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Species–area relationship within benthic habitat patches of a tropical floodplain river: An experimental test

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Abstract The curvilinear relationship between species richness and habitat area (species–area relationship (SAR)) is a fundamental ecological pattern. The relationship is often viewed from a long-term perspective across relatively large spatial scales, reflecting a balance between immigration and extinction dynamics. We explored whether predictions of SAR also manifest over short time periods (days) in benthic habitat patches of a dynamic floodplain river where littoral faunal assemblages are continuously assembled and disassembled with changing water levels. We examined the relationship of patch size with faunal abundance (i.e. fish and aquatic invertebrates), taxonomic richness, trophic group richness and overall assemblage composition. Strong taxa–area relationships emerged despite the relatively short experimental time period (21 days); larger patches had more taxa and trophic groups. For the smallest patches, taxonomic richness was especially sensitive to abundance of individuals; abundance of individuals was a less important predictor of taxonomic and trophic group richness for the largest patches. Despite the relatively short time frame for study within this temporally dynamic ecosystem, our findings indicate a strong SAR for fishes and macroinvertebrates inhabiting patchy habitats in the littoral zone of this tropical river.

Key words: assemblage structure, floodplain river, habitat patch size, Neotropical fish, species diversity, Venezuela.

INTRODUCTION

The relationship between area and the number of species is perhaps the most studied and reliable patterns in ecology (Rosenzweig 1995), and has even been referred as one of the few laws in this field (Connor & McCoy 1979; Coleman 1981). This relationship has been observed across a variety of habitats and organisms, and has been hypothesized to result from a dynamic equilibrium between colonization and extinction rates which depend on habitat isolation and size (see reviews by Connor & McCoy 1979; Lomolino 2000). The species–area relationship (SAR) is mediated by many factors including habitat area (Connor & McCoy 1979; Matias *et al.* 2010), taxonomic groups (Rosenzweig 1995), habitat heterogeneity (Stein *et al.* 2014), trophic diversity (Ryberg & Chase 2007) and disturbance history (Lake 2000; Badano *et al.* 2005).

In tropical floodplain rivers, there is strong seasonal variation in hydrology, with water levels rising or falling throughout the year. The littoral zone of these rivers is composed of a mosaic of habitat patches upon which local communities are assembled and disassembled over days to weeks according to water level fluctuations associated with the annual flood pulse (Arrington & Winemiller 2006; Layman *et al.* 2010). In a study of fish and aquatic macroinvertebrate assemblages in the littoral zone of the Cinaruco River in Venezuela, Arrington and Winemiller (2006) demonstrated non-random structure of fish and macroinvertebrate assemblages in different types of habitats (e.g. sand banks, leaf litter, woody debris) during the falling-water phase of the annual flood cycle. The spatial distribution of the habitat patches (e.g. Arrington *et al.* 2005; Layman *et al.* 2010) and habitat complexity (e.g. Willis *et al.* 2005; Montaña *et al.* 2014) were shown to play an important role in determining assemblage structure. Patch size is likely another driver of assemblage composition but has not been explicitly investigated.

Here, we examined whether species–area relationships are manifest over relatively short time periods in patch habitats within littoral zones in a Venezuelan floodplain river. To test relationships, we constructed habitat patches using bricks. These structures are rapidly colonized by fishes, shrimps and other aquatic macroinvertebrates, thereby allowing us to examine the relationship between patch size and taxonomic and trophic group richness.

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METHODS

Experiments were conducted in littoral zones of floodplain lagoons of the Cinaruco River, a species-rich, moderate blackwater river within the Venezuela's Santos Luzardo National Park, Estado Apure (between latitude 6°32′N and 67°24′W). The Cinaruco is characterized by low nutrients, low pH, high fish diversity and sandy substrate (Arrington *et al.* 2005; Montoya *et al.* 2006). Like other tropical floodplain rivers, the Cinaruco has strongly seasonal hydrology in accordance with pronounced wet and dry seasons. During the wet season (May–October), the riparian zone is flooded, and organisms are dispersed widely through the inundated floodplain. The flood crest typically occurs in September and falls October through December. As water levels start receding, organisms are forced off floodplains into the main river channel and lagoons (Winemiller & Jepsen 1998). During the dry season (January–March), aquatic habitats are reduced to a spatial mosaic consisting of the main channel, side channels and lagoons (Arrington *et al.* 2005). Floodplain lagoons have heterogeneous habitat features including sand, leaf litter, cut banks, partially submerged overhanging vegetation and submerged branches and tree falls. The connectivity of lagoons varies with the hydrological regime, geomorphology and distance from the main channel, but most lagoons are connected to the main river channel from May to December.

