DETERMINISM OF FISH ASSEMBLAG STRUCTURE IN NEOTROPICAL FLOODPLAIN LAKES: INFLUENCE O INTERNAL AND LANDSCAPE LAKE CONDITIONS

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## ABSTRACT

In the neotropics, seasonal flooding renders the floodplain an open system in which many fish species can disperse freely. Consequently, it has been suggested that fish assemblage structure in floodplain lakes is largely stochastic. However, recent studies concluded that fish assemblage structure could be determined mostly by local environmental factors. The present work tested 1) the predictability of fish assemblage structure in lakes of the Mamoré River floodplain, Bolivia, in relation to environmental conditions and 2) the general prediction that fish assemblages are structured following the piscivory-transparency-morphometry (PTM) model originally developed for the Orinoco River. Fish species abundances were quantified in eight lakes of the Mamoré River floodplain, positioned along a spatial gradient of distance to the main river, through five high-

water and four low-water surveys. We found strong relationships between fish assemblage structure and abiotic variables. Spatial variation in fish assemblage structure was stronger than temporal variation. Consistent with predictions of the PTM model, relative abundances of siluriforms and gymnotiforms declined in clearer and deeper water, whereas relative abundances of characiforms and clupeiforms increased, as expected from knowledge on the sensory capabilities of these taxa. Partitioning of variation showed that although internal variables, especially transparency and water depth, play an important role in structuring fish assemblages, landscape variables, specifically temporal variability of water quality and connectivity, also influenced assemblage structure. These results support the notion of hierarchical control of assemblage structure. Landscape variables seem to operate as a primary filter that differentially limits local movement and migration as a function of lake connectivity. A secondary filter reflecting internal processes appears to exert stronger control in well-connected lakes where the migration filter might be weak. At the ordinal level, the distribution of clupeids, gymnotiforms and siluriforms appeared to be shaped by both landscape and internal variables. In contrast, that of characiforms did not seem limited by landscape variables.

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## INTRODUCTION

The structure of fish assemblages is influenced by environmental variations at multiple spatial and temporal scales. Assemblage patterns should therefore be evaluated with respect to the relative contribution of small-scale, local and larger-scale, regional, ecological and Winston 1998). (Angermeier processes Specifically, environmental influences acting at different scales can be viewed as hierarchical filters that control species presence or abundance (Tonn et al. 1990). Species should be influenced differentially as a function of their adaptations to abiotic and biotic selective forces. Abiotic conditions may be influential at all spatial scales, although biotic interactions are likely to operate only at the local scale (Tonn et al. 1990; Keddy 1992). Patterns of control in fish assemblages differ among systems. For example, in Mediterranean streams, variation in fish assemblage structure is mostly explained by large-scale factors (stream size and catchment position) rather than by microhabitat and biotic interactions (Magalhães, Batalha and Collares-Pereira 2002). In small temperate lakes, piscivory and both local and larger-scale environmental variables (water depth, surface area, isolation) influence the structure of fish assemblages (Tonn et al. 1990). Finally, in neotropical floodplain lakes of the Orinoco River, the piscivory-transparency-morphometry model (PTM) proposed by Rodríguez and Lewis (1997) indicates that species distribution and abundance is tightly linked to lake water transparency, which is in turn controlled by lake morphometry. A similar pattern was found in the Araguaia River floodplain, Brazil (Tejerina-Garro, Fortin and Rodriguez 1998).

In most neotropical floodplains, the annual flood cycle of the river is predictable and exhibits marked seasonal fluctuations in water level that constitute one of the main ecological characteristics of floodplain waterbodies (Junk, Bayley and Sparks 1989). Floodplain lakes are mainly isolated during the dry season, but during the wet season, lake interconnections and forest flooding give fish access to a broad range of habitats. Consequently, the alternation of dry and wet seasons produces major change in patterns of

fish abundance and distribution (Lowe-McConnell 1975; Rodríguez and Lewis 1994).

At the floodplain scale, environmental conditions at any given moment and seasonal change in those conditions are spatially heterogeneous. Young oxbow lakes are located near the river channel and retain a channel-like morphology. Over many years, floodplain lakes undergo morphological change and become shallower as a consequence of sediment deposition, colonization by vegetation and flooding attenuation (Amoros et al. 1987). This dynamic physical process is accentuated as the main channel moves away from the lake. Thus, one could expect orderly changes in fish assemblage structure along an age or distance gradient to the main river channel, a relationship driven by changes in lake morphometry, intensity of the flood effect and degree of connection with the main river channel along the gradient. However, Rodríguez and Lewis (1997) and Tejerina-Garro *et al.* (1998) found no influence of landscape variables on structure of fish assemblages and concluded that assemblage structure was determined mostly by internal variables operating locally.

We conducted, over a two-year period, a survey of the structure of fish assemblages in eight lakes of the Mamoré River floodplain, Bolivia, that were positioned along a sharp spatial gradient of landscape conditions. The present work tested: 1) the predictability of fish assemblage structure in the Mamoré River floodplain in relation to both internal descriptors and lake-type categories reflecting landscape conditions and 2) the general prediction that fish assemblages are structured following the PTM model originally developed for the Orinoco River floodplain (Rodríguez and Lewis 1997).



# MATERIALS AND METHODS

STUDY AREA

The Mamoré River is one of the main tributaries of the Madeira River, a major affluent of the Amazon (Figure 1). The Mamoré River drains the southern Bolivian Andes and a vast savannah plain broken by forest gallery. Local climatic conditions are marked by the alternation of a wet (October – March) and a dry season (April – September). A large annual

Table 1: Environmental characteristics (landscape and internal variables) of eight lakes of the Mamoré floodplain. Means (ranges) of internal variables are given for the dry and wet seasons.

