shallow-water communities of tropical lowland rivers that experience prolonged, seasonal flooding are well suited for testing alternative models of community assembly. As water levels rise, aquatic organisms disperse into newly available habitats located higher on riverbanks or in floodplains. As floodwaters recede, aquatic organisms are forced to return to lower-elevation habitats. Reviews of fish community patterns in tropical rivers (Lowe-McConnell 1987; Goulding et al. 1988) have emphasized random associations between fish species and habitats at various spatial scales. Recent research, however, on fish assemblage structure in the Amazon River (Cox-Fernandez 1999; Petry et al. 2003) and floodplain lakes of the Orinoco River (Rodrìguez and Lewis 1997) has identified non-random fish assemblage structure in relation to physical environmental features that vary at the landscape scale. Using multiple regression analysis with a suite of variables indicating habitat states and variability, Mérigoux et al. (1999) were able to explain only a relatively small percentage of variance of fish species richness in lowland creeks in French Guiana. They attributed much of the unexplained variation to a strong influence of rare species. Thus, the role of biotic interactions in the assembly of aquatic communities in tropical river habitats remains an open question, particularly at the local scale.

Here, we test a model that predicts species richness in habitat patches via field experiments on community assembly in the littoral zone of a tropical lowland river. We modified the island biogeography model (MacArthur and Wilson 1967) to predict combined effects of colonization rate and habitat complexity on species density of local patches (Fig. 1). If biological interactions regulate community assembly, then species density increases with increasing habitat complexity because more complex habitats support greater niche diversification (MacArthur 1970; Petren and Case 1998), reduce interference competition (Petren and Case 1998), and stabilize predator–prey interactions (Menge and Sutherland 1987). Therefore, we predict habitat complexity should lower local extinction rates. As colonization rate increases, the number of species should increase until reaching an upper asymptote (MacArthur and Wilson 1967). Thus, we predict a positive interaction (i.e. additive effect) between colonization rate and habitat complexity on species density (Fig. 1). Differences in species density between newly available habitats with low- and high-structural complexity should be greatest when colonization rate is high, because the potential for ecological interactions to inhibit species establishment or persistence is greater when habitats are more saturated. When colonization rates are low, differences in species density between habitats with low- and high-complexity may be minimized by the strong effect of colonization limitation (Sale and Douglas 1984; Tilman 1994; Hurtt and Pacala 1995). Extrapolating from this model and additional literature (Resh et al. 1988; Angermeier and Winston 1998; Olden et al. 2001), we hypothesize that assemblage structure, in a system with so many potential colonizing species, should be more random when colonization rates are low and habitats are relatively unsaturated (i.e. less potential for biotic interactions).

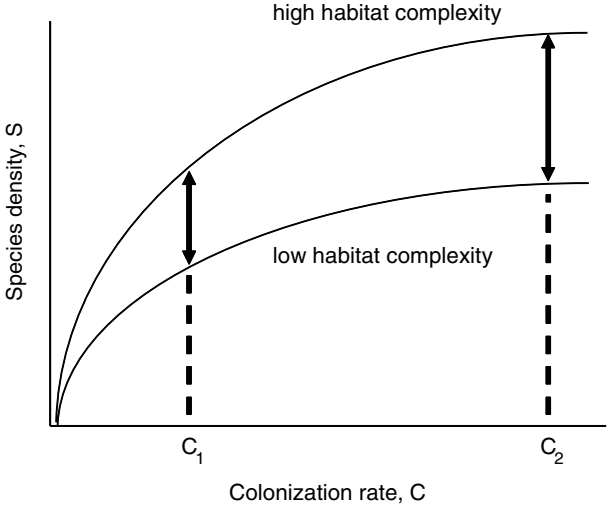

Fig. 1 Conceptual model integrating the influence of colonization rate (C_1 low, C_2 high) and habitat structural complexity on species density (S)

Whereas, habitat features and hydrological disturbance frequency predict local fish assemblage structure in temperate streams (Horwitz 1978; Ross et al. 1985; Schlosser 1987; Poff and Allan 1995; Grossman et al. 1998), hydrologic fluctuations in temperate streams are stochastically intermittent compared to gradual water-level changes that occur in tropical lowland streams (Winemiller 1996; Bürnheim and Cox Fernandez 2001) and rivers (Welcomme 1985; Junk et al. 1989; Arrington and Winemiller 2003). In the Cinaruco River, Venezuela, floodwater recession (~5 m) occurs over a 6-month period (Arrington and Winemiller 2003), and littoral zone organisms that associate with certain substrates or structures are repeatedly forced to vacate habitat patches and colonize new ones (on an order of days to weeks throughout the year). In the littoral zone of lowland tropical rivers, species richness should be higher in habitat patches with greater structural complexity and higher rates of colonization as predicted by the model in Fig. 1. To test this model, we conducted a field experiment in which rocky habitat patches with different degrees of structural complexity were created in the main river channel on shallow-grade sandbanks at variable distances from natural habitats (i.e. sources of colonists). Results supported the model, and a second experiment was conducted to examine temporal dynamics of community assembly.

