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Interconnectedness during high water maintains similarity in fish assemblages of island floodplain lakes in the Amazonian Basin

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ABSTRACT. We conducted a study to test the hypothesis that interconnectedness among island floodplain lakes and the adjacent Solimões River during the flood stage of the hydrologic cycle is enough to maintain similarity in fish species assemblages. Gill net samples were collected during high and low water periods for three consecutive years (July 2004 to July 2006) in four lakes on Paciência Island. Two lakes, Piranha and Ressaca, are connected to the river all year, and the other two, Preto and Cacau, which are in the center of the island, are isolated during low water periods. The abundance, species richness and evenness of the fish assemblages in these lakes did not differ according to their relative positions or the season of the hydrological cycle, which confirmed our hypothesis. However, fish abundance during the dry season was greater than in the flood season. Apparently, the short period of full connection between the lakes is enough to allow the colonization of all fish species, but not to cause similar abundances. Our study indicates that persistence of the species composition of island floodplain lakes is primarily due to the annual replenishment of fish to the lakes during the flood season.

KEY WORDS.Amazonian; diversity; flood pulse; floodplain lakes.

Several studies have been conducted during the past few decades to evaluate the effects of abiotic and biotic factors on the structure and dynamics of fish communities (Chesson 1986, Dunson & Travis 1991, Tejerina-Garro *et al.* 1998, Súarez *et al.* 2001, 2004). In general, it has been accepted that spatial habitat diversity promotes species diversity in fish communities (Hoeinghaus *et al.* 2003, Pouilly & Rodriguez 2004), but temporal aspects, such as seasonal changes in the habitat, have been little studied thus far.

Several hypotheses have been advanced to explain the high fish diversity in the Amazon Basin. Lowe-McConnell (1999) suggested three possibilities: 1) the age and size of the watershed, 2) the high spatial heterogeneity, which promotes a wide range of niches, and 3) the interchange of fauna through the influx of rivers from neighboring basins resulting from geological changes. The Amazonian floodplain is a very dynamic system in which the water level rises and falls seasonally with a range between maximum and minimum annual levels of approximately 15 m near Manaus, which is in the central area of the basin (Filizola *et al.* 2002), creating markedly distinct terrestrial and aquatic phases within the same habitat (Junk *et al.* 1989). This system has been called a "mobile ecotone" by Junk & Soares (2002) due to the movement of the terrestrial-aquatic interface during the course of a hydrological cycle and the resulting dramatic environmental changes in the system.

The hydrodynamic strength of the Solimões River causes large modifications in the river channel, destroying lateral banks by erosion. At the same time, the deposition of material is the main force acting in the formation of new islands and river banks. These floodplain islands contain several lakes, some of which are isolated from one another during the dry season. However, these lakes are interconnected during the flood season, and the duration of the interconnection depends on their distance from the river. Lakes near the shore may never completely lose their connection with the river as the water level falls, while those nearer the center of the island may be isolated until the peak of flood season, and the water level depends exclusively on rainfall and groundwater during the rest of the year.

