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Aquatic habitats of the Upper Paraguay River-Floodplain -System and parts of the Pantanal (Brazil)

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Abstract
The Paraguay-Paraná river system forms an important ecological corridor across South America. Here, we report the first description of the fluvial geomorphology and the physical structure of aquatic habitats along the main channel a 200-km long section of the Upper Paraguay River between Cáceres city and Taiama island (Mato Grosso, Brazil). Four functional sets were identified: (a) main channel and anabranches, (b) floodplain channel, (c) floodplain lake, and (d) aquatic-terrestrial-transition zone. The diversity of functional units was higher in the meandering and transitional sectors (Brillouin index 1.957 and 2.003) than in the straight and fluviolacustrine sectors (Brillouin index 1.562 and 1.577, respectively). In the transversal dimension, the relatively homogeneous habitats of the main channel contrasted with the heterogeneous floodplain habitats. We attribute this morphological diversity to changes in the hydrological connectivity, caused e.g. by drifting large macrophyte mats or by multi-year periods of higher and lower inundation phases.

Key words: Physical habitat, wetland, floodplain, large river, Pantanal, conservation.

1. Introduction

The Paraguay-Paraná river system forms an ecological corridor that crosses the central part of South America from the tropical headwater spring brooks at 15° S (closely linked with Amazonian headwater streams) to the temperate zone of the Río de la Plata estuary (34° S; Marchese *et al.* 2002). The upper catchment of the Paraguay River (Fig. 1) is an important ecological region since it is the largest tributary of the Pantanal wetland (Hamilton *et al.* 1996; da Silva 2000; Junk *et al.* 2005 in press). The Upper Paraguay floodplain has been colonized by human beings for centuries by native tribes such as the Payaguá and Guató (Da Silva, Silva 1995). Since the 18th century, cattle production has been one of the major economic sources in the alluvial landscape, however it has permanently declined since the 1950s. Still, the extensive form of cattle ranching appears to be a sustainable management strategy for the area (Junk, da Silva 2003).

Recently, this river corridor has become a focus of a major navigation project, the Hidrovia Paraguay-Paraná. Several ecologists have drawn attention to potential effects of manipulating the river channel by dredging or rock-blasting and by the already-existing navigation with inappropriate vessels (Ponce 1995; Da Silva 1998; Hamilton 1999; Wantzen *et al.* 1999; Gottgens *et al.* 2001). In spite of the extensive planning efforts, little is known about the riverine organisms and their habitats (PCBAP 1997).

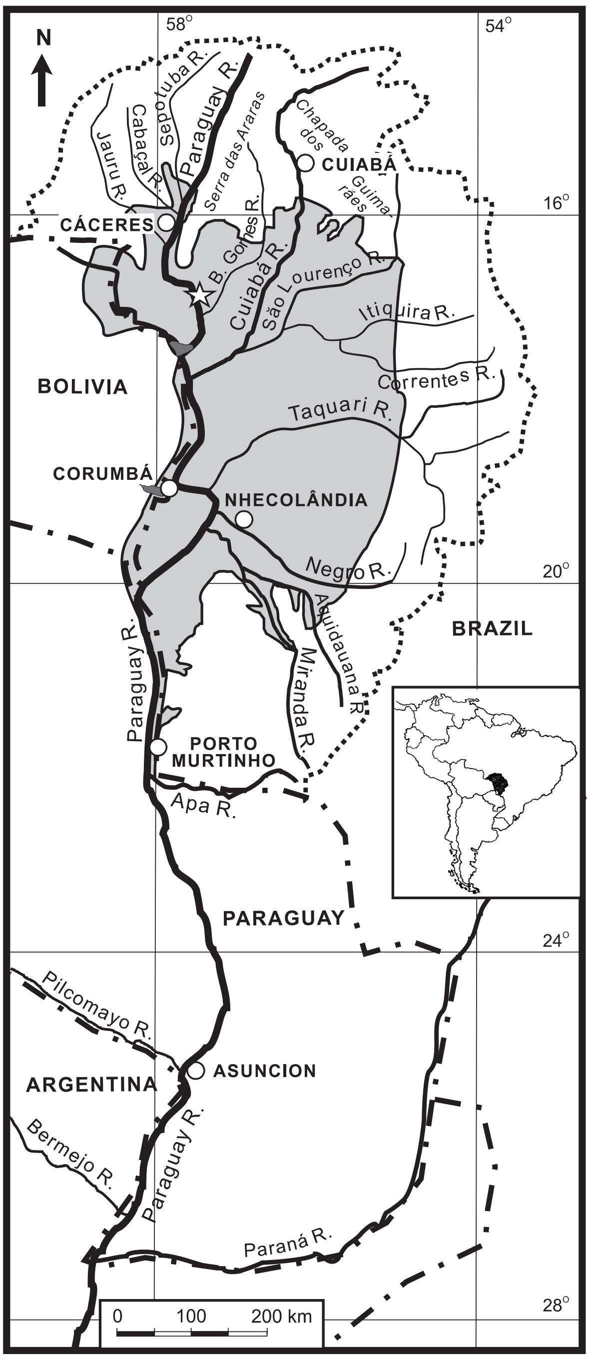


Fig. 1. Research area within the course of the Paraguay River. Dotted line: Upper Paraguay catchment area. Star indicates position of the Taiama ecological station and the southern limit of the studied segment of the river.