Materials and methods

Study site

We tested the species-density model on habitat patches in the littoral zone of the Cinaruco River, a species-rich, backwater, floodplain river with a drainage basin ca. 10,000 km^2 located in Venezuela's plains region (i.e. *llanos*). Variation in assemblage structure in the littoral zone is strongly associated with habitat type (Arrington 2002). Small organisms in shallow waters of the Cinaruco River face a high risk of predation (Layman and Winemiller 2004), and many fish and invertebrate species use physical structures (rocks, woody debris, vegetation) as refuges and foraging substrates (e.g. algivores, detritivores, invertebrate gleaners). Our prior research on the Cinaruco River has documented over 280 fish species, among which, 53 were collected from simulated rock patches during an extensive survey of littoral habitats in the main river channel (Arrington 2002). These patches are rapidly colonized by both fishes and late instars of aquatic macroinvertebrates (e.g. *Macrobrachium* spp., Odonata, Hemiptera, Coleoptera). Recruitment onto these newly available habitat patches is achieved primarily via dispersal and not in situ reproduction. We included both fishes and macroinvertebrates in our "community" analysis because both groups colonize and interact in structurally complex habitats in the littoral zone, and both were consistently collected by our sampling method.

Data collection

To test the relative influence of colonization rate and habitat complexity on community assembly, we conducted a field experiment during the dry season (Feb. 2002), in which experimental habitat patches were constructed with three different distances to the source habitat and two levels of complexity (experiment 1). Experimental habitat patches (rocky patches) were constructed with unglazed ceramic building blocks and were nested within large (>500 m in length) sandbanks located on inside of meanders in the main river channel. Rocky patches were created at three distances (25, 75, and 225 m) from natural source habitats having high structural complexity, i.e. dense, submerged woody debris located on the upstream margin of the broad sandbank on which habitat patches were created. Importantly, we have demonstrated considerable overlap in the taxa that colonize submerged wood and block habitats (Arrington 2002; Willis et al. 2005). During the low-water period of 1999, block habitats (equivalent to the high-complexity patches in the present study) in the river channel ($n=18$) contained 31 species, of which, 87% were collected from submerged wood in the river channel during the same period ($n=24$). Furthermore, correspondence analysis of these samples indicates high similarity in community composition of block and wood habitats (Arrington 2002). Within-habitat community similarity, measured as the inverse of mean within-habitat pairwise Euclidean distance (1/mean ED), was 0.83 for river channel submerged wood samples. Community similarity between river channel block and submerged wood samples was slightly lower at 0.74, whereas the lowest similarity value (0.34) was observed between river channel block and bare sand substrate samples. Thus, distance from source habitat serves as a surrogate for colonization rate, a reasonable assumption given that rocky patches were constructed as islands of structurally-complex firm substrate within broad expanses of shifting sand substrate.

To manipulate habitat complexity, we created patches of firm substrate with low and high structural complexity. We also sampled un-manipulated reference patches, i.e. areas of bare sand substrate with no vertical structure (0.42 m^2). Patches of hard substrate with low- and high-structural complexity were created using unglazed ceramic building blocks. Each block measured 14×18.5×29 cm, was hollow, and had nine internal compartments (3.5×5 cm) that opened on each end of the longitudinal axis of the block. Each constructed habitat was composed of 10 blocks configured consistently (6 blocks on the bottom layer and 4 on the top layer) to cover an area of 0.42 m^2 and a volume of 0.12 m^3. Blocks used in low-complexity patches had their ends sealed with adhesive tape to create solid rectangular structures, whereas the ends of blocks used in the high-complexity patches remained open so that organisms could move inside the blocks as well as around and between them (tape was placed around the circumference of each end of high-complexity blocks to control for potential tape effects). Thus, constructed habitats of both treatments (low- versus high-complexity) had the same volume. Structural complexity of these habitats can be indexed by the total area of exposed external and internal surface relative to a constant plot area: low-complexity patches = 18,003 cm^2; high-complexity patches = 62,373 cm^2. These patches of constructed block habitat simulated key attributes of natural firm habitats (rocks and wood with numerous holes and crevices), while having a controlled area and facilitating efficient sampling.

Each habitat complexity (fixed factor) by proximity to source habitat (fixed factor) treatment was replicated five times on different sandbanks in the main river channel (random factor $n=15$). Five replicates of each of three complexity levels (reference, low, high) and each of three distances yielded 45 sampling units. Treatments were assigned to sampling units on a given river reach at random, except for the last two reaches, for which units were assigned in a manner that achieved a balanced block design. Each block patch was sampled 21 days after construction.

To examine temporal dynamics of patch colonization, experiment 2 was conducted during March–April 2002 (dry season), in which high-complexity habitat patches were constructed 75 m from upstream source habitats (i.e. intermediate proximity to source habitat in experiment 1) on 45 different channel sandbanks (each ≥ 150 m long) at intervals of 1, 2, 4, 6, 12, 18, 24, 30, and 36 days ($n = 5$ replicates per day). Dates of patch construction were staggered so that all patches were sampled only once on day 37. One replicate from the day-4 and day-18 intervals, two replicates from the day-24 interval, and three replicates from the day-30 interval were partially buried by shifting sand and deleted from the analysis, resulting in a total of 38 experimental units.

For both experiments, all block patches were sampled in the same manner during daylight hours with a seine (6.4×1.2 m with 4 mm mesh). For each sample, a 1.5-m^2 area containing the habitat patch was encircled with the seine, blocks were removed from inside the seine and inspected to ensure no organisms were attached, and the seine and its contents were carefully taken ashore for removal of organisms. We then enumerated organism abundance (total number of individuals) and species density (number of species per 1.5 m^2) for each habitat patch sampled. We use the term species density to indicate the number of taxa per unit area on the landscape (Gotelli and Colwell 2001). We consider these values to reflect complete sampling of organisms associated with structurally complex habitat patches. The same encircling protocol was used to sample reference plots in experiment 1.