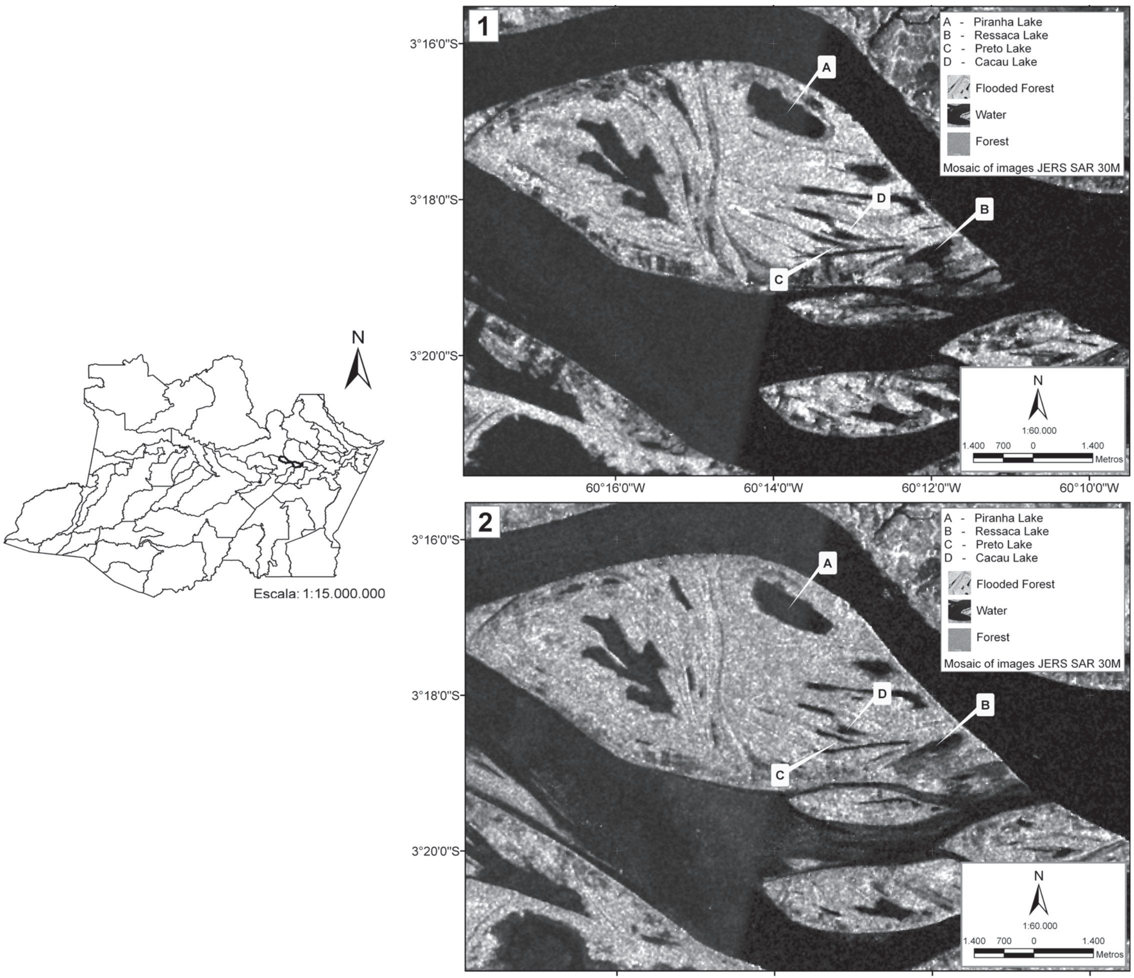
This would be expected to result in the possibility of the formation of metacommunities (Holyoak *et al.* 2005) with relatively independent assemblages of fish species in which coexistence might depend mainly on biotic interactions, such as competition (Amarasekare & Nisbet 2001), based on the definition of Holyak *et al.* (2005) that a metacommunity is a regional set of communities linked by dispersal. However, a critical question about the occurrence of such patterns is how much dispersal is required for a system to be deemed a metacommunity (Holyoak *et al.* 2005).

In this study, we tested the hypothesis that the interconnectedness of lakes that occurs during the flood season is sufficient to assure similarity in their associated fish assemblages, regardless of their spatial position on an island and relative isolation during the low water period.

MATERIAL AND METHODS

We sampled fish in four lakes of Paciência Island (Figs 1 and 2): Ressaca Lake (03°18′54″S, 60°12′37″W), Piranha Lake (03°16′40″S, 60°13′19″W), Cacau Lake (03°96′36″S, 60°38′31″W) and Preto Lake (03°18′46″S, 60°13′8″W). This island is located in the lower stretch of the Solimões River, approximately 50 km from Manaus (Amazonas). Ressaca Lake and Piranha Lake are relatively more recent and remain connected to the Solimões River from the beginning of the flooding season to the end of drying season: therefore, these lakes will be referred to hereafter as type CON (connected). They were formed by the natural deposition of material over the last few decades. In contrast, the Preto and Cacau Lakes are located in the center of the island and are isolated from the Solimões River until the peak of the flood season, when the water is at its maximum depth, and will hereafter be referred as type ISO (isolated).

For three consecutive years, we sampled fish at each lake three times during each season (dry and flood). We assumed that the dry season corresponded to a depth of less than 2 m, as measured close to center of the lake, and the flood season corresponded to depths above 5 m. This criterion is consistent



Figures 1-2. Study area showing Paciência Island and the sampled lakes: Piranha (A), Ressaca (B), Preto (C) and Cacau (D), during the flood season (1) and dry season (2). Dark channels indicating flooded forest are evident in I as an indication of the interconnectedness among lakes and between lakes and the main channel of the river. These convert to terrestrial forest during the low water period (II).

with that proposed by Bittencourt & Amadio (2007) to define seasons of the hydrological cycle in the Central Amazon. Thus, we conducted three samplings during the dry season: October 2004, August 2005, and January 2006; and three samplings for the flood season: July 2004, June 2005, and May 2006.