Unglazed ceramic building bricks were used to construct patches of structurally complex habitat (simulating natural rocky patches). These patches were discrete areas with a similar configurations and vertical profiles that attract certain taxa of aquatic invertebrates and fishes that rely on structurally complex habitats for refuge and feeding (Forman & Godron 1981; Pringle *et al.* 1988). Each brick measured $14 \times 18.5 \times 29$ cm, was hollow and had nine internal (3.5×5 cm) compartments that opened at each end of the longitudinal axis of the block. The arrangement of the compartments creates microhabitats for organisms to colonize both outer and inner surfaces of the brick. Given the three-dimensional arrangement of these habitat patches, we used volume (cm^3) as the measure of patch size. Six treatments were created: one ceramic tile ($25 \times 6.4 \times 0.49$ cm), one brick (=7511 cm^3), two bricks (=15 022 cm^3), five bricks (=37 555 cm^3), 10 bricks (=75 110 cm^3) and 20 bricks (=150 220 cm^3). Patches were replicated in three lagoons (Laguna Larga, Secreta and Escondida) at three different times: December of 2005, February of 2006 and March of 2006. Six sand banks were randomly selected in each lagoon, and treatments randomly assigned to a bank site. The same six banks were used each month, with experimental patches always constructed at 1.2 m depth. For each patch, we arranged the bricks following Arrington *et al.* (2005), in which bricks were positioned parallel (i.e. the water could flow through the bricks) to the direction of the current flow.

Patches were constructed at the beginning of each month and sampled after 21 days. A seine (6.2×1.2 m with 4 mm mesh) was used to encircle each patch to prevent the organisms inside the sampling area from escaping. Bricks were removed from inside the seine, and the seine with its contents was carefully taken ashore for removal of the organisms (for further description of sampling protocol see Arrington *et al.* 2005). Fishes and invertebrates were included in our analysis because both groups are abundant and interact in structurally complex littoral habitats of the Cinaruco (Arrington *et al.* 2005; Layman *et al.* 2010).

Fishes and invertebrates were preserved in 10% formalin, and later identified and counted in the laboratory. Fishes and shrimps were identified to species, whereas aquatic macroinvertebrates were identified to order or family depending on availability of taxonomic keys. Fishes and invertebrates were used for calculations of the Shannon diversity index ($D = -\Sigma_{i=1}\ p_i \ln p_i$) and Evenness index ($E = H'/\ln S$) to interpret results of assemblage diversity in relation to patch size, lagoon and month. Fishes were assigned to functional groups (piscivore, invertivore, invertivore/piscivore, omnivore, algivore/detritivore, mucus feeders, Appendix S1) following Taphorn (1992), Arrington *et al.* (2005), Hoeinghaus *et al.* (2003), Montaña and Winemiller (2009), and FishBase (2012). Specimens are archived in the Museo de Ciencias Naturales de Guanare, Venezuela.

Species richness was regressed against abundance among replicates for each patch size. Number of taxa and number of individual species per patch were log-transformed to meet assumptions of normality. In addition, we tested for differences among the slopes of relationships between species richness and abundance among patch sizes by using the test for homogeneity of slopes (Underwood 1997). We used ANCOVA (patch volume as covariate) to examine differences in species richness and abundance with respect to patch size. Richness and abundance were compared across months, lagoons and their interactions (time × lagoon × patch size).

We also employed the C-score metric (Stone & Roberts 1990; Gotelli 2000), a quantitative index of co-occurrence that allows for inference regarding species interactions (Gotelli 2000; Gotelli & McCabe 2002). Using EcoSim (Gotelli & Entsminger 2001), we calculated C-scores for observed values and then contrasted each with an average C-score resulting from 10 000 random matrix simulations in which rows and columns were maintained (i.e. the fixed-fixed null model or SIM9, Gotelli 2000). Non-significant C-score values suggest that species colonized patches randomly (independent of other species or individuals), whereas C-score values significantly different from zero suggest deterministic mechanisms (e.g. predation or competition) played a role in community assembly (Stone & Roberts 1992; Gotelli 2000).