Because the seine completely encircled the patch, there was a low probability that organisms inside the sampling area could escape, particularly those organisms with affinities for structurally complex habitats. This collecting method, nonetheless, may underestimate the abundance of highly mobile species associated with open sandbank habitats that lack woody debris or rocks. Surveys of open sandbanks based on sixty-three 10-m hauls with the same seine during the 1999 low-water season yielded an average of 2.2 organisms/m^2 (fishes + macroinvertebrates; Arrington 2002), whereas our encircling method captured an average of 1.3 organisms/m^2.

At the time of sampling, we measured water depth (cm) and water velocity (cm/s) at the location of the patch. For experiment 2, we also measured the following habitat variables: distance of patch from shore (m), distance across channel to opposite bank (m), and colonization potential. Colonization potential is based on the amount of submerged wood located in the 200 m of shoreline immediately upstream of each sandbank. We quantified submerged wood using the line intercept method. Transects ($n = 200$) were spaced every 1 m and extended 5 m from the shoreline towards the middle of the channel. The quantification of submerged wood upstream of sandbanks was designed to indicate the size of the source habitat for species associated with structurally complex habitat patches.

Statistical analyses

The effect of habitat complexity and proximity to source habitat on the number of species in patches was evaluated using analysis of variance (ANOVA). For experiment 1, our statistical model was *response* = *reach* (blocking factor) + *proximity to source habitat* (fixed factor) + *habitat complexity* (fixed factor) + *proximity to source habitat* × *habitat complexity* interaction. Raw data violated parametric assumptions, so values were transformed [square-root ($x + 0.5$)]. Although a few transformed values exhibited minimal deviations from normality, we proceeded with parametric tests because transformed values were not heteroscedastic.

Furthermore, we used the same statistical model to examine patterns of species density for two subsets of the littoral fish assemblage that represent different levels of vagility and dispersal potential. Loricariid catfishes are relatively sedentary (Power 1984), benthic fishes that consume algae and detritus. These catfishes are covered by bony plates that reduce buoyancy and swimming efficiency. The second subset was small invertebrate-feeding fishes (invertivores) of the littoral zone, a group represented mostly by characiform, siluriform and perciform species (Arrington 2002), that are more efficient swimmers with substantially greater dispersal capabilities than loricariids. We restricted our comparison to invertivorous species normally associated with complex habitats and not areas of open sand, i.e. taxa that were collected in less than half of dry-season channel sand samples (Arrington 2002).

Data from experiment 2 were analyzed with the C-score metric (Stone and Roberts 1990) to test for statistically significant non-random assemblage organization (i.e. not independent species co-occurrence) in rocky patches colonized for short (1–4 day), intermediate (6–18 day), and long (24–36 day) time intervals. Because our limited sample sizes per sampling day offered limited statistical power (Nick Gotelli, personal communication), we composed three species-by-sample presence/absence matrices, with each matrix containing all replicate samples from a single time interval (short, intermediate, long) in order to assess larger temporal changes in community structure. Using EcoSim (Gotelli and Entsminger 2001), we calculated the C-score for the observed matrix and then compared it with C-score values resulting from 20,000 matrix randomization simulations, in which row and column totals were maintained (SIM9, Gotelli 2000). By maintaining row and column totals, the number of occurrences of each species and the number of species in each sample is equal in both the original dataset and in all null (simulated) communities. Both the C-score metric and the simulation constraints we employed have sound statistical properties and are relatively insensitive to measurement error (Gotelli 2000). Non-significant C-scores denote independent (e.g. random) species co-occurrence patterns, while statistically significant C-scores may indicate either more or less pair-wise species co-occurrence than

expected by chance. Significantly negative C-scores indicate more co-occurrence than expected by chance, which should occur when species are positively associated, i.e. aggregated (Stone and Roberts 1992). Significantly positive C-scores indicate less co-occurrence than expected by chance and are concordant with deterministic processes structuring the community (Gotelli and McCabe 2002). At our experimental scale, significantly positive C-scores may result from (1) species segregation due to habitat affinities, and/or (2) species interactions (Gotelli and McCabe 2002). We present standardized C-scores (standardized effect size [SES]) for each matrix, because these values scale the results in units of standard deviation and allow between-assemblage comparisons of the degree of non-random organization (Gotelli and McCabe 2002).

If a significant C-score resulted from the above analysis, we (1) identified species pairs that contributed to the significance of the test, and (2) used step-wise multiple linear regression to evaluate the influence of measured habitat characteristics on the occurrence pattern for each species identified in step 1. The C-score represents the mean number of ''checkerboard units'' (Stone and Roberts 1990) between all pair-wise combinations of species in the original matrix (Gotelli 2000); therefore, we considered species pairs with an observed number of checkerboard units in the 95th percentile (largest 5%) of all pair-wise combinations as contributing significantly to the significance of the C-score test. Using these species (species pairs in the 95th percentile of checkerboard units) from the time interval where the C-score was found to be significant, we performed a step-wise multiple linear regression analysis in which each species' density was the dependent variable and habitat measures (see above) were independent variables. If a significant linear regression was observed (between the abundance of a species and measured habitat variables) during the time interval with significant C-score, we then tested the significance of the same relationship using pooled samples from the time intervals with non-significant C-score values. For regression analysis, habitat variables were $\log_e$ transformed (except depth, which was transformed by taking the reciprocal of depth squared) and then standardized. Transformed and standardized habitat variables met the assumptions for parametric statistics.