Six gill nets (20 m long x 2 m high, with 20, 30, 40, 50, 60 and 70 mm stretched mesh) were deployed at each lake for approximately 10 hours from 10:00 am to 8:00 pm to catch fishes exhibiting both diurnal and nocturnal behavior. The fish caught were identified to the level of species and deposited in the fish collection of the Federal University of Amazonas.

A mixed model of one-way ANOVAs with repeated measures for multiple samplings was used to evaluate differences in species assemblage parameters. The spatial position of each lake (CON = Ressaca and Piranha Lakes; ISO = Cacau and Preto Lakes) was used as the independent factor, and abundance, species richness, and evenness were used as response variables. Evenness was calculated as: E = H'/ln S.

After detection of violation of homogeneity of variance by Levene's Test, the abundance and species richness data were log-transformed to avoid heterocedasticy. We used Mauchly's test for sphericity, and when it was violated, we employed the epsilon of Greenhouse-Geiser to fit the degrees of freedom (Girden 1992). We did not use lake area as a factor in our analyses due to its wide variation during the year as the water rose and fell and the full connection of these lakes when we sampled them during the flood season (Figs 1 and 2).

We performed a detrented correspondence analysis – DCA (Hill & Gauch 1980) to identify potential patterns in fish community structure among the lakes. This analysis was chosen to avoid the arch effect, a common feature in the results of correspondence analyses (Manly 2005).

To evaluate the stability of community dynamics in CON and ISO-lakes, we measured the rate of change in species composition, or species turnover, estimating the percent turnover as proposed by Davies *et al.* (2005): $(C_{obs} + E_{obs})/(S_i + S_{i+1})$ x 100, where, C_{obs} is the number of species present in the flood season but not in the dry season (i.e., the number of species observed to colonize with the flood pulse); E_{obs} is the number of species absent in the flood season but present in the dry season (i.e., the number of species observed to migrate as the water level rises); S_i is the number of species observed in the dry season; and S_{i+1} is the number of species observed in the flood season.

RESULTS

We captured 2,019 fish during the six sampling events, which were distributed among 92 species, 68 genera, 19 families and 6 orders (Tab. I). The order Characiformes was the dominant group, with 47 species belonging to seven families. Siluriformes was the second most frequent order, with 20 species belonging to 4 families. We did not detect any differences in species composition among the lakes in the DCA analysis (Fig. 3).

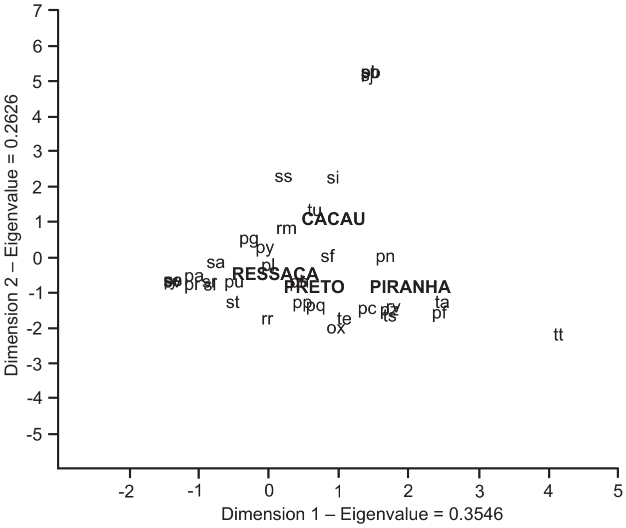


Figure 3. Detrented correspondence analysis with lake name and species (codes given in table I).

The greatest species richness and abundance were observed in Ressaca Lake (Tab. II), but the other three lakes exhibited no pattern related to their spatial position with respect to either of these two variables. In fact, the two ISO lakes, Preto and Cacau, had somewhat higher mean species richness than Piranha Lake (CON). Abundance, species richness and evenness were also relatively constant in Preto Lake. In this lake, the evenness was always higher than 0.60, indicating an assemblage that is quite stable from one season to another. The other three lakes showed great variability, including within the same season.