While almost all large river systems in Europe and North America have been regulated, the Paraguay river is still in a nearly pristine stage and may be useful as a natural model for restoration planning in similar systems of the tropical zone. Moreover, insights from largely preserved river systems may be used to develop models for restauration planning in those rivers where pristine reference sites have been lost. The Rhine River, for example, has been largely regulated by canalizing and sluice construction in the nineteenth and twentieth centuries (Van Dijk *et al.* 1995; Simons *et al.* 2001; Nienhuis *et al.* 2002). In studies on preserved sections of European and North American temperate zone rivers, fluvial landscape dynamics and connectivity between main channel and floodplain have been identified as key factors in controlling habitat heterogeneity and biotic diversity (Ward, Stanford 1995; Tockner, Ward 1999; Arscott *et al.* 2000; Pringle 2001; Amoros, Bornette 2002). This relationship allows one to ordinate floodplain habitat types and to apply organism-habitat relationships for the monitoring of biotic integrity and the success of river rehabilitation, *e.g.* by using woody vegetation (Deiller *et al.* 2003), macrophytes (Bornette *et al.* 1994; Vanderpoorten, Klein, 1999), benthic invertebrates (Marten, 2001), and fish (Simons *et al.* 2001). Few studies of this kind exist in neotropical river systems (*e.g.* Marchese *et al.* 2002), however they are urgently needed as habitat destruction proceeds very fast. As a baseline for further detailed studies on biotic communities and their ecological interactions, it is necessary to describe the physical habitats within the framework of spatial and temporal scales (*e.g.* Petts, Amoros 1996; Ward *et al.* 2002), based upon the following questions: What are the major landscape units of the river and its floodplains? What are the driving forces that cause the development and succession of these units? Which forms of connectivity exist along the channel (longitudinal dimension) and between the channel and floodplain (lateral dimension)? Which key taxa can be used as indicators for the subunits of the major structures?

The goal of this paper is to contribute to answering these questions, thereby providing quantitative information on aquatic habitat structures and their distribution along 200-km of the Upper Paraguay River between Cáceres city and Taiama island reserve, Brazil (Fig. 1), and to give recommendations for the conservation and sustainable management of the system.

2. Materials and methods

Site description

The Upper Paraguay River is conventionally taken as the area located upstream of the mouth of the Apa River (Fig. 1). Along 1873 km, it has several tributaries the largest being the Sepotuba, Cabaçal, Jauru, Cuiabá, Taquari, and Miranda rivers. Its basin covers about 496 000 km^2 of Brazil, Bolivia, and Paraguay (14°-23° S and 53°-60° W). Tectonic activities such as subsidence and uplift movements have produced the geomorphological and hydrological conditions of the Upper Paraguay Basin (Ussami *et al.* 1999). The predominant Upper Precambrian formations in the basin are covered by extensive Quaternary deposits. Several rock outcrops of quartz and quartz/feldspar sandstones emerge in the main channel (on average every 40 km), which have an important regulating effect on the river level (Ponce 1995). The slope of this fluvial segment varies between 0.7 and 6.5 cm km^{-1} (Ponce 1995).

The prevailing climate in the Paraguay upper catchment is dry to subhumid, the mean annual rainfall is about 1180 mm, 85% of which falls during the rainy season (EDIBAP, 1979). The potential evapotranspiration is about 1370 mm (Tucci *et al.* 1999). The discharge at Cáceres ranges from 140 to 1281 $m^3 s^{-1}$, with a mean discharge of 382 $m^3 s^{-1}$ (Ponce 1995). The low runoff coefficient of the Upper Paraguay (0.07) is a direct consequence of the hydrological relationships between the river as a drainage system and the Pantanal as a reservoir system. Therefore, the overall flood propagation from Cáceres above the Pantanal to Porto Murtinho below takes 130-150 days, or 0.09-0.11 m s^{-1} (Ponce, 1995). This causes a delay of the flooding maximum in the northern part of the wetland (January-February) in reaching the southern part (May-June). However, both the maximum and the minimum river stage (Fig. 2) and, consequently, the inundation phases (Hamilton *et al.* 1996) show a large multiannual variability. The studied river segment encompassed approximately 200 km from the city of Cáceres to the Ecological Reserve Station on the Taiama Island (for a detailed picture of the studied area, see satellite image in Fig. 3).