	Season	Coitarama	Suarez	Florida	Potrero	Siquero	Verdun 2	Tiuco	Verdun 1
						_			
Supra-lake variables									
Lake-type / Position		Savannah	Savannah	Edge	Edge	Forest	Forest	Mamoré	Mamoré
Estimated age (year)		>100	>100	>100	>100	>20	>20	<20	<20
Distance Mamoré (km)		5	6	4.5	4	1.3	1.2	0.1	0.15
				temporary/	temporary/	temporary/	temporary/	permanent	permanent
Connectivity		isolated	isolated	forest	channel	channel	channel		
Lake Penmeter		8.08	10.99	4.11	3.4	6.13	4.06	9.94	8.81
Lake area		3.43	4.2	0.28	0.39	0.67	0.37	1.19	1.01
Lake shape		1.23	1.51	2.2	1.55	2.11	1.88	2.57	2. <b>48</b>
Temporal variation (CVPCA)		-1.35	-0.84	1.5	1.53	-0.35	0.64	-0.61	-0.11
Whole-lake variables				•					
Temperature (é C)	Dry	27.7	28.8	25.9	25.9	29.1	27.7	27.7	28.4
		(26.7-29.3)	(26.8-32.9)	(20.3-31.6)	(19.4-32)	(28.8-29.4)	(26.7-28.6)	(24.6-29.6)	(26.8-30.3)
, , , , , , , , , , , , , , , , , , ,	Wet	28.4	28	27.6	27.2	28.3	27.7	28.7	28.5
. ·		(24.4-31.1)	(24.1-30.5)	(26.4-28.7)	(23.1-30.6)	(25.7-30.2)	(27.4-28.3)	(26.8-32)	(28.1 <b>-29.2</b> )
Water depth (m)	Drv	1.5	1.2	- - 0.7	0.6	4.4	0.9	8.7	4.9
		(1.5-1.5)	(1.1-1.3)	(0.6-0.8)	(0.4-1)	(2.3-6.4)	(0.7-1.2)	(6.1-11.6)	(3.4-6.5)
•	Wet	1.7	1.4	- 2.4	1.5	6.4	5.6	11.9	10.5
		(1.6-1.8)	(1.3-1.5)	(0.6-4.6)	(0.5-3.7)	(3.5-8.5)	(3:6-8.1)	(9.2-17)	(9.5-11.7)
Secchi transparency (cm)	Drv	. 36	. 13.8	- 83	12.5	19.1	19.3	77.6	-33.2
,		(27.3-43.3)	(10-23.3)	(8.3-8.3)	(5-29)	(9.7-25)	(14.7-24)	(48.7-139)	(22.7-48.3)
	Wet	42.2	38.5	40.6	29.1	45:4	64.6	73.2	63.8
		(35.7-51.3)	(31-49)	(13.3-68)	(8.7-76)	(31-60)	(46.7-80)	(41.3-106	(27-85)
								-	
pH	Dry	6.8	6.9	5.5	6	6.9	6.6	7.8	7.2
		(6.6-7)	(6.7-7.4)	(5.4-5.5)	- (5.7-6.5)	. <b>(6.8-7)</b>	(6.1-7.2)	(7.2-8.7)	(6.9-7.7)
	Wet	6.5	6.6	6.5	6.1	6.4	6.5	7.1	6.7
		(6.4-6.7)	(6.3 <b>-6.8</b> )	(6.3-6.7)	(5.5-6.8)	(5.9-6.7)	(6.4-6.6)	(6.8-7.5)	(6.4-7.1)
Conductivity (micros/s)	Dry	17 ·	20	90	- 49	86	74	228	150
		(16-19)	(16-24)	(73-107)	(39-55)	(66-97)	(42-105)	(160-277	(103-237)
	Wet	16	19	65	36	43	70	139	97
	.	(15-1 <b>8</b> )	(14-26)	-(56-76)	(27-60)	(30-76)	-(51-91)	(85-158)	(73-113)

flood, potentially extending over ca. 150 000 km<sup>2</sup> (Denevan 1980), generally occurs at the end of the wet season (December – April) and can last as long as three or four months (Loubens, Lauzanne and Le Guennec 1992).

The study area is situated in the central part of the Mamoré River floodplain (14°30' - 14°52'S; 64°51'- 65°01'W) near the city of Trinidad. Eight lakes were studied that correspond to four different ecological lake-types (Figure 1, Table 1): six are oxbow lakes situated in the forest gallery at varying distances from the Mamoré River; the remaining two are savannah lakes:

- Mamoré: Lakes Tiuco and Verdun 1, situated near the Mamoré River, were formed about 10 years ago and have a morphology similar to that of the river channel. They are permanently connected to the Mamoré River by way of a short channel (< 100 m).
- Forest: Lakes Siquero and Verdun 2, situated in the middle of the forested floodplain, were formed more than 20 years ago. They are temporarily connected to the Mamoré River by way of a small tributary that drains the savannah and the floodplain. The tributary is over 1 km long and runs through one or two other lakes before reaching the Mamoré River.
- Edge: Lakes Potrero and Florida, situated at the forested floodplain edge, were formed more than 50 years ago (according to local people). Lake Florida was connected to the Mamoré River only by floodwater. Lake Potrero was connected indirectly to the Mamoré River by way of a short channel that converged with a small temporary tributary. Both lakes are more than 4 km distant from the Mamoré River.

 Savannah: The last two lakes, Coitarama and Suarez, were situated in the savannah adjacent to the floodplain. They were estimated to have formed more than 100 years ago. In years with a typical hydrologic cycle, they are isolated yearround, but they likely connect with the Mamoré River in years with exceptionally high water level.

Lakes close to the river may be subject to flooding by whitewater drained by the Mamoré River (Loubens *et al.* 1992; Ibañez 2000) and are largely influenced by annual water level fluctuations. Local rainwater feeds lakes remote from the river, the savannah and edge lake types, which therefore have characteristics, intermediate between white and blackwaters.

## FISH SAMPLING AND ENVIRONMENTAL MEASUREMENTS

Fish were sampled using thirteen gillnets with a wide range of mesh sizes (25 m long by 2 m high; mesh sizes: 10, 15, 20, 25, 30, 35, 40, 50, 60, 70, 80, 90 and 110 mm). Sampling was conducted during five periods of wet season (March 1998, March 1999, May 1999, March 2000, May 2000) and four periods of dry season (July 1998, October 1998, September 1999, December 1999). For each sampling (lake-period combination), gillnets were left in place for two hours in the evening (17:00-19:00) and two hours in the morning (5:00-7:00). Gillnets were placed perpendicular to the shore at approximately the same locations throughout the study.

Captured fishes were fixed in buffered formaldehyde (4 percent) and later preserved in buffered ethanol (75 percent). In the laboratory, fish were identified to species, or only to genus when taxonomic knowledge was inadequate for reliable specific identification, by reference to voucher specimens left by a previous taxonomic research project (Lauzanne and Loubens 1985; Lauzanne, Loubens and Le Guennec 1991) at the Trinidad fish collection (CIRA-UTB), the Museo Nacional de Historia Natural, La Paz and the Musée National d'Histoire Naturelle, Paris.

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Environmental variables were assigned to two categories. Eight variables characterizing lake internal conditions in individual lakes: temperature, water depth, transparency, conductivity, pH, lake area, perimeter and shape (calculated as Perimeter/  $(4\xiArea)^{0.5}$ ). Three variables correspond to landscape

conditions (features external to the lake) that may influence internal biotic and abiotic processes and that are related to the position of the lake in the floodplain: connection type, distance to the main river channel and temporal variability of water quality. On each sampling occasion, five internal variables: temperature, water depth, transparency (Secchi disk), conductivity (electronic conductimeter WTW model LF31) and pH (colorimetric pH meter HACH), were measured at three points (referenced by GPS) in the deepest area of the lake. Temporal variability of water quality was quantified by means of coefficients of variation (CV) of the five landscape variables. Lake scores on the first axis of a PCA on the covariance matrix of the five CVs were used as an overall measure of temporal variation (CVPCA). Lake area, shape, perimeter and distance to the main channel were estimated from a photographic image (ERS satellite; pixel resolution 12.6 m).

#### STATISTICAL ANALYSES

Species represented by <5 individuals and <3 occurrences were excluded from the analysis (103 species were conserved of a total of 140). Given that fishing effort was constant, catch per unit effort (CPUE) was calculated for each species and sampling occasion as the total number of individuals captured in all gillnets. Transformations were performed as required to better conform to statistical assumptions. CPUE data were transformed as In (X+1) or, for proportions, as arcsin (p<sup>o5</sup>). The environmental variables Secchi transparency, water depth and conductivity were log-transformed.