RESULTS

We collected 34, 34 and 32 species of fish from constructed habitat patches in Laguna Larga, Escondida, and Secreta, respectively. Common taxa (Table 1) included characids (e.g. *Aphyocharax alburnus*, *Microschemobrycon casiquiare*, *Moenkhausia copei*), small benthic catfishes (e.g. *Ochmacanthus alternus*, *Tatia concolor*, *Platydoras costatus* and *Microglanis poecilia*), pike cichlids (*Crenicichla lugubris* and *C.* aff. *wallacii*) and an omnivorous anostomid (*Anostomus ternetzi*).

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Table 1. Taxonomic richness (S), number of individuals (abundance, A), Shannon–Weiner diversity (D), evenness index (E) and number of trophic groups (TG) collected from patch habitats

	Patch volume (cm^3)	Laguna Larga					Escondida					Secreta				
		S	A	D	E	TG	S	A	D	E	TG	S	A	D	E	TG
December	78	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	7 511	4	4	0.1	0.1	3	3	9	0.1	0.2	0	8	38	0.2	0.2	3
	15 022	6	9	0.1	0.1	3	11	24	0.1	0.1	3	12	42	0.2	0.1	5
	37 555	14	218	0.7	0.6	3	13	42	0.2	0.1	3	11	23	0.1	0.1	5
	75 110	14	47	0.2	0.1	5	11	233	0.9	0.8	6	15	159	0.3	0.3	6
	150 220	19	60	0.1	0.1	5	25	426	2.7	1.9	6	23	416	2.6	1.9	7
February	78	2	3	0.0	0.2	0	2	4	0.1	0.2	2	2	2	0.0	0.1	1
	7 511	3	5	0.1	0.1	2	2	2	0.0	0.1	2	2	2	0.0	0.1	2
	15 022	9	89	0.0	0.0	3	7	11	0.1	0.1	3	8	24	0.1	0.2	4
	37 555	10	104	0.0	0.0	4	9	30	0.2	0.2	3	13	33	0.2	0.1	5
	75 110	18	320	5.2	4.1	4	20	315	1.6	1.2	5	9	168	0.4	0.4	5
	150 220	21	493	3.4	2.6	6	20	218	0.7	0.6	5	23	369	2.1	1.5	6
March	78	2	5	0.1	0.2	0	2	5	0.1	0.2	2	3	7	0.1	0.2	0
	7 511	4	7	0.1	0.1	2	5	5	0.1	0.1	1	3	13	0.1	0.2	2
	15 022	7	11	0.1	0.1	3	5	16	0.1	0.2	2	5	21	0.1	0.2	3
	37 555	8	31	0.2	0.2	3	7	68	0.1	0.1	4	8	27	0.2	0.2	4
	75 110	12	66	0.1	0.1	4	14	123	0.1	0.1	4	16	102	0.0	0.10	4
	150 220	22	156	0.3	0.2	5	20	206	0.6	0.5	5	20	152	0.3	0.2	6

Common invertebrate taxa included macroinvertebrates (e.g. naucorid hemipterans, Odonata, Ephemeroptera and Coleoptera) and the small shrimp *Macrobrachium* cf. *dierythrum*. Some species, for example, *Acestrorhynchus minimus* and *Sternopygus macrurus*, were collected only during the onset of the dry season (December); other species, for example, four species of *Hemigrammus* and two species of cichlids (*Apistogramma* sp. and *Geophagus abalios*), were captured from patches only during the peak of the dry season (February–March). Twenty-two taxa were collected in all three sampling periods (Table 2).

As expected under SAR predictions, taxonomic richness and organism abundance varied significantly among patch sizes, with larger patches containing more taxa (Table 2, Appendix S2). Number of trophic groups, taxonomic diversity (D) and evenness (E) also tended to increase with increasing patch size (Table 1). When relationships between organism abundance and taxonomic richness were examined within replicates for a given patch size, larger habitats had both greater number of individuals and taxa ($r = 0.82$, $P < 0.001$, Fig. 1). Slopes were significantly different among patches of different sizes (test for homogeneity of slopes, $F_{5,2} = 8.81$, $P < 0.001$). For the smallest patches, taxonomic richness was especially sensitive to abundance of organisms (e.g. steeper slopes, 78.4 cm^3: b = 0.34, Fig. 1), whereas abundance was a less important predictor of taxonomic and trophic group richness for the largest patches (150 220 cm^3: b = 0.008, Fig. 1). Results from ANCOVA showed support for patch size being related to taxonomic richness