We detected no significant differences in fish abundance, species richness and evenness between the CON and ISO lakes (Tab. III). There was, however, a significant difference in the abundance between sampling periods, but we did not find effects of the interaction between the lake type and sampling periods.

We found a p-value of 0.07 for the time factor on species richness in the ANOVA. However, the sphericity condition was not accepted and we used the epsilon of Huynh-Feldt as a correction factor. This correction factor reduces the degrees of freedom and improves the probability of type I error. Thus, this result should be interpreted cautiously, and an effect of the hydrological season on the richness could have been present.

The estimates of turnover percent were 47.25, 60.01, 52.94 and 52.05% for the Ressaca, Piranha, Cacau and Preto lakes, respectively.

DISCUSSION

Our working hypothesis was not refuted because connectedness was a poor predictor of the structure fish commu-

Table I. Sampled species in Ressaca, Piranha, Cacau and Preto Lakes. We also report common names (as available), codes employed in the DCA (Fig. 2), and the number of individuals sampled in each lake.

	Species	Common name (Code)	Lakes			
			Ressaca	Piranha	Cacau	Preto
Osteoglossiformes						
Osteoglossidae	*Osteoglossum bicirrhosum* (Cuvier, 1829)	Aruanã branco (ob)	4	0	4	7
Clupeiformes						
Pristigasteridae	*Ilisha amazonica* (Miranda Ribeiro, 1920)		0	1	0	0
	Pellona castelnaeana (Valenciennes, 1847)	Apapá-amarelo (pc)	14	7	0	0
	Pellona flavipinnis (Valenciennes, 1836)	Apapá-branco (pf)	43	44	0	2
Characiformes						
Curimatidae	*Curimata inornata* Vari, 1989	Branquinha (cn)	30	0	0	0
	Curimata vittata Kner, 1859	Branquinha (cv)	2	1	11	20
	Curimatella meyeri (Steindachner, 1882)		2	0	0	0
	Cyphocharax plumbeus (Eigenmann & Eigenmann, 1889)	Branquinha (cp)	0	5	0	0
	Potamorhina altamazonica (Cope, 1878)	Branquinha (pa)	251	7	22	8
	Potamorhina latior (Spix & Agassiz, 1829)	Branquinha (pl)	0	2	2	4
	Potamorhina pristigaster (Steindachner, 1876)	(pp)	0	0	1	3
	Psectrogaster amazonica Eigenmann & Eigenmann, 1889	Branquinha (pz)	3	5	6	4
	Psectrogaster rutiloides (Kner, 1859)	Branquinha (pr)	181	7	1	5
Prochilodontidae	*Prochilodus nigricans* Agassiz, 1829	Curimatã (pn)	27	11	6	0
	Semaprochilodus insignis Jardine, 1841	Jaraqui escama-grossa (si)	14	6	31	13
	Semaprochilodus taeniurus (Valenciennes, 1817)	Jaraqui-escama-fina (st)	5	0	0	0
Anostomidae	*Anostomoides laticeps* (Eigenmann, 1912)	Aracu (al)	1	1	0	0
	Leporinus fasciatus (Bloch, 1794)	Aracu-flamengo (lf)	0	1	0	0
	Leporinus friderici (Bloch, 1794)	Aracu (li)	0	2	2	2
	Leporinus spp.	Aracu (lp)	0	0	1	0
	Leporinus trifasciatus Steindachner, 1876	Aracu (lt)	4	1	2	4
	Rhytiodus argenteofuscus Kner, 1858	(ra)	0	0	0	1
	Rhythiodus microlepis Kner, 1858	(rm)	3	1	10	8
	Schizodon fasciatus Spix & Agassiz, 1829	Aracu-comum (sf)	13	11	10	6
	Schizodon vittatum (Valenciennes, 1850)	Aracu-pororoca (sv)	0	0	0	1
Hemiodonditae	*Anodus elongatus* Agassiz, 1829	Cubiu (ae)	0	3	0	1
	Hemiodus sp.	Orana-fleixeira (he)	0	2	31	10
	Hemiodus sp.1	(hi)	0	0	1	0
	Hemiodus aff. *microlepis*	(hs)	14	29	13	0
Characidae	*Brycon amazonicus* (Agassiz, 1829)	Matrinxã (ba)	60	4	16	24
	Brycon melanopterus (Cope, 1871)	(bm)	0	0	7	7
	Chalceus erythrurus (Cope, 1870)	Arari (ce)	7	0	26	27
	Colossoma macropomum (Cuvier, 1818)	Tambaqui (cu)	16	0	2	1

Continue

Table I. Continued.