Multivariate relationships between assemblage structure and environmental variables were quantified by canonical correspondence analysis (CCA), (Ter Braak 1986); (programme CANOCO, version 4), a direct ordination technique based on chi-square distances for the species data. Inclusion of predictor variables was based on a forward selection procedure with cutoff p value = 0.05. Statistical significance of species-environment relationships in the CCA was obtained by means of Monte Carlo tests implemented in CANOCO (1 000 permutations).

The variation-partitioning method of Borcard, Legendre and Drapeau (1992) was used to determine the fraction of the variation in the species matrix that could be explained by the landscape variables (pure "spatial" effect), the internal variables (pure "environmental" effect) and a "shared" effect of landscape and internal variables (variation explained jointly by spatial and environmental variables), as well as the fraction of variation not explained by these three components ("unexplained"). The variation is partitioned by dividing the inertia (sum of all eigenvalues) of constrained (partial) CCAs of the species matrix by the total inertia of a correspondence analysis of the species matrix (Borcard *et al.* 1992).

Partitioning of variation was also used to examine further the pure "spatial" component. First, the effect of the significant environmental variables was partialled out, leaving only the "pure" spatial variation and the unexplained variation. Then, forward selection was used to determine which landscape variables contributed significantly to explaining the "pure" spatial variation.



■ Figure 2. Boxplot of internal variables (pH, temperature, conductivity, water depth, Secchi transparency), by lake type. Lake types are ordered along the horizontal axis according to their distance to the Mamore River channel.

As a test of the general prediction of the PTM model, scatterplots were used to depict the relationships between relative abundance of major taxa (CPUE proportion; arcsine transformed) and transparency (Rodríguez and Lewis 1997).

### RESULTS

# TEMPORAL AND SPATIAL VARIATION OF LAKE INTERNAL CONDITIONS

Variation in water depth, Secchi transparency and conductivity showed clear temporal and spatial structure (Figure 2, Table 1). Savannah lakes, showed very limited variation in water depth both within and between wet and dry periods (range 20 cm); for the other (oxbow) lakes, environmental variation generally increased with distance to the river (Figure 2). Depth of oxbow lakes also diminished with increasing distance to the river, reflecting the temporal evolution of lake morphology along a gradient ranging from recently abandoned river channel to total dry-out.

Temporal variability of Secchi transparency and conductivity showed spatial patterns similar to that for water depth, as did the composite measure of temporal variability based on five environmental variables (CVPCA, Table 1). The six oxbow lakes were generally deeper, clearer and had lower conductivity during the wet season than during the dry season, contrasting with savannah lakes, which showed more limited seasonal variation (Table 1). pH, conductivity, Secchi transparency and water depth generally decreased systematically with the increasing distance to the river; however, the savannah lakes, although further from the river than oxbow lakes, had high pH and Secchi transparency relative to their distance from the river.

#### FISH ASSEMBLAGE STRUCTURE

A total of 38 292 fish, distributed among 140 species, were caught (Table 2). The 103 species selected for quantitative analysis represented more than 99.8 percent of the total number of individuals. A few very abundant species accounted for more than half of the catch: the small tetra *Moenkhausia dichroura* (30.7 percent), the armored catfish *Hypoptopoma joberti* (9.5 percent), the curimatid *Potamorhina latior* (5.4 percent), the characid "sardines" *Triportheus* 

Table 2: List of 140 fish species captured in eight lakes of the Mamoré floodplain. Occurrence, total number of individuals captured, and relative abundance are given for each species, by lake type.

Order, Family						Relative Ab of analys	undance (%) ed species
Species, Authority	pisci.	Total catch number	occurrence (n=57)	Sāvannah -{2 lakes, n=15)	Edge 2 lakes, n=14)	Forest (2 lakes, n=13)	Mamoré (2 lakes, n=15)
Beloniformes				-	-		
Belonidae							
Potamorrhaphis cf. eigenmanni		3	3				
Miranda-Ribeiro, 1915		-				•	
Characiformes				88.61	64.53	39.48	59.04
Acestrorhynchidae							
Acestrorhyrichus spp.	Ś	387	26	1.93	0.29	0.19	0.35
Anostomidae				مىرىمەر ئ	· · ·		
Leporinus friderici friderici (Bloch, 1794)		86	24	0.30	0.16	0.14	0.19
Leporinus trifasciatus Steindachner, 1876		1	1			··· ·	
Rhytiodus microlepis Kner, 1858		107	13	0.04	1.10	0.31	0.37
Schizodon fasciatus Spix & Agassiz, 1829		154	33	0.48	0.68	0.11	0.46
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Order, Family						Relative Al	oundance (%) sed species
Species, Authority	pisci	Total catch number	occurrence (n=57)	Savannah (2 lakes, n=15)	Edge 2 lakes, n=14)	Forest (2 lakes, n=13)	Mamoré (2 lakes, n=15)
Characidae							
Agoniates cf. anchovia Eigenmann, 1914	Š	9	3	0.00	0.00	0.01	0.10
Aphyocharax anisitsi Eigenmann &		338	3	0.02	8.78	0.00	0.00
Rennedy, 1903							
Brycon ci. cephaius (Genther, 1869)		3	2	••	••		
Charax gibbosus (Linnaeus, 1758)	Š	19	11	0.03	0.26	0.02	0.03
Roeboldes affinis (Génther, 1868)	Š	968	42	4.00	2.07	0.49	2.00
Roeboides bisenalis (Garman, 1890)	Š	11	3	0.00	0.16	0.00	0.06
Roeboldes myersii Gill, 1870	Š	277	31	0.76	1.02	0.65	0.59
Piabucus melanostomus Holmberg, 1891		3	1	••			
Astyanax abramis (Jenyns, 1842)		2	2				••
Astyanax bimaculatus (Linnaeus, 1758)		48	10	0.19	0.42	0.00	0.00
Ctenobrycon spilurus (Valenciennes, 1850)		183	19	0.13	3.48	0.23	0.06
Gymnocorymbus ternetzi (Boulenger, 1895)		2	2	••			
Hemigrammus sp.	1	4	1				
Markiana nigripinnis (Perugia, 1891)		35	10	0.17	0.05	0.03	0.00
Moenkhausia dichroura (Kner, 1858)		11748	43	61.26	12.47	4.74	3.80
Parecbasis cyclolepis Eigenmann, 1914		431	17	0.00	1.41	2.19	2.19
Phenacogaster sp.	1	4	2.	••		]	
Triportheus albus Cope, 1872		1336	35	0.29	0.92	2.19	13.46
Triportheus angulatus (Spix & Agassiz, 1829)		1831	48	4.48	7.44	2.17	7.37
Triportheus culter (Cope, 1872)		3	1				
Triportheus sp.	-	4	3				
Colossoma macropomum (Cuvier, 1818)		35	11	0.08	0.45	0.01	0.05
Metynnis hypsauchen (Méller & Troschel, 1844)		13	- 8 -	0.04	0.03	0.05	0.00
Metynnis maculatus (Kner, 1858)		30	8 -	0.17	0.00	0.00	0.00
Myleus tiete (Eigenmann & Norris, 1900)		3	3		••		
Aylossoma aureum (Agassiz, 1829)		32	10	0.02	0.00	0.06	0.28
Aylossoma duriventre (Cuvier, 1818)	· .	157	19	0.06	0.18	0.66	1.00
Piaractus brachypomus (Cuvier, 1818)		4	4		·		
ygocentrus nattereri Kner, 1858	Š	397	39 <sup>-</sup>	0.46	4.06	1.35	0.46
errasalmus compressus Jégu, Leéo &	\$	21	16	0.07	0.05	0.04	0.04
antos, 1991					1.	ļ.	
errasalmus eigenmanni Norman, 1929	Ś	115	21	0.61	0.03	0.08	0.01
errasalmus elongatus Kner, 1858	Š	23	14	0.01	0.03	0.06	0.19
errasalmus hollaridi Eigenmann, 1915	Š	372	45	0.35	1.68	1.29	1.61
errasalmus rhombeus (Linnaeus, 1766)	Š	474 -	42 -	0.68	0.37	1.50	2.60
errasalmus spilopleura Kner, 1858	Š	37	12	0.20	0.05	0.01	0.00
optella compressa (Génther, 1864)		235	20	1.29	0.08	0.08	0.03
tethaprion crenatum Eigenmann, 1916		163	14	0.06	0.26	1.45	0.06
etragonopterus argenteus Cuvier, 1816	7	4	0.01	0.00	0.04	0.01	
	1			1	1	1	1