Results

Thirty-four fish species and 7 macroinvertebrate species were collected in experiment 1, and 36 fish species and 4 macroinvertebrate species in experiment 2 (44 fish and 7 invertebrate taxa overall). The maximum number of species on a patch was 13 and 10 in experiments 1 and 2, respectively. Results from experiment 1 reveal that proximity to source habitat and habitat complexity each significantly influenced the number of species in habitat patches. Local habitat patches with closer proximity to source habitat (i.e. higher colonization rates) yielded more species (Fig. 2a, $F_{2,19} = 4.33$, $P = 0.028$), and more complex habitats contained more species ($F_{2,19} = 88.5$, $P < 0.001$). Reach (beach sampled) and the proximity to source habitat by habitat complexity interaction term were both non-significant (reach $F_{14,19} = 1.19$, $P = 0.355$; interaction $F_{4,19} = 0.732$, $P = 0.581$). Species density was not significantly correlated with water depth (mean, range; 82 cm, 70–105; $F_{1,40} = 1.138$, $r^2 = 0.028$, $P = 0.293$) or water velocity (24 cm/s, 1–54; $F_{1,40} = 0.004$, $r^2 = 0.000$, $P = 0.947$).

Total organism abundance was strongly associated with habitat complexity but not with proximity to source habitat (complexity $F_{2,19} = 56.0$, $P < 0.001$, proximity to source habitat $F_{2,19} = 0.34$, $P > 0.7$). For total organism abundance, the effect of reach (blocking factor) was significant ($F_{14,19} = 2.4$, $P = 0.04$). Total organism abundance was not significantly correlated with water velocity (water velocity $F_{1,40} = 0.865$, $r^2 = 0.021$, $P = 0.358$,); however, total organism abundance was weakly associated with water depth (water depth $F_{1,40} = 5.209$, $r^2 = 0.115$, $P = 0.028$).

Neither loricariids nor members of our invertivore group were present in any of our samples from reference plots, though these fishes obviously crossed large areas of open sand to colonize patches of hard substrate with high structural complexity. Species density of low vagility taxa (i.e. loricariids) was affected by both habitat complexity (Fig. 2c, $F_{2,19} = 13.0$, $P < 0.001$) and proximity to source habitat ($F_{2,19} = 3.0$, $P = 0.07$), with species density significantly greater among habitats positioned most closely to source habitat (planned contrast, near versus far distance, $P = 0.024$). Species density of highly vagile taxa (i.e. invertivores) was significantly associated with habitat complexity (Fig. 2b, $F_{2,19} = 62.0$, $P < 0.001$), but not with proximity to source habitat ($F_{2,19} = 1.8$, $P > 0.19$; i.e. vagile species rapidly colonized all three distances, although mean species density was slightly lower in habitats farthest from sources). The interaction between proximity to source habitat and habitat complexity was not significant for either loricariids ($F_{4,19} = 1.32$, $P = 0.298$) or invertivores ($F_{4,19} = 1.33$, $P = 0.295$). Relative abundance of loricariids, in contrast to invertivores, was strongly associated with proximity to source habitat ($\chi^2 = 40.04$, df = 2, $P < 0.0001$). Abundance of slow-moving loricariid fishes was successively greater with proximity to source areas, but abundance of invertivores peaked at the intermediate distance.

Experiment 2 evaluated community assembly through time and tested the idea that species interactions influenced patch occupancy. Aquatic organisms were sampled over nine different time intervals from high-complexity patches constructed on sandbanks at the intermediate distance from source habitat (i.e. colonization rate). Mean organism abundance and mean species density (Fig. 3a) increased until day 30, and then declined on day 36. Species density and organism