Functional classification

In this paper, we adopt the ordination of the fluvial landscape structure developed in the Fluvial Hydrosystem Concept (Petts, Amoros, 1996). The ecohydrological condition of the fluvial hydrosystem and its subsystems depends on the dynamic interactions of hydrogeomorphological and biological processes. The term "functional sectors" describes river segments differentiated by changes in valley width and gradient, while the terms "reaches or stretches" are used for any other segments of the river. Within each sector, several functional sets (larger ecological units of 5-50 km extension) were delineated according to their position in the main channel or in the floodplain and according to specific landforms (Table I). The functional units (medium-sized ecological units of 2-20 km maximum extension) were divided based on a combination of toposequence (i.e. according to site-specific characteristics, *e.g.* bank strip) and chronosequence (i.e. according to developmental characteristics, *e.g.* oxbow lake, floodplain forest). A functional unit (small-sized ecological units of 0.2-2 km maximum extension) encompasses specific mesohabitats such as rocky beds, gravel or sand patches, scour holes, and macrophyte stands, i.e. characteristic associations of vegetation represent additional criteria for the division of different mesohabitats. In the Pantanal, these associations are often characterized by a monodominant species (Schessl 1999, and see below).

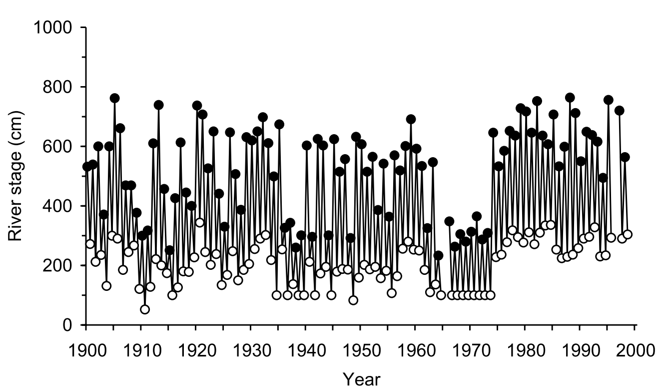
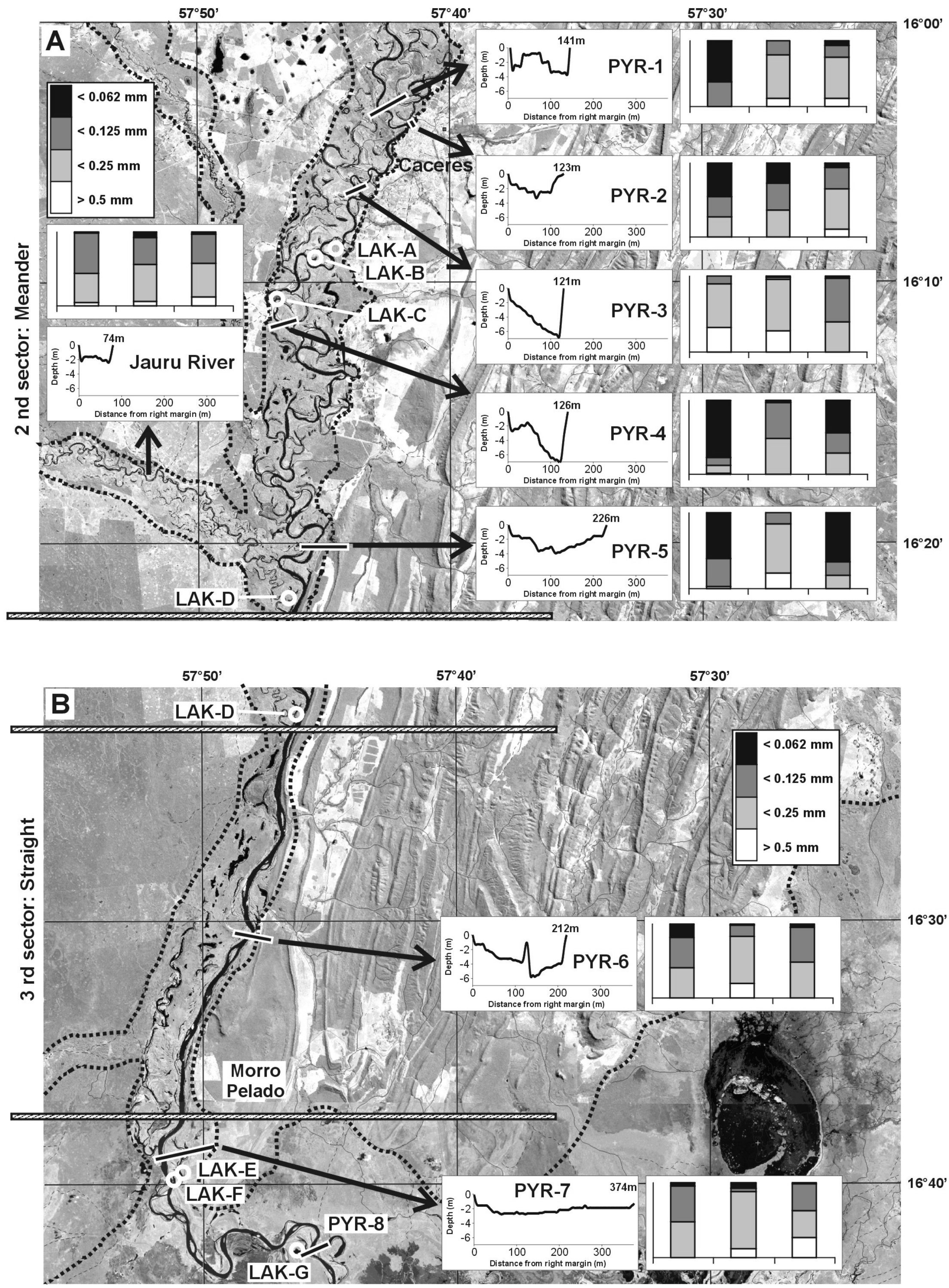