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Order, Family						Relative Al	bundance (%) sed species
Species, Authority	piscL	Total catch number	occurrence (n=57)	Savannah (2 lakes, n=15)	Edge 2 lakes, n=14)	Forest (2 lakes, n=13)	Mamoré (2 lakes, n=15)
Curimatidae		1					
Curimata sp.		27		0.15	0.00	0.00	0.03
Curimatella albuma (Méller & Troschel		1060	27	5.91	0.00	0.00	0.03
1844)		1005		5.01	0.10	0.01	0.40
Curimatella, dorsalis (Eigenmann &		55	3	0.21	0.00	0.20	0.00
Eigenmann, 1889)				0.21	0.00		
Curimatella immaculata (Ferné ndez-Yé pez,		38	5	0.00	0.00	0.01	0.48
1948)		}				}	
Curimatella meyeri (Steindachner, 1882)		131	17	0.51	0.08	0.41	0.03
Curimatella sp.	1	431	7	2.48	0.00	0.00	0.05
Potamorhina altamazonica (Cope, 1878)		135	31	0.04	0.81	0.49	0.66
Potamorhina latior (Spix & Agassiz, 1829)		2058	34	0.05	9.59	7.54	12.52
Psectrogaster amazonica Eigenmann &		95	7	0.07	1.91	0.11	0.00
Eigenmann, 1889					·	ł	
Psectrogaster curviventris Eigenmann &		119	15	0.18	0.10	0.56	0.40
Kennedy, 1903		1				1	
Psectrogaster rutiloides (Kner, 1858)		395	25	0.08	1.81	1.70	1.96
Psectrogaster sp.		2	2		•••		
Steindachnenna sp.		14	5	0.00	0.05	0.00	0.15
Cynodon gibbus Spix & Agappin 1900		1					
Hydrolycus scombernides (Cuvior 1916)	S	29	8	0.02	0.13	0.20	0.01
Rhaphiodon vulpinus Spix & Agassiz 1820	s	65	17	0.01	0.37	0.33	0.24
, 1023		69	23	0.00	0.08	0.30 0.	49
Erythrinidae							{
Hoplerythrinus unitaeniatus (Agassiz, 1829)		1	1				
Hoplias malabaricus (Bloch, 1794)	- <b>Š</b>	100	18	0.29	0.76	0.18	0.05
-			-				
Gasteropelecidae	ł					l	÷
Thoracocharax stellatus (Kner, 1858)		20	9	0.00	0.03	0.17	0.04
Hemiodontidae		-				1	
Anodus elongatus Agassiz, 1829		938	28	0.01	0.37	6.61	3.85
Lebiasinidae							l,
Pyπhulina vittata Regan, 1912	ļ	1.	. 1	••	••		
Prochilodontidae		. •	-				· ·
Prochilodus nigricans Spix & Agassiz, 1829		133	_ 28	0.50	0.31	0.19	0.22
Chuna Manuara				, ·			]
viuperionnes		-		3:15	1.65	14.08	11.90
Clupeldae			-				
Pellona casteinaeana Valenciannos 1947		40-					
Pellona flavipinnis (Valenciennes 1926)	S	187	24	0.26	0.00	0.20	1.60
Contractines, 1000/	S	968	42	2.89	1.39	0.88	4.31
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Determinism of fish assemblage structure in neotropical floodplain lakes:

Order, Family	1					Relative Al	bundance (%) sed species
Species, Authority	pisci	Total catch number	occurrence (n=57)	Savannah (2 takes, n=15)	Edge 2 lakes, n=14)	Forest (2 lakes, n=13)	Mamoré (2 lakes, n=15)
	•						
Engraulidae		l					
Anchoviella cf. carrikeri Fowler, 1940		2	1		••		
Engraulidae sp.		1701	28	0.00	0.26	13.00	5.99
Gymnotiformes				0.58	5.87	1.10	0.36
Apteronotidae	.						
Adontostemarchus sachsi		73	10	0.00	0.08	0.69	0.06
Apteronotus albifrons (Linnaeus, 1766)		9	5	0.05	0.00	0.00	0.00
Sternarchorhyrichus sp.		2	2				
Gymnotidae		1.					
Gymnotus carapo Linnaeus, 1758		4	3 ·				
Hypopomidae							
Brachyhypopomus cf. brevirostris (Steindachner, 1868)		15	5	0.03	0.08	0.05	0.01
Rhamphichthyidae							
Rnampnichthys rostratus (Linnaeus, 1766)		19	9	0.05	0.13	0.02	0.04
Sternopygidae							
Allen 1942)		1	1				
Eigenmannia humboldtii (Steindachnor 1878)							
Eigenmannia virescens (Valenciennes 1940)		52	9	0.04	0.92	0.05	0.06
Stemopyqus macrurus (Bloch & Schneider 1901)		259	28	0.35	4.35	0.22	0.14
Lional Schneider, 1801)		29	16	0.05	0.31	0.06	<sup>-</sup> 0.04
Perciformes		;		0.35	3.09	0.52	3.65
Cichlidae							
stronotus crassipinnis (Heckel, 1840)		. 2	1		·		
Chaetobranchopsis orbicularis		3	- 2				
Steindachner, 1875)		· •	<b>.</b> .				
haetobranchus flavescens Heckel, 1840		2	2	-			
Aequidens sp.		1	2				
Frenicichla sp.							
ichla monoculus Soix & Agassiz 1831			. 1.				
renicichia cf. semicincta Steindachner 1802		19	12	0.09	0.00	0.00	0.04
atanoperca jurupan (Heckel 1840)	·	3	3		••		••
claenidae		4	3				
achypons Infilis (Méller & Troschol 1949)			-	!	•	•	- 
lagioscion squamosissimus (Heckel, 1840)	Ś	1 492	1 38	0.26 3	.09	0.52	3.61
euronectiformes				·			
chiridae							
hirus achirus (Linnaeus 1759)							
Linnaeus, 1/00)		1	1			••	