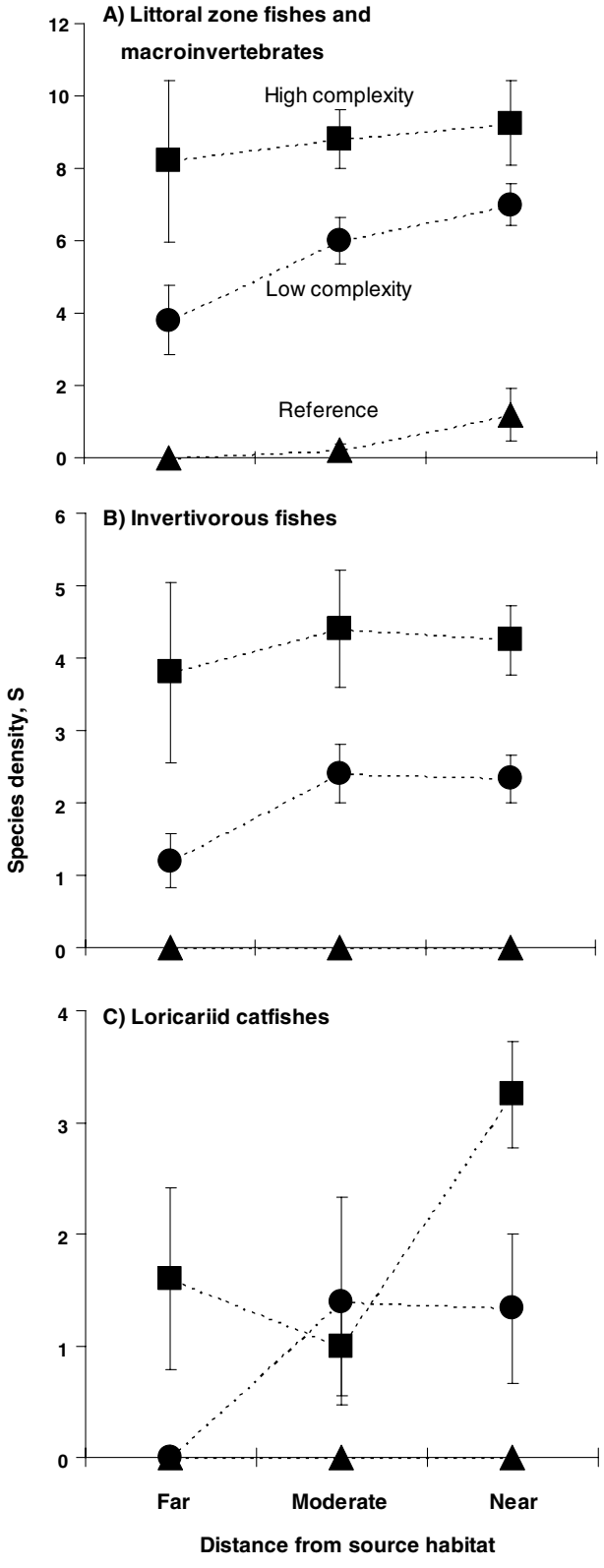

Fig. 2 Species density (S, no. species per 1.5 m^2) for **a** all littoral zone fishes and macroinvertebrates, **b** vagile invertivorous fishes, and **c** relatively sedentary loricariid catfishes in relation to distance from source habitats (i.e., colonization rate) and habitat structural complexity (*squares* high complexity, *circles* low complexity, *triangles* reference plots, i.e. sand substrate with no structures). Means ± SE

abundance were highly correlated ($F_{1,36} = 100.59$, $r^2 = 0.86$, $P < 0.001$). Mean species density on day 24 was equal to the value (8.7) obtained in the first experiment from patches of high-complexity and intermediate proximity to source habitat after 21 days. We tested bivariate relationships between both sample species density and total organism abundance and local environmental parameters (colonization potential [mean = 136, range = 4–200], distance across channel [mean = 277 m, range = 70–500], distance to shoreline [mean = 14 m, range = 1–67], water velocity [mean = 16 cm/s, range = 0–45], water depth [mean = 64 cm, range = 49–115]). None of these bivariate relationships were statistically significant (Table 1). Dominant taxa in short and intermediate samples (days 1–12) were small characids with high vagility (e.g. *Microschemobrycon casiquiare*, *M. callops*, and *Hemigrammus micropterus*) and a small loricariid, *Farlowella vittata*. Species typically associated with structurally complex habitats (Willis et al. 2005) dominated samples from day 24 (e.g. omnivorous anostomid fishes, the small pseu-

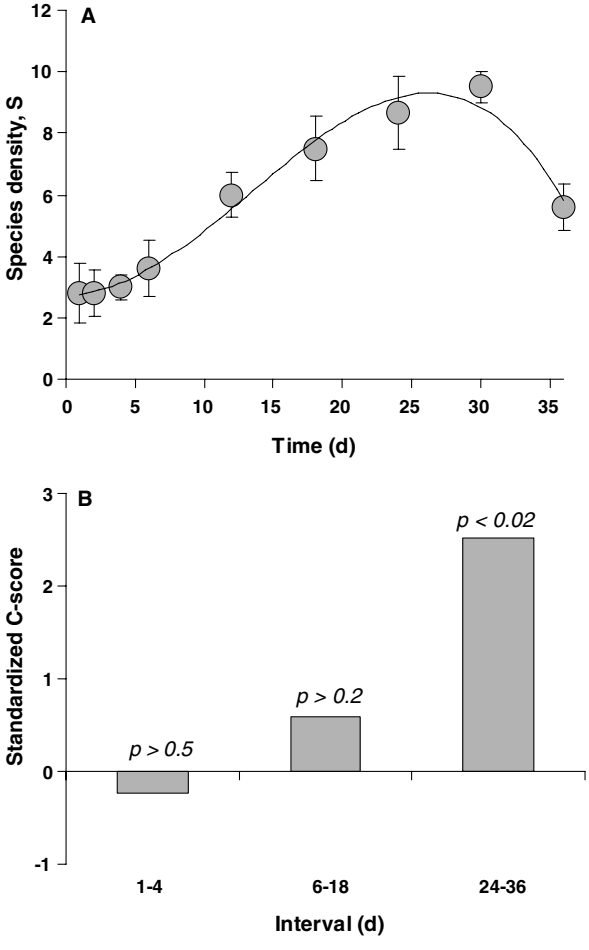

Fig. 3 Plots of **a** Species density (mean ± 1 SE) in relation to time since creation of habitat patch (regression model is $S = -0.0007(t)^3 + 0.03(t)^2 - 0.01(t) + 2.75$; $r^2 = 0.98$), and **b** standardized C-scores indicating degree of non-random assemblage structure for habitat patches of varying time intervals since creation