	Species	Common name (Code)	Lakes			
			Ressaca	Piranha	Cacau	Preto
	Gymnocorymbus thayeri Eigenmann, 1908	Lambari (gt)	0	0	0	1
	Metynnis hypsauchen (Müller & Troschel, 1844)	Pacu (mh)	0	0	0	1
	Moenkhausia intermedia Eigenmann, 1908	Lambari (mi)	1	0	0	0
	Myleus torquatus (Kner, 1858)	Pacu (mt)	0	0	1	3
	Mylossoma aureum (Agassiz, 1829)	Pacu (mu)	2	7	0	1
	Mylossoma duriventre (Cuvier, 1818)	Pacu (md)	9	8	6	13
	Piaractus brachypomus (Cuvier, 1818)	Pirapitinga (pb)	0	0	2	0
	Pygocentrus nattereri Kner, 1858	Piranha-caju (py)	18	3	9	9
	Roeboides myersii Gill, 1870	Zé-do-ó (ry)	2	1	1	1
	Serrasalmus altispinis Merckx, Jégu & Santos, 2000	Piranha-seca (sa)	2	1	9	2
	Serrasalmus elongatus Kner, 1858	Piranha mucura (se)	3	2	0	2
	Serrasalmus rhombeus (Linnaeus, 1766)	Piranha-preta (sr)	3	6	3	3
	Serrasalmus spilopleura Kner, 1858	Piranha-tucupi (ss)	41	1	25	12
	Triportheus albus Cope, 1872	Sardinha-comum (ta)	45	50	3	21
	Triportheus angulatus Spix & Agassiz, 1829	Sardinha-papuda (tu)	74	38	55	18
	Triportheus elongatus (Günther, 1864)	Sardinha-comprida (te)	8	9	2	8
Acestrorhynchidae	*Acestrorhynchus falcirostris* (Cuvier, 1819)	Dentudo (af)	7	3	18	23
Cynodontidae	*Hydrolycus scomberoides* (Cuvier, 1819)	(hs)	1	0	0	0
	Rhaphiodon vulpinus Spix & Agassiz, 1829	Peixe-cachorro (rv)	2	2	1	2
Erythrinidae	*Hoplerythrinus unitaeniatus* (Agassiz, 1829)	Jeju (hu)	0	0	0	2
	Hoplias malabaricus (Bloch, 1794)	Traíra (hm)	5	1	2	1
Siluriformes						
Callichthyidae	*Hoplosternum littorale* (Hancock, 1828)	Tamoatá (hl)	6	0	6	10
Loricariidae	*Dekeyseria amazonica* Rapp py-Daniel, 1985	Acari (da)	1	0	0	0
	Pterygoplichthys pardalis (Castelnau, 1855)	Acari-bodó (lp)	9	0	0	0
	Loricaria cataphracta Linnaeus, 1758	(lc)	0	0	15	2
Pimelodidae	*Hypophthalmus edentatus* Agassiz, 1829	Mapará (hy)	1	1	0	1
	Hypophthalmus marginatus Valenciennes, 1840	Mapará (ht)	0	0	0	2
	Pimelodina flavipinnis Steindachner, 1877	Mandi-moela (po)	0	0	1	0
	Pimelodus blochii Valenciennes, 1840	Mandi (ph)	2	2	1	8
	Pinirampus pirinampu (Agassiz, 1829)	Piranambu (pp)	0	2	0	2
	Pseudoplatystoma fasciatum (Linnaeus, 1766)	Surubim	1	0	0	0
	Pseudoplatystoma tigrinum (Valenciennes, 1840)	Caparari (pt)	2	1	1	0
	Sorubim lima (Bloch & Schneider, 1801)	Bico-de-pato (sl)	2	0	1	0
Doradidae	*Hassar wilderi* Kindle, 1895	Botinho (hw)	0	1	0	0
	Lithodoras dorsalis (Valenciennes, 1840)	Bacu-pedra (ld)	1	0	0	0
	Oxydoras niger (Valenciennes, 1840)	Cuiu-cuiu (ox)	1	2	0	0
	Pterodoras lentiginosus (Eigenmann, 1917)	Bacu (pl)	7	0	1	0

Continue

Table I. Continued.