Order, Family						Relative Abundance (%)	
Species, Authority		Total	occurrence	Savannah	Edge	Forest	Mamoré
•	pisci.	catch number	(n=57)	(2 lakes, n=15)	2 lakes, n=14)	(2 lakes, n=13)	(2 lakes, n=15)
Rajiformes	ļ						
PotamotrygonIdae							
Potamotrygon cf. motoro (Méller & Henle, 1841)		17	11	0.05	0.16	0.01	0.01
Siluriformes				7.26	24.71	44.81	25.04
Ageneiosidae	]						
Ageneiosus inermis (Linnaeus, 1766)	Ś	72	16	0.00	0.08	0.59	0.17
Ageneiosus brevis Steindachner, 1881		384	9	0.00	0.24	3.94	0.04
Ageneiosus sp.	5	14	5	0.00	0.00	0.13	0.03
Ageneiosus ucayalensis Castelnau, 1855		11	1				
Tympanopleura sp.	5	246	15	0.00	0.10	1.95	0.75
Aspredinidae	j .						
Bunocephalus sp.		1	1				
Auchenipteridae			1				
Auchenipterus nuchalis (Spix & Agassiz, 1829)	[ .	289	21	0.00	0.29	1.73	1.48
Centromochlus sp.		144	15	0.00	0.00	0.38	1.39
Entomocorus benjamini Eigenmann, 1917		307	22	0.39	5.42	0.16	0.23
Epapterus dispilurus Cope, 1878		124	15	0.00	0.42	0.98	0.21
Trachelyopterus striatulus (Steindachner, 1877)		68	17	0.12	1.13	0.02	0.03
Tatia aulopygia (Kner, 1858)		1	1				
Callichthyidae			-		-	1	
Brochis splendens (Castelnau, 1855)		44	3	0.00	0.00	0.46	0.01
Corydoras sp.		64	4	0.00	0.00	0.59	0.10
Dianema longibarbis Cope, 1872		5	4	0.00	0.05	0.02	0.00
Hoplosternum littorale (Hancock, 1828)		3	1				
Megalechis thoracata (Valenciennes, 1840)		17	6	. 0.01	0.10	0.13	0.00
	· .		•				
Doradidae			•				
Anadoras weddellii (Castelnau, 1855)		19	. 4	0.00	0.45	0.02	0.00
Astrodoras asterifrons (Kner, 1853)		1	1				
Doras sp.		178	22	0.02	1.28	1.08	0.30
Opsodoras sp.		120	9	0.00	0.00	1.00	-0.33
Platydoras costatus (Linnaeus, 1758)	-	10	5	0.06	0.00	0.00	0.00
Dxydoras niger (Valenciennes, 1821)		30	13	0.05	0.42	0.00	0.06
Pterodoras granulosus (Valenciennes-1821)	:	. 4	4				
rachydoras paraguayensis (Eigenmann &		114	17	0.09	1.62	0 10	0.23
Vard, 1907)	-			0.09	1.02	0.19	
		-					
		]					1

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Order, Family				-		Relative At	oundance (%) sed species
Species, Authority	piscl.	Total catch number	occurrence (n=57)	Savannah (2 lakes, n=15)	Edge 2 lakes, n=14)	Forest (2 lakes, n=13)	Mamoré (2 lakes, n=15)
+ Heptapteridae							
Pimelodella spp.							
		720	30	3.88	0.58	0.20	0.15
Loricarlidae				0.00	0.00		
Hypoptopoma joberti (Vaillant, 1880)		3644	29	0.01	3.35	25.76	13.97
Hypostomus sp.		18	11	0.05	0.05	0.01	0.08
Pterygoplichthys sp.	}	129	27	0.22	2.04	0.13	0.01
Hemiodontichthys acipenserinus (Kner, 1853)	1	15	11	0.02	0.26	0.01	0.00
Rineloricaria cf. lanceolata (Génther, 1868)		7	5	0.01	0.03	0.03	0.03
Sturisoma nigrirostrum Fowler, 1940		107	10	0.00	0.03	0.86	0.32
Loricaria cf. simillima Regan, 1904		119	16	0.47	0.05	0.07	0.37
Loricariichthys maculatus (Bloch, 1794)		164	34	0.51	0.97	0.21	0.24
Pseudohemiodon laticeps (Regan, 1904)		43	9	0.06	0.00	0.19	0.19
Ancistrus sp.		7	6	0.00	0.00	0.04	0.04
Pimelodidae							
Hemisorubim platyrhynchos	Š	8	7	0.01	0.03	0.01	0.05
(Valenciennes, 1840)							
Leiarius marmoratus (Gill, 1870)		1	1				
Phractocephalus hemioliopterus		1	1				
(Bloch & Schneider, 1801)							
Pimelodina flavipinnis Steindachner, 1876		1	1				
Pimelodus gr. maculatus-blochi		479	40	1.16	4.03	0.54	0.95
Pinirampus pirinampu (Spix & Agassiz, 1829)	Š	46	16	0.00	0.03	0.35	0.15
Pseudoplatystoma fasciatum (Linnaeus, 1766)	Š	28	15	0.03	0.13	0.10	0.10
Pseudoplatystoma tigrinum (Valenciennes, 1840)	Š	24	11	_0.01	0.39	0.01	0.09
Sorubim lima (Bloch & Schneider, 1801)	S .	196	19	0.01	0.58	1.08	0.91
Hypophthalmus edentatus Spix & Agassiz, 1829		109	33	0.05	0.37	0.36	0.67
Hypophthalmus marginatus Valenciennes, 1840		166	23	0.01	0.18	1.06	0.75
Calophysus macropterus (Lichtenstein, 1819)	Š	84	17 ·	0.00	0.00	0.41	0.58
Total catch number and relative abundance		5757		13.0	17.2	12.9	21.2
of plscivores (30 species)					· .		

angulatus and T. albus (respectively 4.8 percent and 3.5 percent) and an unidentified species of anchovy, Engraulidae sp. (4.5 percent). Seventeen species had abundances exceeding 1 percent of the total catch (Table 2).

The proportions of individual species, major orders and piscivores differed among lake-types (Table 2). Characiforms dominated savannah lake assemblages (88.6 percent) whereas siluriforms dominated forest lakes (44.8 percent) and were relatively uncommon in the savannah lakes (7.3 percent). Clupeiforms were common in forest and Mamoré lakes.

Gymnotiforms were mostly captured in floodplain edge lakes. Similarly, relative abundance of most species differed among lake-types (Table 2). As an example of extreme patterns, the relative abundance of *M. dichroura* increased from the Mamoré lakes to the savannah lakes and the relative abundance of *T. albus* declined along the same gradient. Other species colonized preferentially one lake-type, such as *Aphyocharax anisisti*, which was present almost exclusively in floodplain edge lakes and *Anodus elongatus* and Engraulidae sp., which were captured mostly in forest and Mamoré lakes.

# RELATIONSHIPS BETWEEN ASSEMBLAGE STRUCTURE AND ENVIRONMENTAL CONDITIONS

Six environmental variables (conductivity, shape, water depth, Secchi transparency, temperature and lake area) were retained among the eight internal variables by the forward selection procedure in the CCA analysis. The CCA revealed a significant overall relationship between species CPUE and environmental internal variables (n = 57 lake-date combinations; p < 0.001), with the first three canonical axes jointly explaining 80.8 percent of the variation in the speciesenvironment relationship (respectively 50.8, 20.4 and 9.7 percent; Table 3).