Fig. 2. Stage hydrograph of the Paraguay River of the past 100 years from Porto Ladário near Corumbá. Maximum values: full circles, minimum values: open circles. Source: Brazilian Navy.

Determination of functional sets and units and sampling procedure

Data were taken on a sampling trip from Cáceres to the Taiama island in November 2000, during the annual minimum of the Upper Paraguay water regime. The studied river segment was divided into relatively homogeneous morphological reaches characterized as straight, meander or anastomosing sectors. The sampling stations were selected according to their representative position within the different sectors as well as in relation with some



important features such as cities, major tributaries, bedrock outcrops, or floodplain lakes. Sampling points in the Paraguay River, PYR-1, PYR-2 and PYR-3 were situated above, within, and below the city of Cáceres, respectively, PYR-4 in a meander and PYR-5 in a straight stretch above the mouth of the Jaurú river which was sampled in a straight sector. PYR-6 and PYR-7 were sampled in straight sectors above and below the rocky outcrops of Morro Pelado. The lowermost sampling stations were PYR-8 and PYR-9, both of which were taken in mean-

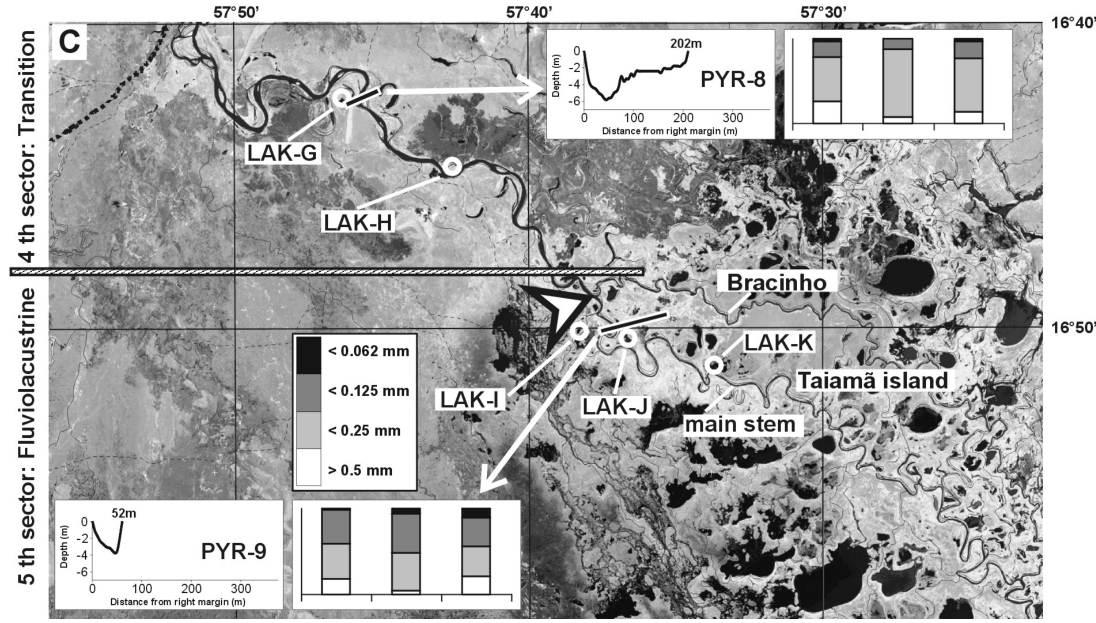


Fig. 3. Landsat TM image of the Paraguay River between Cáceres and Taiama island (Nov. 99). The image has been rectified and north-positioned. 10 minutes latitude (= distance between horizontal lines) correspond to a distance of 18.52 km. The headwater area sector 1 is not shown.
A) Meandering sector 2;
B) straight sector 3 and the beginning of transition sector 4;
C) end of transition sector 4, and anastomotic sector 5.
The floodplain area is indicated by a dotted line in A) and B). In the lower sectors 4 and 5, the floodplain area exceeds the image size. Borders between sectors are marked with striped bars.
Inserts: depth profiles and grain size distribution of the sampling positions within the left, middle, and right part of the channel. Shading of the bars refers to different grain sizes.
Abreviations:
PYR, river sites;
LAK, lakes.
Arrowhead indicates bifurcation of the river into the southern mainstem and the northern "Bracinho" channel which embrace the Taiama island.

ders, above and below the bifurcation of the Paraguay River (Fig. 3). The sampling sites in the floodplain lakes water bodies, and physical and chemical characteristics of the water are given in Marchese *et al.* (2005).

Habitat types and GPS (Global Positioning System, Garmin Quest, accuracy 30m) data were recorded on a field protocol which was based upon visible physical habitat characteristics and occurrence of characteristic plant assemblages (categories given in Table I), and fitted on a Landsat TM satellite image from November 1999. Additional field observations were noted by teams of 2 students per side of the vessel which noted the positions and habitats of conspicuous animal and plant species during the expedition. These data were completed with field observations from earlier studies in the area. Aquatic macrophyte species were identified in all lakes using a transect method (Bini *et al.