	Species	Common name (Code)	Lakes			
			Ressaca	Piranha	Cacau	Preto
Auchenipteridae	*Ageneiosus inermis* (Linnaeus, 1766)	Mandubé (ai)	1	2	0	0
	Ageneiosus ucayalensis Castelnau, 1855	Mandubé (au)	0	3	1	0
	Auchenipterus nuchalis (Spix, 1829)	Mandi-peruano (an)	1	1	0	0
	Centromochlus heckelii (Filippi, 1853)	Carataí (ch)	0	13	0	0
	Trachelyopterus galeatus (Linnaeus, 1766)	Cangati	14	0	3	2
Gymnotiformes						
Gymnotidae	*Gymnotus* sp.1		1	0	0	0
	Gymnotus sp.2		1	0	0	0
Rhamphichthyidae	*Rhamphichthys rostratus* (Linnaeus, 1766)	Sarapó (rr)	1	0	0	0
Perciformes						
Sciaenidae	*Plagioscion squamosissimus* (Heckel, 1840)	Pescada (pq)	4	4	0	0
Cichlidae	*Acarichthys heckellii* (Muller & Troschel, 1849)	Acará (ak)	0	0	2	1
	Acaronia nassa (Heckel, 1840)	Acará (as)	0	0	1	1
	Astronotus crassipinnis (Heckel, 1840)		0	0	0	1
	Chaetobranchus flavescens Heckel, 1840	Acará-branco (cf)	2	0	0	0
	Chaetobranchopsis orbicularis (Steindachner, 1875)	(co)	4	0	0	0
	Cichla monoculus Agassix in Spix & Agassiz, 1831	Tucunaré (cc)	3	0	12	1
	Cichla ocellaris Schneider, 1801	Tucunaré (ci)	1	0	3	1
	Cichlasoma amazonarum Kullander, 1983	Acará-cascudo (cz)	4	0	0	0
	Geophagus proximus Castelnau, 1855		1	0	0	0
	Mesonauta festivus (Heckel, 1840)	Acará (mf)	5	0	0	2
	Pterophyllum scalare (Valenciennes, 1823)	Acará-bandeira (ps)	1	0	0	0
	Satanoperca acuticeps (Heckel, 1840)	Acará-bicudo (su)	0	0	1	0
	Satanoperca jurupari (Heckel, 1840)	Acará-bicudo (sj)	3	0	1	0
Total			997	315	392	315

Table II. Mean and standard deviation of ecological parameters for both seasons of the hydrological cycle (Dry and Flood). Lake types: (CON) connected year-round to the river; (ISO) isolated from the river and other lakes during the low water period.

Ecological measures	Lake							
	Ressaca (CON)		Piranha (CON)		Cacau (ISO)		Preto (ISO)	
	Dry	Flood	Dry	Flood	Dry	Flood	Dry	Flood
Abundance	178.3 ± 60.451	183.0 ± 129.67	72.3 ± 58.84	41.7 ± 22.50	103.0 ± 71.08	34.7 ± 10.69	61.0 ± 10.44	44.3 ± 29.36
Species richness	28.33 ± 2.517	20.33 ± 2.517	16.33 ± 5.033	10.00 ± 1.732	21.33 ± 7.638	9.00 ± 2.646	18.67 ± 4.041	16.33 ± 4.163
Evenness	0.563 ± 0.074	0.353 ± 0.196	0.597 ± 0.179	0.727 ± 0.150	0.640 ± 0.131	0.553 ± 0.182	0.667 ± 0.055	0.750 ± 0.072

nities that inhabit island floodplain lakes. The two lakes that were relatively isolated from the main river during low water (Cacau and Preto) did not systematically differ from those that remained connected to the river (Ressaca and Piranha) with respect to abundance, species richness, and evenness.

Assuming that a metacommunity is composed of several metapopulations, we extrapolate the definition of metacommunity proposed by SALE *et al.* (2006) as a system in which:

Table III. Summary of results of ANOVAs with repeated measures employing abundance, species richness, and evenness as response variables. Position = CON or ISO; time = sampling date. Statistically significant effects ($p < 0.05$) are indicated in bold type.

Effect	df[2]	Abundance		Richness		Evenness	
		F	p	F	p	F	p
Position	1/2	0.604	0.518	0.152	0.734	0.636	0.509
Time	5/10	4.574	**0.020**	6.819	0.070[1]	0.432	0.817
Time*Position	5/10	0.687	0.644	0.670	0.659	0.334	0.881

[1] The sphericity condition was not accepted, so the epsilon of Huynh-Feldt (GIRDEN 1992) was used to fit the degrees of freedom.
[2] Degrees of freedom are shown in the format n1/n2, were n1 is the degrees of freedom of the effect, and n2 is the degrees of freedom of the error.