The CCA ordination shows a segregation of lake-types (spatial effect) on the first two axes (Figure 3). The temporal effect (dry vs. wet season) is reflected in a systematic shift in sample positions that is consistent across lake-types, but small relative to overall variation among samples. Savannah lakes were grouped in the lower left part of the CCA graph and differed markedly from the oxbow lakes in assemblage structure as well as in area, shape and conductivity. Savannah lakes also showed limited seasonal variation relative to oxbow lakes. Samples from oxbow lakes were concentrated in an elliptical cluster aligned with gradients in Secchi transparency and water depth. The

Table 3: Results of canonical correspondence analysis (CCA) linking abundance of 103 fish species transformed as ln(CPUE + 1), to six internal variables in eight lakes of the central Mamoré floodplain (n = 57 lake-date combinations). Monte Carlo tests for significance of first canonical axis and for all axes together: p < 0.001 (n = 1,000 permutations).</li>

	Axis1	Axix2	Axis3
Eigenvalue	0.382	0.154	0.073
Cumulative% of explained variance of species-Env.relation	50.76	71.16	80.83
Species-Env. correlation (r)	0.951	0.915	0.811
Canonical coefficients		÷	
Temperature	0.058	-0.062	0.098
Water depth	0.924	-0.304	-0.678
Secchi transparency	-0.038	-0.280	1.220
Conductivity	-0.145	0.256	-0.134
Area	-0.556	-0.761	-0.532
Shape	0.019	-0.209	-0.348
Correlations of environmental variables with ordination axes			
Temperature	0.171	-0.236	-0.048
Water depth	0:823	-0.433	-0.082
Secchi transparency	0.502	-0.523	0.457
Conductivity	0.658	0.196	-0.226
Area	-0.505	-0.759	-0.123
Shape	0.723	0.028	-0.309

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■ Figure 3. Graphical output of canonical correspondence analysis (CCA) linking abundance of 103 fish species, transformed as In(CPUE + 1), to six internal variables in eight lakes of the central Mamoré floodplain (n = 57 lake-date combinations). Ordination plots for samples (A), environmental variables (B), and individual species (C) are presented separately to avoid cluttering.

cluster spanned from dry season samples of floodplain edge lakes (upper left portion of the plot) to wet season samples of Mamoré lakes (lower right).

Species points in the ordination plot correspond approximately to the mode of their distributions along the environmental gradients (Ter Braak 1986). Patterns of distribution at the ordinal level can be broadly characterized as follows. The savannah lake samples were dominated mostly by characiform species that werenot well represented in the oxbow lakes. All other species were associated mainly with the transparencywater depth gradient (TWD gradient): species found in more turbid and shallow conditions were located in the upper left portion of the ordination plot, whereas species found in clearer and deeper conditions were located in the lower right portion of the plot. Characiform species were evenly distributed between the two portions of the TWD gradient and the savannah lakes samples. Siluriform species were almost absent from the savannah lakes (only 4 of 39 species were present), but were distributed more or less uniformly along the TWD gradient. Gymnotiforms were most abundant in turbid, shallow waters. In contrast, the three clupeiform species had highest abundance in clearer, deeper waters.

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## Variation partitioning

Table 4: Partitioning of variation in abundance of 103 fish species, transformed as in(CPUE + 1), at two spatial scales (landscape and internal). The total inertia (sum of eigenvalues) is partitioned into four fractions, three of which correspond to explained variance (landscape, internal, shared), and an unexplained fraction.

		% of total	partitioning
	Inertia	variation	of explained
		explained	variation (%)
1) Total variation (CA fish)	2.39		
2) CCA Fish vs Whole-lake	0.754	31.5	
3) CCA Fish vs Supra-lake	0.572	23.9	
4) Partial CCA Fish vs Whole-lake/Supr-lake	0.398	16.7	
5) Partial CCA Fish vs Supra-lake/Whole-lake	0.216	9.0	
6) Total explained variation (2+5=3+4)	0.970	40.6	
Unexplained variation (1-6)	1.42	59.4	
Whole-leke variables effect (4)	0.398		41.0
Supra-lake variables effect (5)	0.216		22.3
Shared effect (2-3=3-4)	0.356	ļ	36.7
			· · · · · · · · · · · · · · · · · · ·

In principle, partitioning of variation could be used to estimate the relative contribution not only of the two spatial scales, but of seasonal change as well. However, to simplify the interpretation and because CCA results showed that in the study system seasonal variation was very limited relative to spatial variation, partitioning of variation was conducted only between the two spatial scales. Landscape and internal variables jointly explained 40.6 percent of variation of the species matrix (Table 4). The unexplained variation corresponds to stochastic fluctuations as well as other biotic or abiotic effects not included in the analysis. The explained variation was partitioned into three components: 41 percent corresponded to internal variables, 22.3 percent to landscape variables and 36.7 percent to a shared influence of both types of variables.



■ Figure 4. Graphical output of partial canonical correspondence analysis (CCA) linking abundance of 103 fish species, transformed as In(CPUE + 1), to two landscape variables in eight lakes of the central Mamoré floodplain (n = 57 lake-date combinations). The effect of the six significant internal variables was partialled out. Ordination biplots are given separately for individual species and environmental variables. Nocon = connectivity, CVPCA = temporal stability of internal variables (see text).

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In the partial CCA that controlled for internal variables, two landscape variables were retained by the forward selection procedure: the overall measure of temporal variation, CVPCA (p < 0.001) and a binary variable indicating the presence or absence of a connection to the main river channel, NOCON (p = 0.003) (Figure 4). However, the position of the connectivity variable very near the origin of the ordination plot relative to the overall dispersion, suggests that the effect

of connectivity was not large. Furthermore, there was no obvious pattern relating connectivity to the distribution of major taxa on the plot. In contrast, the distributions of gymnotiforms and characiforms were associated with variable CVPCA even after the effect of internal variables had been removed; the former were associated with fluctuating conditions whereas the latter were associated with more stable conditions (Figure 4).



■ Figure 5. Arcsine-transformed relative abundance of major taxa and piscivores in relation to water transparency. Each data point represents one lake-date combination (open circles: savannah lakes; filled circles: oxbow lakes). Solid lines are lowess regression curves for the oxbow lakes. Lowess regression curves for similar data from the Orinoco (Rodré guez & Lewis 1997) and Araguaia (Tejenna-Garro *et al.* 1998) floodplains are given also.

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Applicability of the PTM model to the Mamoré floodplain

Variation of relative abundance of major orders along the gradient of transparency in the Mamoré oxbow lakes appeared broadly similar to those for the Araguaia and Orinoco floodplains (Figure 5). Secchi transparency was strongly associated with the abundance of clupeiforms (positive relationship) and gymnotiforms (negative relationship). Characiforms had highest relative abundance in clearer lakes, whereas siluriforms had highest relative abundance in more turbid lakes, but the relationships appeared weaker (with broader scatter) for these two groups in the Mamoré than in the Araguaia and Orinoco floodplains.

Characiforms were common and siluriforms uncommon in savannah lakes (15 samples) relative to oxbow lakes (42 samples). Fish assemblages in savannah lakes do not respond to the same environmental gradients as in oxbow lakes, e.g. abundance trends for characiforms and siluriforms in relation to transparency are neutral or opposite those in oxbow lakes and the Orinoco and Araguaia floodplains.