* 1999), terrestrial vegetation was identified from one-hour-surveys at the unflooded sites and fish were sampled with cast nets at two floodplain lakes and two floodplain channels per functional sector. As the purpose of this paper is a characterization and quantification of the landscape units, only the most conspicuous species are reported here, and detailed publications will follow on fish, birds and plants. Along the transects, depth profiles were recorded in 5 m intervals using a Humminbird Max-10 portable echosounder which has an accuracy of 0.10 m. As depths less than 1 meter revealed unprecise echosoundings, they were measured with a sounding rod. Bed sediments were sampled with a Tamura grab (five samples per site) at the center and on both banks of the main channel cross-sections. Granulometry was completed using dry sieving (mesh 1000, 500, 250, 125, 63 µm).

On the satellite image, the area and length of functional units larger than a pixel size (30x30 m), and the areas of the functional sectors were measured using a vector-based digital-imaging program developed at the University of Konstanz (Institute of Limnology and Department of Electronics, unpublished). The average channel width was registered at 11 equidistant sites per

Table I. Functional organisation of the Upper Paraguay hydrosystem

FUNCTIONAL SET	FUNCTIONAL UNIT	MESOHABITAT
Main channel + anabranche	1) CENTRAL CHANNEL STRIP	- substrate-defined patches - mobile sand bedform - rocky outcrop
	2) BANK STRIP	- meander scour pool - substrate-defined patches - slackwater area - logjam - aquatic vegetation belt
	3) BAR (point, midchannel, lateral)	- substrate-defined patches - slackwater area
	4) ISLAND (lateral, midchannel, scroll)	- substrate-defined patches - chute channel - island lake - scroll lake
	5) TRIBUTARY CONFLUENCE	- tributary-main channel ecotone - scour hole - downstream shoal area
	6) FLOATING SUBSTRATA	- floating macrophyte patches - driftwood
Floodplain channel	7) CENTRAL CHANNEL STRIP	- as for 1
	8) BANK STRIP	- as for 2
	9) SMALL F.P. CHANNELS (permanent/ temporary)	- substrate -defined patches - confluence scour hole - logjam - aquatic vegetation belt
Floodplain lake (permanent/ temporary)	10) OXBOW LAKE (directly/ indirectly connected, isolated) 11) DEPRESSION LAKE	- open water - vegetated shoreline - vegetation-free shoreline - substrate-defined patches - macrophyte-defined patches
	12) SWAMP 13) POND	- macrophyte-defined patches - open water
ATTZ	14) CAMPO 15) FLOODPLAIN FOREST	- macrophyte-defined patches - floodgradient-defined patches - tree vegetation
	16) LEVEE	- tree vegetation - macrophyte-defined patches

functional sector. Floodplain size was measured for sectors 2 and 3. In sectors 4 and 5, the riverine floodplains are transient with the wetlands of the Pantanal; therefore, the analysis of the functional units was arbitrarily limited to a 15-km wide corridor along the river channel. Sinuosity (S) was calculated as the ratio of total active channel lenght to valley lenght (sinuosities of 10 km-long reaches averages) between the channel and valley lengths (Schumm 1972). Diversity of habitats was calculated taking the specific functional units as "species" in the index, in analogy to Arscott *et al.* (2000). We used the Brillouin index because all functional units of the study area were registered and therefore other indices which require random sampling did not apply (Magurran 1987). The Brillouin index is calculated as:

$$HB = \frac{\ln N! - \sum \ln_i !}{N}$$

with N=total sample size, and ni=number of individuals of the ith category. HB rarely exceeds 4.5 and its values are generally lower than the Shannon index of diversity because HB describes a known collection (Magurran 1987).