1) local communities inhabit discrete habitats patches; and 2) interval dispersal is neither so low as to negate significant demographic connectivity nor so high as to eliminate any independence of local community dynamics, including a degree of asynchrony with other local communities. Apparently, the short interval of full connection among all lakes during the peak of flood season is enough to prevent metacommunity assortment.

However, it is necessary to identify the importance of each factor in the structuring of floodplain fish communities. SÚAREZ *et al.* (2001) studied fish communities in Pantanal lagoons and concluded that the most important factors influencing fish community organization were macrophyte cover, abundance of piscivorous species, and the depth of the lagoons. However, these authors conducted their sampling during the dry season, after the lagoons were isolated. In contrast, we conducted sampling during both the dry and flood seasons, and our results indicate a lack of patterns in the structure of the fish assemblages among lakes during these periods. Our findings, therefore, support the hypothesis that the annual period of connection between the lakes and with the river during the peak of the flood season is enough to assure a similar opportunity of occurrence for all species in the lakes, independent of their isolation during the dry season. Any interactive assortment of predators or other factors that may occur during lake isolation is, therefore, mitigated by connectedness during high water period. Additionally, SIQUEIRA-SOUZA & FREITAS (2004) studied floodplain lakes of the Solimões River and observed the occurrence of species typical of lotic environments swimming in schools during the flood season.

In systems of large rivers with adjacent forested floodplains, the flood pulse is quite predictable (JUNK *et al.* 1989) and floodplains represent spawning and nursery grounds for many fish species as a result of the occurrence there of increased heterogeneity of habitats, food supply, and shelter against predators (GOULDING 1980, LOWE-MCCONNELL 1999). Thus, dispersion during high water seems to be an adaptive strategy of some fish species to exploit the variety of habitats available in the system. Fish diversity in floodplain lakes is related to habitat availability (PETRY *et al.* 2003). For instance, FREITAS & GARCEZ (2004) studied the fish assemblages in the connection canals between lakes and rivers and found the predominance of species that are able to use canals to quickly colonize more favorable environments, such as lakes.

Studies conducted in the Amazon floodplain indicate that seasonal changes due to flood pulses modify the relative influence of lentic and lotic waters on fish community structure (JUNK 1984) and that fish communities in lentic systems seem to be temporally more stable than those in lotic systems (MERONA 1987). The constancy of our percent turnover estimates supports this idea, indicating that changes in species composition are relatively constant for all lakes that occupy the same island. Thus, we were able to observe the influence of seasonal changes on assemblage structure. In our opinion, the observed stability in fish assemblage composition of the studied island floodplain lakes is due to the annual replenishment of fish to the lakes during the flood season. We conclude that the absence of streams in the drainage basin of these lakes is a key factor in explaining this homogeneity in the fish assemblages.

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LITERATURE CITED

AMARASEKARE, P. & R.M. NISBET. 2001. Spatial heterogeneity, source-sink dynamics and the local coexistence of competing species. **American Naturalist 164**: 572-584.

BITTENCOURT, M.M. & S.A. AMADIO. 2007. Proposta para a identificação rápida dos períodos
hidrológicos em áreas de várzea do rio Solimões-Amazonas nas proximidades de Manaus. **Acta Amazonica 37**: 303-308.

CHESSON P.L. 1986. Environmental variation and the coexistence of species, p. 240-256 *In*: J. DIAMOND & T.J. CASE (Eds). **Community Ecology.** Harper and Row, 688p.

Davies, K.F.; B.A. Melbourne; C.R. Margules, C.R. & J.F. Lawrence. 2005. Metacommunity structure influences the stability of local beetle communities, p. 170-188 *In*: M. Holyoak; M.A. Leibold & R.D. Holt (Eds). **Metacommunities: Spatial Dynamics and Ecological Communities.** Chicago, University of Chicago Press, 520p.

Dunson W.A. & J. Travis. 1991. The role of abiotic factors in community organization. **American Naturalist 138**: 1067-1091.