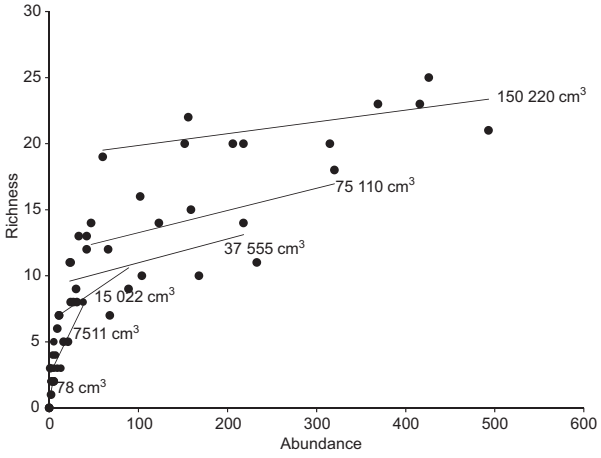

Fig. 1. Regressions of the relationships between taxonomic richness and organism abundance for patches of different sizes. Slopes for patch volume replicates were: 150 220 cm^3 = b: 0.008, 75 110 cm^3 = b: 0.01, 37 555 cm^3 = b: 0.02, 15 022 cm^3 = b: 0.02, 7511 cm^3 = y: 0.15, 78.4 cm^3 = b: 0.34.

($F_{5,2} = 264.2$, $P < 0.0001$) and organism abundance ($F_{5,2} = 5.99$, $P < 0.018$); no differences were observed for richness or abundance among different lagoons ($F_{5,2} = 0.70$, $P < 0.52$) or time periods ($F_{5,2} = 1.28$, $P < 0.08$). We also ran analyses excluding all macroinvertebrates, and results were qualitatively similar.

Results from the C-score analysis had just one value (December, patch size 15 022 cm^3) significantly

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Table 2. Abundance, by month and patch size, of the 22 most common taxa

	December						February						March					
Patch volume (cm^3)	78	7511	15 022	37 555	75 110	150 220	78	7511	15 022	37 555	75 110	150 220	78	7511	15 022	37 555	75 110	150 220
Aphyocharax alburnus					1	3			3		5	2			2			7
Microschemobrycon casiquiare			14	2		3			60	4	123	153					26	83
Moenkhausia copei		26	7			41		3	15	11	51	22			10	52	75	35
Anostomus ternetzi			1	4	1	1			1	1	1							
Pseudanus gracilis			1	7	26	23			1	4	1	8				1	2	2
Auchnenipterichthys longinamus		1	4	1	8	7			1			4						1
Trachycorystes trachycorystes		1	2		1	3												
Tatia concolor		7	5	35	153	263		2	13	65	286	380		5	3	7	51	76
Cetopsis sp.				3		9			1	2	2	4						1
Acanthodoras sp.			1		2	4				3	1	1				1	2	8
Platydoras costatus		4	5	7	14	20		1	3	3	8	7			1	1	2	5
Scorpiodoras sp.				1	1	5						5					5	10
Dekeyseria scaphirhincha				5	3	5				1	3	3						2
Microglanis poecilus		3	8	16	21	22			2	3	11	13			1		5	8
Ochmacanthus alternus			2	1		2						5		2			1	2
Cephalosilurus apurensis			2	2		2			1	1								
Crenicichla lugubris			1		5	8			1	2	3	5				1		3
Crenicichla aff. *wallacii*		2	5	9	16	29		2	6	19	23	26		2	5	15	16	25
Invertebrates																		
Hemiptera (Naucoridae)			2	5	4	6	2		1	3	15	11	7		2	4	1	7
Ephemeroptera				3		11	4			2		2	8					9
Odonata		1				3	2				1	3	2	5	2		3	
Decapoda (*Macrobrachium* cf. *dierythrum*)		4	13	170	160	408		2	14	33	177	380		10	19	29	99	218

Table 3. Results of the co-occurrence analyses (C-scores and standardized effect size (SES)) indicating the degree of non-random assemblage structure for habitat patches in the Cinaruco River across three months