## DISCUSSION

The results revealed strong relationships between fish assemblage structure and abiotic environmental features in eight lakes of the Mamoré floodplain. Fish assemblages were structured primarily along a marked spatial gradient correlated with internal and landscape variables. Spatial variation was stronger than temporal variation, as evidenced by large differences between lake-types relative to seasonal differences within lake types. Consequently, temporal variation was not interpreted on the basis of differences between dry and wet seasons, but remained indirectly included by way of the landscape variable CVPCA, an indicator of the amplitude of seasonal fluctuations in each lake. Ordination results showed major effects of water transparency and water depth on fish assemblage structure and less marked effects of pH, conductivity and temperature. In contrast to studies in other river systems, fish assemblage structure in

the Mamoré floodplain, surveyed during wet and dry seasons, also seemed to be influenced by landscape variables.

Structural complexity and hydrological dynamics of the floodplain provide a broad range of habitat conditions that support high fish diversity (Welcomme 1985; Lowe-McConnell 1987). Seasonal connectivity renders the floodplain an open system in which many species can disperse. Consequently, assemblage structure in lakes can change seasonally and yearly as a function of variation in ecological conditions and reproductive success of species. Several studies have failed to link patterns of fish distribution to lake characteristics in neotropical floodplains (Bonetto Cordiviola de Yuan and Pignalberi 1970; Cordiviola de Yuan 1980; Lowe-McConnell 1987; Saint-Paul et al. 2000) and the assemblages have often been viewed as stochastic, mainly because of their strong interannual variability (Lowe-McConnell 1964; Cordiviola de Yuan 1980; Goulding. Carvalho and Ferreira 1988; Merona and Bittencourt 1993). However, differences between fish assemblages of white and black water lakes have been reported (Marlier 1968; Rodríguez and Lewis 1994; Saint-Paul et al. 2000) and fish assemblage structure in neotropical floodplains has been interpreted in relation to water quality variables that reflect instantaneous and local conditions, such as temperature, pH and oxygen concentration (Kramer et al. 1978; Junk, Soares and Carvalho 1983; Welcomme 1985; Goulding et al. 1988; Henderson and Crampton 1997). Welcomme (1985) suggested that lake morphometry plays a role in structuring fish assemblages, as exemplified by influence of lake size and bottom type on fish species composition and body size. Two recent studies that examined the effects of water quality, lake morphometry and landscape-level features (distance to main river channel, connectivity, forest cover) on fish assemblages of the Orinoco (Venezuela) and Araguaia (Brazil) floodplains, found that assemblage structure was associated mostly with two internal variables, water transparency and lake depth (Rodríguez and Lewis 1997; Tejerina-Garro et al. 1998).

Both studies concluded that fish assemblage structure during the dry season was controlled primarily by internal variables, with no detectable influence of landscape variables. Because of high variability in the inter-annual hydrologic conditions and high potential connectivity between the lakes, it might be expected that the spatial position of lakes does not play a major role in assemblage structure. Given that many fish can migrate, fish could be assumed to colonize lakes according to internal conditions, with little influence of lake position on the floodplain. However, lakes of the Mamoré floodplain are spatially structured at both internal and landscape levels, countering the previous assumption. Although flooding and dispersal could potentially lead to homogenisation of fish assemblages across the floodplain, the gradual evolution of lakes along the successional gradient determined by their spatial position relative to the Mamoré River (and related landscape variables) results in spatial heterogeneity of internal attributes and assemblage structure (relative abundances of major taxa and piscivores).

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A salient result was the marked difference in fish assemblages and environmental conditions between savannah lakes and oxbow lakes, which indicates that the savannah lakes are not subject to the same ecological and physical dynamics as the oxbow lakes. Savannah lakes are large, shallow isolated lakes characterized by high stability of internal conditions. Except for their low conductivity, they have water quality characteristics comparable to those of oxbow lakes. Fish assemblages in savannah lakes changed relatively little between seasons. In contrast to oxbow lakes, savannah lakes yielded few siluriforms and gymnotiforms and characiforms were dominant. Because savannah lakes remain isolated for long periods of time, local species extinction may not be compensated by colonization as readily as in lakes with higher connectivity. As a consequence, species abundance and survival in isolated lakes may depend more on ecological attributes conferring local adaptation than on replenishment by recurrent movement or colonization events. Several characiform species seemed adapted to these conditions.

CCA showed that oxbow lakes were arranged along successional gradient of internal conditions, especially transparency and water depth. Mamoré lakes were deeper and clearer; lakes at the annual floodplain edge were more turbid and shallower. Oxbow lakes of the Mamoré floodplain are subject to annual isolation and flooding. These lakes may favour species able to respond to contrasting habitat conditions by moving or adopting ecological strategies. Several previous studies have suggested that exchanges of fish among lakes and the main river channel during the wet season lead to stochastic reassortment of species among the lakes. In contrast, species distributions showed clear patterns for clupeiforms, which were associated with more transparent and deeper lakes near to the Mamoré River and gymnotiforms, which were mostly associated with more turbid, shallower lakes at the forested floodplain edge. However, no clear pattern was apparent in the oxbow lakes for characiform and siluriform species, which were distributed more or less evenly along the lake gradient.

CCA provides modal positions of individual species on the lake-type and TWD gradient. However, the ordination plot for species distributions is not robust to random fluctuation in the position of rare species and, more generally, does not weigh species in relation to their abundances. In contrast, the relation between relative abundance of major taxa and water transparency integrates abundance over species, so that rare species do not unduly influence the analysis.

The results for major taxa in the Mamoré River floodplain appeared concordant with predictions of the piscivory-transparency-morphometry (PTM) model, originally developed for floodplain lakes of the Orinoco River (Rodríguez and Lewis 1997) and subsequently tested in the Araguaia River floodplain (Tejerina-Garro *et al.* 1998) (Figure 4). In the present study, an interaction of sampling methodology with water transparency could have influenced patterns of relative abundance. Although species that are not visually oriented might have equal probability of capture in clear and turbid lakes, visually oriented fishes might be

able to detect gillnets more readily in clear water and thus be more vulnerable to capture in turbid water (K. Winemiller pers. comm.). However, predictions of the PTM model seem robust and general, because similar results were obtained in three different floodplain systems (Orinoco, Araguaia, Mamoré) sampled with different gears (electrofishing, minnow traps and gillnets and gillnets respectively). A general pattern arising from the comparison of results from these three systems is that relative abundances of siluriforms and gymnotiforms decline with increasing water clarity, whereas relative abundances of characiforms and clupeiforms increase. These results are consistent with the interpretation that differences in sensory capabilities (whether prevailing sensory modes are visual vs. chemical, tactile, or auditory) strongly influence species distributions along a gradient of water transparency (Rodríguez and Lewis 1997; Tejerina-Garro et al. 1998).