Filizola, N.; J.L. Guyot; M. Molinier; V. Guimarães; E. Oliveira & M.A. Freitas. 2002. Caracterização Hidrológica da Bacia Amazônica, p. 35-53. *In:* A.A.F. Rivas & C.E.C. Freitas (Eds). **Amazônia: Uma Perspectiva Interdisciplinar.** Manaus, Editora da Universidade do Amazonas, 270p.

Freitas, C.E.C. & R.C.S. Garcez 2004. Fish communities of natural channels between floodplain lakes and Solimões-Amazonas River. **Acta Limnologica Brasiliensia16**: 1-7.

Girden, E.R. 1992. **ANOVA: Repeated Measures.** New York, SAGE University Paper, Séries: Quantitative Applications in the Social Sciences, 88p.

Goulding, M. 1980. **The Fishes and the Forest: Explorations in Amazonian Natural History.** Los Angeles, University of California Press, 250p.

Hill, M. O. & H.G. Gauch. 1980. Detrended correspondence analysis, an improved ordination technique. **Vegetatio 42**: 47-58.

Hoeinghaus, D.J.; C.A. Layman; D.A. Arrington & K.O. Winemiller. 2003. Spatial and temporal variation in fish assemblage structure in tropical floodplain creeks. **Environmental Biology of Fishes 67**: 379-387.

Holyoak, M.; M.A. Leibold; N. Monquet; R.D. Holt & M.E. Hoopes. 2005. Metacommunities: A framework for large-scale community ecology, p. 1-31. *In*: M. Holyoak; M.A. Leibold & R.D. Holt (Eds). **Metacommunities: spatial dynamics and ecological communities.** Chicago, University of Chicago Press. 520p.

Junk, W.J. 1984. Ecology of the várzea floodplain of Amazonian white-water rivers, p. 215-244. *In*: H. Sioli (Ed.) **The Amazon: limnology and landscape ecology of a mighty tropical river and its basin.** The Hague, W. Junk Publishers, 800p.

Junk, W. J. & M.G.M. Soares. 2002. Freshwater fish habitats in Amazonia: state on knowledge management and protection. **Aquatic Ecosystem Health & Management 4**: 437-451.

Junk, W.J.; P.B. Bayley & R.E. Sparks. 1989. The flood pulse concept in river floodplains systems. **Canadian Special Publication on Fisheries and Aquatic Science 106**: 110-127.

Lowe-McConnell, R. 1999. **Estudos Ecológicos de Comunidades de Peixes Tropicais.** São Paulo, Editora da Universidade de São Paulo, 416p.

Manly, B.F.J. 2005. **Multivariate statistical methods: a primer.** New York, Chapman & Hall/CRC, 3rd ed., 208p.

Merona, B. 1987. Aspectos ecológicos da ictiofauna no baixo Tocantins. **Acta Amazonica 16/17**: 109-124.

Petry, P.; P.B. Bayley & D.F. Markle. 2003. Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. **Journal of Fish Biology 63**: 547-579.

Pouilly, M. & M.A. Rodríguez. 2004. Determining of fish assemblage structure in neotropical floodplain lakes: influence of internal and landscape lake condition, p. 243-265. *In*: R. Welcomme, & T. Petr (Eds). **Proceedings of the Second International Symposium on the Management of Large Rivers for Fishes (LARS2).**Bangkok, FAO Regional Office for Asia and the Pacific.

Sale, P.F.; I. Hanski, I. & J.P. Kritzer. 2006. The merging metapopulation theory and marine ecology: establishing the historical context, p. 3-28. *In*: J.P. Kritzer & P.F. Sale (Eds). **Marine Metapopulations.** Elsevier, San Diego, 576p.

Siqueira-Souza, F.K. & C.E.C. Freitas. 2004. Fish diversity of floodplain lakes on the lower stretch of the Solimões river. **Brazilian Journal of Biology 64**: 501-510.

Súarez, Y.R.; M. Petrere & A.C. Catella. 2001. Factors determining the structure of fish communities in Pantanal lagoons (MS, Brazil). **Fisheries Management and Ecology 8**: 173-186.

Súarez, Y.R.; M. Petrere & A.C. Catella. 2004. Factors regulating diversity and abundance of fish communities in Pantanal lagoons, Brazil. **Fisheries Management and Ecology 11**: 45-50.

Tejerina-Garro, F.L.; R. Fortin & M.A. Rodríguez. 1998. Fish community structure in relation to environmental variation in floodplain lakes of the Araguaia River, Amazon Basin. **Environmental Biology of Fishes 51**: 399-410.

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