Table 1 Bivariate relationships between local environmental parameters and species density and organism abundance

Environmental parameters	Species density			Organism abundance		
	F	r^2	P	F	r^2	P
Colonization potential	2.137	0.056	0.152	0.267	0.007	0.609
Distance across channel	0.207	0.006	0.652	0.268	0.007	0.608
Distance to shoreline	1.132	0.03	0.294	1.264	0.034	0.268
Water velocity	0.321	0.009	0.574	0.003	0.000	0.956
Water depth	2.254	0.059	0.142	2.812	0.074	0.102

Note that none are significant

dopimelodid catfish *Microglanis poecilus*, and naucorid hemipterans) through day 36 (loricariids, carnivorous cichlids and pimelodids).

Results from the C-score analysis indicated increasing levels of non-random community organization over time (Fig. 3b). We failed to reject the null hypothesis of random (i.e. independent) species co-occurrence for communities sampled during the short (days 1–4 standardized effect size [SES] = −0.023, $P > 0.55$) and intermediate (days 6–12 SES = 0.58, $P > 0.27$) time intervals. In contrast, fishes and aquatic macroinvertebrates had significantly less co-occurrence (large C-score) than expected by chance (SES = 2.52, $P = 0.016$) in communities assembled for 24–36 days. There were 406 pair-wise interactions among the 29 taxa (25 fishes, 4 macroinvertebrates) collected from block patches sampled on days 24–36. Eleven taxa contributed to the 95th percentile of checkerboard units (non-co-occurrence) from these pair-wise interactions (Table 2). Nine of these 11 species (82%) showed a significant relationship between measured habitat characteristics and abundance in samples from the long time interval (days 24–36; Table 3). Importantly, none of these species-specific relationships were significant ($P > 0.05$; see Table 3) when tested using samples pooled from the short and intermediate time intervals (days 1–18) for which the C-score analysis indicated apparent random co-occurrence patterns among species. Habitat characteristics were not statistically different between the long and short–intermediate time intervals (colonization potential $F_{1,36} = 2.25$, $P = 0.142$; distance across channel $F_{1,36} = 0.421$, $P = 0.521$; distance to shoreline $F_{1,36} = 0.856$, $P = 0.361$; water velocity $F_{1,36} = 0.119$, $P = 0.732$; water depth $F_{1,36} = 3.72$, $P = 0.062$). Furthermore, there was no statistically significant change in abundance between the short–intermediate (days 1–18) and the long (days 24–36) time interval (Table 4). However, one predator species, *Crenicichla* af. *wallacii*, did show a substantial, though non-significant, increase in abundance over these time periods. Differences in community organization, therefore, do not appear attributable to among-interval differences in microhabitat characteristics or statistical artefacts due to changing abundances of the species.

Discussion

Experimental manipulations of proximity to source habitat and the structural complexity of simulated rocky patches in the littoral zone of the Cinaruco River revealed significant effects of both factors on fish and macroinvertebrate species density (experiment 1). We observed an increase in species density as both proximity to source habitat and habitat complexity increased in block patches constructed in the littoral zone. Results from experiment 1 are consistent with the well-established relationship between colonization rate and species

Table 2 Identification of 19 species pairs with the largest number of checkerboard units (95th percentile of the observed number of checkerboard units) for samples collected during the long time interval (days 24–36)

	Panaque maccus	*Parotocinclus eppleyi*	*Pekoltia* sp.	*Pimelodella* sp. 1	*Pimelodella* sp. 2	*Crenicichla* af. *wallacii*	*Geophagus* sp.
Odonata		9		12	9		
Creagrutus phasma	8		9	8			
Microschemobrycon callops	8					12	
Moenkhausia copei	12	9	8			10	
Panaque maccus							12
Parotocinclus eppleyi							12
Pekoltia sp.					8		8
Pimelodella sp. 1						8	10
Pimelodella sp. 2						18	

Values presented are observed pair-wise checkerboard units. The co-occurrence patterns (i.e. number of checkerboard units) of these species drove the significance of the C-score analysis for the long time interval, which indicated significantly less co-occurrence among species than expected by chance

Table 3 Forward step-wise regression of habitat characteristics on species abundance