	78 cm^3			7511 cm^3			15 022 cm^3			37 555 cm^3			75 110 cm^3			150 220 cm^3		
	C-score	*P*	SES	C-score	*P*	SES	C-score	*P*	SES	C-score	*P*	SES	C-score	*P*	SES	C-score	*P*	SES
December	0.0	1.0	0.000	0.40	1.0	0.001	**0.47**	**0.001**	**6.02**	0.53	0.53	–0.03	0.30	0.8	–0.44	0.28	1.0	–0.88
February	0.33	1.0	0.000	0.90	0.65	–0.001	0.55	0.29	0.43	0.41	1.0	–0.72	0.27	0.5	0.15	0.20	1.0	–0.98
March	0.0	1.0	0.000	0.66	0.26	1.03	0.63	0.43	0.3	0.42	0.19	0.21	0.43	0.2	0.87	0.34	1.0	–0.97

Values in parenthesis correspond to the *P*-values. The one significant value is in bold text.

different from zero (see Table 3). The non-significant C-scores suggests colonization did not deviate from random colonization patterns, that is, there was little inferential evidence for deterministic mechanisms, such as predation or competition, influencing assemblage structure.

DISCUSSION

Our experimental manipulations revealed that patch size was an important variable explaining variation in taxonomic richness and organism abundance in structurally complex habitats within littoral habitats of lagoons in the Cinaruco River floodplain. Strong richness-patch size relationships emerged despite the relatively short time period for patch colonization in this temporally dynamic floodplain river. We suggest the most likely factors contributing to this pattern are effects of patch size on immigration rates, diversity of microhabitats that serve as refugia and higher prey abundance for predatory taxa within larger patches. We discuss each of these possibilities below.

Greater diversity of organisms in larger habitat patches is hypothesized to be due to the positive correlation between immigration rates and patch size (Gilpin & Diamond 1976; Simberloff 1976; Lomolino 1990). Larger patches are thought to serve as more likely targets for both passive and actively dispersing fishes and invertebrates. As such, with a greater number of immigrant individuals, more species would be expected on larger patches regardless of local biological interactions. Some rare species, such as catfish (e.g. *Scorpiodoras*, *Dekeyseria* and *Cetopsis*), were found only on the largest patches. These species have relatively low vagility, suggesting that large patches increase the likelihood of encountering that habitat and/or once settled they are less likely to leave.

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The availability of microhabitats (e.g. more holes and crevices inside the block structure) also increases with patch size (Underwood & Chapman 1996). These microhabitats provide fishes refugia, consequently reducing predation efficiency (Savino & Stein 1982; Angermeier & Schlosser 1989). Larger patches had a disproportionate number of small catfishes (e.g. auchenipterids, doradids and pseudopimelodids) which can move into spaces within the patches to reduce predation risk from larger predators such as peacock cichlids (*Cichla* spp.) and pimelodid catfishes (*Pseudoplatystoma fasciatum*, *Phractocephalus hemilioipterus*). In contrast, diurnal, invertivorous characids that are active swimmers within the water column occurred even in the smallest patches. For these fishes, patch size per se is not as important because they are not utilizing the internal refugia provided by the larger patches. Larger patches also provide greater surface area for accumulation of fine organic matter and algae that are food for macroinvertebrates and fishes. For instance, larger patches had greater abundance of shrimp (*Macrobrachium* cf. *dierythrum*) that utilize these resources. In turn, the shrimp serve as food for small benthic predators (e.g. *Crenicichla* aff. *wallacii*). As such, these predators can forage directly within the patch, further increasing the diversity of fishes found on the largest patches.

The C-score analysis suggests that species interactions were not important in structuring the communities. As such, of the above discussed drivers, the immigration explanation seems most likely to explain the observed patterns. Arrington *et al.* (2005) performed an experiment in the same river system in which patch complexity and distance to colonization source were manipulated. They determined that assemblages in these artificial patches had essentially random composition during the first 1–18 days of colonization, but assemblages after 24–36 days had significantly non-random structures (i.e. competition or predation affected assemblage composition). Our data are consistent with the non-random patterns of assembly, which Arrington *et al.* (2005) suggest is the result of 'equilibrium' densities of organisms not being reached. Given the fine scale and the short time at which these assemblages are formed in this dynamic floodplain river, species interactions may not be the dominant determinant of assemblage structure, yet general community patterns, like SAR, may be a useful framework for assessing species composition in these dynamic patch habitats.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Trophic classification of the collected fish and invertebrate species.

Appendix S2. Abundance of each species collected in habitat patches.

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