Similar to earlier findings, in the Mamoré floodplain some apparent exceptions can be explained by specific adaptations (Rodríguez and Lewis 1997). For example, several of the characiforms that are common in turbid waters are surface specialists (Triportheus, Hydrolycus, Cynodon) (Goulding 1980) or have lateral line adaptations to turbid environments (Roeboides) (Sazima 1983). Cichlids are visually oriented fishes that are mostly associated with transparent waters. They are poorly represented in the Mamoré and only the distribution of Cichla monoculus was included in our analysis (Table 2). Although C. monoculus had few occurrences, all individuals were captured in relatively transparent waters in the savannah and Mamoré lake samples. This result agrees with Rodríguez and Lewis' (1997) observation that cichlids had a unimodal distribution peaking in relatively clear lakes and is also consistent with the PTM interpretation. Interestingly, the relative abundance of "other taxa" in the Orinoco (mostly Plagioscion, Achirus and Potamorrhaphis), Araguaia (Osteoglossum, Plagioscion) and Mamoré (Plagioscion, Potamotrygon) floodplains declines with increasing transparency, suggesting that generally these taxa are most abundant in turbid waters.

In the Orinoco floodplain, piscivorous species, with the exception of Acestrorhynchus, showed decreasing abundance or unimodal (Cichla and Boulengerella) distributions in relation to transparency (Rodríguez and Lewis 1997). A similar result applies in the Mamoré floodplain, where the relative abundance of the most abundant piscivores remains relatively constant around 20 percent in turbid waters (Secchi depth <20 cm), but then declines progressively to < 5 percent as water transparency increases beyond 20 cm (Figure 5). This 20 cm threshold is also apparent in the Orinoco floodplain for predators and knifefishes (Figures 2 and 3 in Rodríguez and Lewis 1997). There may thus exist a threshold for visual search at that transparency level that drives an ecological switch in foraging modes (and perhaps in predator avoidance tactics as well). Many piscivores seem well adapted for foraging in low transparency conditions and even species morphologically adapted for visual hunting have developed special strategies for foraging in turbid waters (e.g. cynodontids, Roeboides; Rodríguez and Lewis 1997).

The two Mamoré savannah lakes did not conform to the PTM model. Although intermediate in transparency, they supported relatively few siluriforms and gymnotiforms. This lack of support for the PTM model might be attributed to the lack of connection of these lakes with the rest of the system during the annual flood. Savannah lakes probably do not undergo the seasonal cycle of recolonization followed by culling of vulnerable prey by piscivores as postulated by the PTM model. This result suggests that siluriforms and gymnotiforms may require, in addition to a favourable optical environment, ecological conditions such as seasonal access to the lakes from the river. By way of comparison, "morichal" lakes in Venezuela are adjacent to the floodplain, but have no seasonal connections to floodwater. Morichal lakes are small, highly transparent lakes of low conductivity within formations of the palm Mauritia flexuosa and fed mainly by seepage. Similar to Mamoré savannah lakes, morichal lakes are generally dominated by characiforms and have low relative abundance of siluriforms and gymnotiforms.

Partitioning of variation showed that although internal variables, especially transparency and water depth, play an important role in structuring fish assemblages, landscape variables such as distance to the river, connectivity and environmental variability also influenced assemblage structure. Because the measured internal variables do not completely characterize landscape conditions and conversely, the landscape variables do not fully account for variation in internal features, the two sets of variables are complementary. The Mamoré findings support the notion of hierarchical control of assemblage structure, similar to the sequence of "filters" proposed by Tonn *et al.* (1990).

Landscape variables (likely distance from the river channel and its corollary, flood period) operate as a primary filter that differentially limits dispersion to the savannah lakes, possibly affecting siluriforms more strongly than characiforms. Internal processes appear to exert stronger control in the oxbow lakes, where the colonization filter might be weak. Landscape filters also may play a role in the distribution of clupeiforms and gymnotiforms, both of which were mostly associated with specific lake-types, but in this case internal variables can be invoked to interpret species distributions. In contrast, landscape filters may not operate for siluriforms and characiforms in oxbow lakes; these species appeared more influenced by internal variables, especially transparency. Because of marked differences in connectivity between savannah and oxbow lakes, colonization or migration may be the processes most likely affected by landscape differences in this system.

Other processes, however, such as tolerance to environmental fluctuation (as quantified by CV) may be affected as well. The savannah lakes present relatively stable conditions, whereas among the oxbow lakes environmental variability increases with distance to the Mamoré River. The floodplain edge lakes had the lowest stability and also had extreme low values for water depth (<0.5 m in the samples; some lakes can dry out entirely at the end of the dry season in years with low rainfall). Changes in fish assemblage structure along an environmental gradient of harshness-stability determined by periodic hypoxia were described for bog lakes in northern Wisconsin, USA (Rahel 1984); a similar gradient driven by periodic hypoxia and dessication was found for oxbow lakes in Texas, United States (Winemiller *et al.* 2000).

In the Mamoré floodplain, the relatively large proportion of variation (36.7 percent; Table 4) associated with the "shared" component in the CCA indicated that effects of lake type and lake internal environmental conditions are partly confounded, as is likely the case in other floodplain systems. Although the influence of landscape conditions on assemblage structure is partly mediated through their relationship to internal features such as transparency and depth, which in the Mamoré floodplain vary predictably with lake position, landscape variables also contributed to the "pure" spatial component of variation in assemblage structure, which was unrelated to the measured environmental variables and accounted for 22.3 percent of total variation (Table 4). The partial CCA that examined the "pure" spatial component shed additional light on the role of landscape conditions, by showing that gymnotiforms were associated with fluctuating environmental conditions whereas characiforms were associated with more stable environmental conditions (Figure 4). None of the other major taxa showed a patterned distribution on the partial CCA plot. Although interpretable in principle on the basis of life-history strategies (r-K continuum, generalist-specialist, bethedging) at the ordinal level, these results do not mesh smoothly with previous categorizations of Neotropical fishes.

An analysis of patterns of covariation of ten life-history traits for 71 fish species in the Venezuelan llanos revealed a strong phylogenetic effect on life history strategies (Winemiller 1989). In that study, gymnotiforms were classed as "seasonal" (characterized by synchronized reproduction during the early wet season, high fecundity, absence of parental care, breeding migrations); cichlids were mostly "equilibrium" (parental care and aseasonal reproduction); characiforms were mostly "seasonal" with some "opportunistic" (rapid colonization, early maturation, continuous

reproduction, small clutches); finally, siluriform species were split between the "seasonal" and "equilibrium" categories. Winemiller (1989) noted specific instances of fishes with divergent strategies in an environment that should favour only one of the strategies and suggested differential species trophic adaptations, perceived variation in resource abundance and predation pressure. If this explanation applies broadly, information on trophic linkages may complement that on abiotic environmental fluctuations when interpreting life history adaptations of fish species to spatial heterogeneity in the floodplain.

In conclusion, internal variables are linked to processes that modify assemblage structure via biotic and abiotic interactions within individual lakes, whereas landscape variables reflect processes related mostly to movement of fish among lakes and habitat selection based on large-scale landscape features. At the ordinal level, clupeids, gymnotiforms and siluriforms had distributions that may be controlled by both internal and landscape variables. In contrast, the distribution of characiform did not seem limited by the landscape variables. In the Mamoré River floodplain, characiforms seemed to have the greatest potential for colonization, as reflected by their distribution across all lake-types. Siluriforms were more spatially restricted, possibly in relation to their migratory requirements. Gymnotiforms and clupeids had the lowest potential for colonization, as inferred from their limited spatial distributions in this relatively open system.

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