Species	Significant variables	Long time interval (days 24–36)				Combined short and intermediate time interval (days 1–18)			
		ANOVA (P)	r^{2a}	Beta coefficient ($\pm$SE)	P	ANOVA (P)	r^{2a}	Beta coefficient ($\pm$SE)	P
Pimelodella sp. 1	Complete model	0.003	0.83			0.345	0.02		
	Distance across channel			1.808 (0.264)	<0.001			−0.047 (0.106)	0.664
	Colonization			−0.390 (0.124)	0.020			−0.040 (0.122)	0.747
	Depth[c]			−0.313 (0.112)	0.031			0.249 (0.135)	0.077
Moenkhausia copei	Distance across channel	0.005	0.64	−1.500 (0.398)	0.005	0.625	0.01	−0.050 (0.102)	0.625
Parotocinclus eppleyi	Distance across channel	0.015	0.54	0.643 (0.209)	0.015	0.573	0.01	−0.038 (0.067)	0.573
Crenicichla af. *wallacii*	Depth[c]	0.017	0.53	0.542 (0.180)	0.017	0.708	0.01	−0.040 (0.107)	0.708
Microschemobrycon callops	Complete model	0.017	0.60			0.558	−0.03		
	Depth[c]			−0.325 (0.121)	0.320			0.000 (0.067)	0.997
	Colonization			−0.310 (0.131)	0.490			−0.065 (0.061)	0.296
Pimelodella sp. 2	Depth[c]	0.022	0.50	−0.246 (0.087)	0.022	0.763	0.00	0.009 (0.030)	0.763
Creagrutus phasma	Complete model	0.042	0.82			0.424	−0.01		
	Distance to shore			−0.243 (0.038)	<0.001			−0.111 (0.119)	0.361
	Depth[c]			−0.085 (0.034)	0.042			−0.02 (0.134)	0.884
Pekoltia sp.	Distance across channel	0.043	0.42	0.595 (0.248)	0.043	0.085	0.11	0.129 (0.072)	0.085
Odonata	Depth[c]	0.052[b]	0.40	0.218 (0.095)	0.052	0.458	0.02	−0.042 (0.056)	0.458
Geophagus sp.	None significant								
Panaque maccus	None significant								

Beta coefficients show the relative contribution of significant habitat variables ($P<0.05$) on observed species abundance. Only those species with the largest number of pair-wise checkerboard units (Table 2) were analyzed (see Methods)

[a] Adjusted r^2 is presented if model contains more than one independent variable

[b] Presented though marginally significant

[c] Because depth was reciprocally transformed, a positive beta indicates the species was associated with shallower rocky patches

Table 4 Species occurrence and abundance data for the nine species that exhibited a significant relationship between individual abundance and habitat characteristics during the long time interval (Table 3)

Number of occurrences			Total abundance		t-test
Days 1–18	Days 24–36		Days 1–18	Days 24–36	P
6	3	*Creagrutus phasma*	12	3	0.943
5	4	*Parotocinclus eppleyi*	8	6	0.612
5	5	*Pimelodella* sp. A	17	25	0.091
5	4	*Moenkhausia copei*	17	27	0.386
7	6	*Crenicichla* af. *wallacii*	13	23	0.067
2	2	*Microschemobrycon callops*	4	8	0.352
1	3	*Pimelodella* sp. B	1	4	0.168
2	5	*Panaque maccus*	2	12	0.172
4	4	Odonata	4	5	0.221

The P value is the result of a t-test comparing the abundance of individuals sampled during days 1–18 with the abundance of individuals sampled during days 24–36; a separate t-test was performed for each species

density (MacArthur and Wilson 1967; Simberloff and Wilson 1969) and habitat complexity and species density (Petren and Case 1998). Proximity to source habitat and habitat complexity apparently interacted in an additive manner to influence species density in block patches; this result occurred whether we evaluated the entire community, highly vagile fishes (invertivores), or low-vagility fishes (loricariids). A possible explanation for this pattern is that high rates of patch colonization mitigated the effects of selective exclusion as species densities approached patch saturation (Schoener 1988). Furthermore, interspecific variation in vagility significantly affected fish species density in relation to proximity to source habitat but not habitat complexity.

Experiment 2 revealed temporal dynamics of community assembly, with newly created patches (1–18 days old) revealing apparently random, or independent, species co-occurrence patterns, and older patches (24–36 days old) with significantly non-random species co-occurrence patterns (Fig. 3). In newly created block patches, species' occurrences were independent of occurrences of other species as well as measured microhabitat characteristics. In older, more saturated patches, the community shifted from random to non-random (i.e. not independent) organization, with abundances of individual species increasingly correlated with habitat characteristics. As more and more individuals arrived on local patches, abundances of potential com-

petitors and predators increased, which may have resulted in altered patterns of microhabitat use. The fact that none of the significant species abundance-habitat relationships observed during the long time interval (days 24–36) were found to be significant during the short and intermediate time intervals (days 1–18) seems to indicate that species interactions may have driven observed habitat shifts (Schoener 1988). Thus, it appears that species-specific responses to environmental variation (*sensu* Grossman et al. 1998) resulted, in part, because of biotic interactions.

Assemblage composition in local patches exhibited substantial variation in both experiments. Some of this variation in assemblage composition probably was associated with stochastic elements of colonization (Syms and Jones 2000), especially among newly formed patches that were unlikely to have approached equilibrium species densities (Simberloff and Wilson 1969). To some degree, all communities are constrained by their physical environments (Grossman et al. 1998; Wilson 1999; Oberdorff et al. 2001), though observed abundances of individual species in newly formed block patches were not significantly associated with our measured habitat variables. However, species abundances, for nine of the eleven species that contributed to the significance of the C-score test were significantly correlated with measured habitat characteristics as patches aged (days 24–36) and community assembly progressed. If some species inhibit patch occupancy by others, as our experiment 2 results indicate, the sequence of species arrival may yield alternative assemblage trajectories. For example, *Pimelodella* sp. 2 (catfish) never co-occurred with *Crenicichla* af. *wallacii* (pike cichlid) in block patches established for more than 24 days (9 of 10 patches occupied by one, but never both, species; Table 2). Both of these species feed heavily on small shrimp (unpublished data from stomach contents analysis), a resource associated with structurally complex habitats in the littoral zone (Arrington 2002). Non-random co-occurrence patterns also could be driven by prey response to predation threat (Layman and Winemiller 2004). For example, *Crenicichla* af. *wallacii* consumes small fish and never co-occurred with a potential prey fish, *Microschemobrycon callops*, on patches established $\geq$ 24 days (8 of 10 patches occupied by one, but never both, species; Table 2).