3. Results

Alluvial rivers are very sensitive indicators of valley slope change. In the case of the Upper Paraguay River, very abrupt changes are visible on the satellite image (Fig. 3). The reach between Cáceres city and the mouth of the Jaurú River shows a meandering pattern (PYR-1 - PYR-5 in Fig. 3a). Downstream, probably due to a decreasing valley gradient, the supply of coarser bedload by the jauru river, and the geological constrains originated by the nearness of the Sierra Simao Nunes mountains on the east river bank lead to a marked reduction of channel sinuosity and the development of a straight course (PYR-6 in Fig. 3b). Downstream of Descalvado area, the river again develops a meandering-anastomosing pattern due to a slightly decreasing gradient, when the Paraguay River enters to the Pantanal depression (PYR-7 in Fig. 3b, PYR-8 - PYR-9 in Fig. 3c). Thus, the Upper Paraguay River can be divided into four functional sectors: meandering, straight, transitional and fluvio-lacustrine sectors, which range from 12 000 to >40 000 ha in size (Fig. 3a-c).

Functional sectors

1) The ***headwater sector*** encompasses the area from the basin divide to the mouth of the Sepotuba River 3 km upstream the City of Cáceres (not shown in Fig. 3). The river section has tortuous meanders with a high sinuosity (S=2.3), and the floodplain is scarcely developed due to the narrowness of the valley.
2) The ***meandering floodplain sector*** encompasses the area from the Sepotuba River outlet to the mouth of the Jaurú River, about 70 km below the City of Cáceres (Fig. 3a). The main channel shows also a high sinuosity (S=2.2), due to irregular meanders (length 500-1500 m, width 800-2000 m) which are about twice as large as those of the upstream reach. In this sector, the river developed a fringing meander floodplain, with a high density of shallow lakes mainly originated by meander cutoffs or abandonment of the channel through sedimentation, and to a lesser degree by avulsion. The right bank tributaries, the Padre Inácio and Jaurú Rivers, also built fringing floodplains while the left bank tributaries, which have their headwaters in the Serra das Araras mountains, are smaller and intermittent without floodplain formation.
3) The ***straight sector*** occurs from the mouth of the Jaurú River to the Morro Pelado hills (Fig. 3b). Sinuosity is very low, reaching 1.1 downstream of the Jaurú River outlet. Within the large straight reaches, the channel bars and islands have created a low degree of braiding. While the floodplain on the right bank is well developed, large sections of the left margin are steep, including the bedrock outcrops at Simao Nunes, Barranco Vermelho, and Descalvado, which have only scarcely developed floodplains at most. Most alluvial lakes were located on long reaches of the former main channel, 2-4 km west from the present mainstem.
4) In the ***transition sector*** from Morro Pelado to the upriver edge of Taiamá island, the main channel shows irregular meanders and a slightly higher sinuosity (S=1.4) in relation to the upriver reach (Fig. 3c). Scattered islands and sand bars, mainly point bars, are typical of this river reach. The alluvial floodplain is strongly reduced in size due to geological constraints, showing a low density of lentic water bodies, which originated mainly by meander neck cutoffs (oxbow lakes).
5) The apex of the Taiamá island marks the beginning of the ***fluvio-lacustrine sector*** (Fig. 3c). Alternating reaches of irregular and tortuous meanders, strongly increase the main channel sinuosity (S=2.1). The alluvial area shows a complex pattern of lentic water bodies which have been originated both by tectonic subsidence and the present river dynamics (Ussami *et al.* 1999). To the north and south of the Taiama Island, we found a high density of large round and irregular depression lakes some of which are interconnected by floodplain channels.

Functional sets

The river sectors varied in the relative composition of functional sets (Tables I and III). The area within the banks of the main channel formed the ***main channel and anabranch set*** (Table I), while the floodplain area beyond the banks is composed by three functional sets. The larger channels of the ***floodplain channel set*** (Table I) had a similar functional composition as the main channel; however, in the smaller channels the differentiation between central and bank strips was not clear. The distinction between these two sets was made because anabranches and mainchannel may switch their positions within very short periods (days to weeks) due to shifting of bed sediment (dunes) and log depositions. On the contrary, the floodplain channels have a more stable structure in general (however which also can become quickly modified due to stochastic events from the drifting macrophyte mats, see below). ***Floodplain lakes*** (Table I) showed a hydrological heterogeneity because of different degrees of connectivity with the main channel. The ***aquatic-terrestrial transition zone*** (ATTZ, Table I) included a gradient from aquatic to terrestrial functional units. During our study, the water levels were well below the bankfull stage and the borders between these four functional sets arose clearly due to the visible contours of the waterbodies at their minimum water level and the remnants of desiccated macrophyte vegetation and shells of aquatic invertebrates which were found in the dry parts of the ATTZ. Earlier observations have shown that during the inundation phase, large alluvial areas become connected by flood water, developing a mosaic of variable depth and low- and fast-flowing aquatic habitats.

A) **The main channel and anabranch functional set**

Braided reaches consist of two or more channels divided by bars and islands, with one of them usually being permanent and carrying the larger discharge. This primary flow is designated as the main channel and the others flanking channels as anabranches (Fig. 4). Both have generally a similar functional composition, however in the studied section slow-flowing anabranches contained high percentages of fine bed sediments and a large amount of woody debris and logjams. Channel islands were poorly developed and no more than two anabranches in each section were detected.

B) **Floodplain channel functional set**

Floodplain channels or secondary channels are the drainage network of the alluvial plain. They may be permanent or temporary, and the degree of intermittence of the temporary channels is linked with the annual hydrological behaviour of the parent river.

Point bars were the typical habitats observed in the meandering reaches of floodplain channels. Most floodplain lakes were interconnected with the inflowing and outflowing channels. Earlier fieldwork revealed that they may change their flow direction according to the river level fluctuations.

C) **Floodplain lake functional set**

All studied lakes were very shallow, with maximum depths less than 2 m during the dry season. The majority of these water bodies originated from the abandonment of the channel reaches or from basins located on tectonic sunken blocks of the floodplain (Fig. 5). In the fluvio-lacustrine sector, we found large and irregular lakes formed by the annexation of several lentic basins. The connectivity of floodplain lakes with the main channel followed a continuum from permanently connected lakes to those lakes that exchange surface water only during maximum flood peaks. Three types of hydrological connections between running and standing water bodies were found: 1) direct connection, through a mouth or a levee erosion breach, 2) indirect connection, through a longer secondary channel or a channel-lake reach and 3) isolation or temporary connection occurring by overflow during the flooding phases. No lake of the study area was completely isolated from surface water exchange.

Table II. Seral stages and plant species involved in the formation of floating vegetation mats ("*batumes*") based on own data and Pott and Pott (2003)

Stage description	Age (Months)	Plant height (cm)	Organic layer (cm)	Species
Agglomeration of aquatic macrophytes	0 - 6	5 - 30	0 - 10	Eichhornia azurea, E. crassipes, Salvinia auriculata, Utricularia gibba, Pistia stratiotes, Limnobium stoloniferum
Matrix formation	6 - 12	10 - 50	5 - 50	Oxycaryum cubense, Cyperus giganteus, Paspalum repens, Eleocharis sp., Polygonum acuminatum, Pontederia parviflora,
Lower shrubs development	12 - 24	20 - 80	20 - 100	Discolobium pulchellum, Aeschynomene spp., Ludwigia nervosa
Tree and climbers	12 - 36	50 - 300	50 - 300	Cecropia pachystachya, Tabebuia insignis, Mikania micrantha

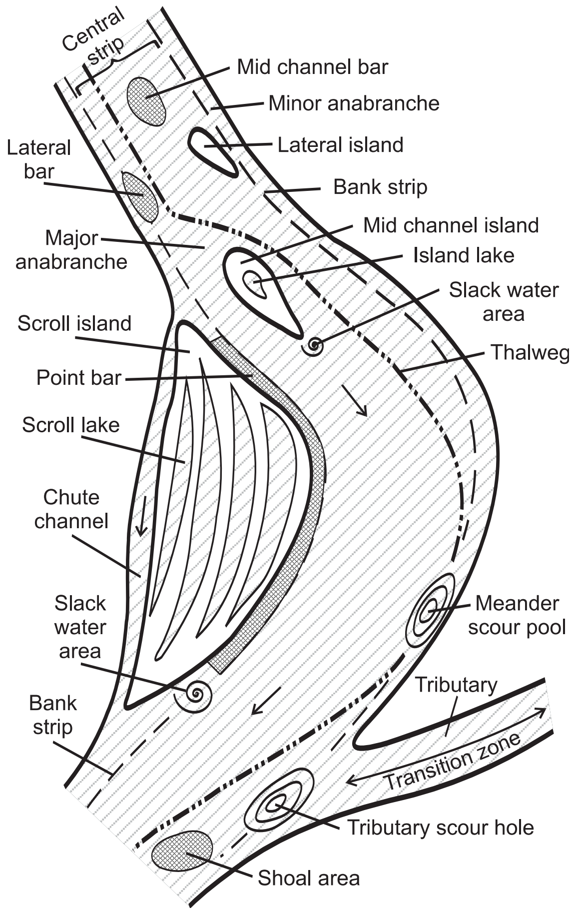


Fig. 4. Functional units and mesohabitats of the main channel and anabranch functional set of the channel in the Upper Paraguay River. See text for discussion.