Had our study only examined patches colonized over the long time interval (days 24–36), we would have failed to realize the apparent influence of biotic interactions on habitat shifts and incorrectly identified species-specific responses to environmental variation as the sole driving force organizing these local communities. In a long-term study of temperate stream fish assemblage dynamics (Grossman et al. 1998), environmental variability (i.e. discharge) was identified as the predominant influence on fish assemblage structure and habitat use patterns. Differences in findings from our study and that of Grossman et al. (1998) are likely due to different disturbance regimes (i.e. hydrologic flow variation) in the two systems, a result predicted by Schlosser (1987). The Cinaruco River is a large floodplain river that experiences substantial (> 5 m) annual water level fluctuations; however these water level changes occur gradually and predictably (Arrington and Winemiller 2003). In contrast, discharge variation in temperate streams is often relatively unpredictable and rapid (Poff and Allan 1995). It appears that in tropical floodplain rivers seasonal water level fluctuations are sufficiently gradual to permit species accrual in habitat patches such that biotic interactions influence patch occupancy.

Like tropical river fishes, coral reef fishes have been the source of debate over determinants of assemblage structure. An early view of random species associations determined by recruitment and establishment of post-larvae (Sale and Douglas 1984) has given way to a model in which combinations of stochastic and deterministic ecological factors influence different life stages and species abundance patterns (Ebeling and Hixon 1991; Syms and Jones 2000). Resident predators and competitors influence the recruitment success of juveniles settling onto the reef in a species-specific manner, thus imposing determinism on future community structure (Shulman et al. 1983; Almany 2003). Fish assemblage dynamics on coral reefs differ from those in tropical rivers in important ways. Most reef fishes have pelagic eggs and larvae that eventually settle onto reefs as juveniles. Recruitment onto reefs can have a significant stochastic component, and reefs are relatively stable habitats that experience infrequent but large-scale disturbances (e.g. ENSO-related climatic effects, hurricanes). Once established on a patch reef, a fish may remain there for years, with availability of food and/or refuges having density-dependent effects on populations (Hixon and Beets 1993; Robertson 1996). In contrast, species assemblages of patchy habitats in the littoral zone of tropical rivers derive from frequent spatial reshuffling, mostly by adult fishes, as water levels rise and recede. Like coral reefs, tropical, floodplain rivers have macrofaunal assemblages influenced by stochastic as well as deterministic processes, and relative influence of these factors depends on patch characteristics, e.g., amount of time submerged at a suitable depth.

Streams are dynamic landscapes composed of a mosaic of habitat patches (Townsend 1989; Schlosser and Kallemeyn 2000; Taylor and Warren 2001; Amoros and Bornette 2002) with constituent biota adapted to exploit the high turnover rates of habitat patches (Robinson et al. 2002). Evaluations of within- and among-patch dynamics in streams have shown the relative importance of both deterministic and stochastic processes influencing local community assembly (Taylor 1996; Angermeier and Winston 1998). Environmental instability, such as the stochastic hydrologic variability that characterizes temperate streams, typically results in a greater influence of stochastic processes structuring assemblages (Poff and Allan 1995; Grossman et al. 1998). Competition and predation seem to exert a greater influence on assemblage dynamics in systems with more predictable disturbance (i.e. hydrologic) regimes, such as large lowland rivers

(Schlosser 1987; Rodríguez and Lewis 1997; Layman and Winemiller 2004). The gradual water level change in tropical floodplain rivers produces a dynamic re-shuffling of local communities much like that described by Townsend (1989) under "mobility control". In our mobility-controlled communities, landscape architecture and local patch characteristics (e.g. structural complexity, water depth, and velocity) influence community membership in habitat patches that are continuously becoming more or less suitable for a suite of species as water levels gradually change. During local community assembly in the shallow littoral zone, biotic interactions appear to strengthen species responses to fine-scale environmental filters (Table 2) (Tonn et al. 1990) as patches become saturated. Community dynamics in newly formed habitat patches seem to be dominated by dispersal. In older patches, when saturation is more likely, community dynamics probably are influenced by dispersal and the spatial distribution of both abiotic and biotic features. In summary, our patch-scale field experiments reveal that the degree to which biotic interactions influence community assembly in littoral habitats of a lowland tropical river is influenced by both the distribution of habitats on the landscape (affecting colonization rates) and physical habitat characteristics.

Acknowledgements We thank D. Taphorn and the Museo de Ciencias Naturales, UNELLEZ for logistic and taxonomic assistance. Jonathan Armbruster graciously verified our loricariid identifications. We thank M. Hixon, T. Lacher, and B. Langerhans for constructive comments on the manuscript. We gratefully acknowledge Tour Apure and members of the Cinaruco River Fishing Lodge for providing logistic accommodations. A. Medina, Walt Arrington, T. Hibbitts, and M. Woods provided assistance with sampling. Specimens were collected under legal authority of permits issued by Venezuela's Ministerio de Ambiente y Recursos Naturales Renovables. This research was supported by National Science Foundation grants DEB 0107456 and 0089834 and a U.S. Environmental Protection Agency STAR Fellowship.

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