D) **Aquatic-terrestrial transition zone (ATTZ) functional set**

The term ATTZ has been introduced by Junk *et al.* (1989) in order to delineate the periodically flooded area that is connected to a permanent water body by a moving littoral zone that migrates along with water level fluctuations. The elevation along the gradient determines the inundation time of the habitat. If the definition were to be applied strictly, almost the entire floodplain area would fall into this category. Therefore, we use the term ATTZ here to describe functional units that generally dry out completely during the annual low-water period and become flooded during the high-water period (Fig. 6), although functional units of the floodplain lake set also may fall dry periodically during severe droughts. As the topographic gradient of the riverine landscape is very low, wide floodplain areas become flooded at the same time. Moreover, multi-year patterns of relatively high and relatively low inundation levels (Fig. 2) markedly shift the border between floodable areas and *terra firme*. We identified field-like flatlands, floodplain forests, and levees as functional units of the ATTZ (Fig. 6, Table. I).

Functional units, aquatic mesohabitats, and characteristic species

A) **Functional units of the main channel**

1) The ***central channel strip*** occupied 95-98 % of the wetted perimeter, being characterized by a mobile sand bed with dunes and sand bars (Fig. 4). Sand-dune heights up to 3 m in the channel center were measured. The concentration of fine particles (<0.125 mm) and organic matter was lower than in the bank strip (see inserts in Fig. 3). Only a few organisms, such as the oligochaete *Narapa bonettoi* and some copepods were found in these mobile sands (Marchese *et al.* 2005).
2) The habitat conditions of the ***bank strips***, which were located along the banklines, varied largely between the concave and convex sides of river meanders. In the studied segment, the erosional bank mesohabitats of the concave margins and straight reaches formed vertical clayey banks which were colonized by burrowing organisms, such as kingfishers (*Ceryle torquata*, *Chloroceryle amazona*), crabs (Trichodactylidae), and otters (*Lontra longicauda*) above the water line and mayfly larvae (*Campsurus* sp.) and loricariid catfish below it. Bank slumping was often observed, indicating fast habitat changes. At few meters distance from the concave bank sides, we measured scour pools up to 7 m depth (see inserts in Fig. 3a, Profile PYR-3) which are used as refuges by large pimelodid catfish species (*e.g.*, the jaú, Paulicea luetkeni) during low river stages (Machado, unpublished data).

Wherever hydraulic conditions allowed the attachment of aquatic plants by rooting or by retention on large woody debris, dense belts of floating macrophytes such as *Eichhornia azurea* and *E. crassipes*, developed along the river banks. Their roots were densely colonized by shrimps, and small fishes such as gymnotiforms and small chararids.

3) ***Channel bars*** units encompassed lateral and mid-channel bars as well as the point bars. They are often associated with slackwater areas where finer sediments and organic matter become deposited, providing favorable conditions for lentic species, such as large native mussels (*Anodontites trapesialis*, *Castalia ambigua*, Marchese *et al.* 2005) and freshwater stingrays (*Potamotrygon* sp.). During our survey in the dry season, large sand beaches were exposed and colonized by terrestrial plants and animals, especially skimmers (*Rhynchops*

Table III. Dimensions of functional units, functional sets, and floodplain of the sectors 2 -5 of the Upper Paraguay River. Data shown only of those units which were discernible from the Landsat TM picture (pixel size 30x30 m). In sectors 4 and 5, ATTZ and riverine floodplain merge with the Pantanal wetland, therefore, the surveyed areas were deliberately limited. Abbreviations: N - number, AVG - average unit size±standard deviation, AHAF - Unit area per floodplain; AHAR - Unit area per River length.

	Area ha	N	AVG ha	AHAF ha km^{-2}	AHAR ha km^{-1}	Area ha	N	AVG ha	AHAF ha km^{-2}	AHAR ha km^{-1}
	Sector 2					**Sector 3**				
MAN-BAR	90	37	2 ± 2	0.4	1.1	81	17	5 ± 3	0.7	2.7
MAN-ISL	60	9	7 ± 7	0.3	0.7	51	4	13 ± 9	0.4	1.7
MAN-SCR	237	5	47 ± 36	1.1	2.8	35	1		0.3	1.2
FCH-LAR	514	32	16 ± 18	2.4	6.2	48	5	10 ± 5	0.4	1.6
FCH-SMA	72	33	2 ± 3	0.3	0.9	28	26	1 ± 1	0.2	0.9
FLA-DEP				0.0	0.0				0.0	0.0
FLA-OXD	418	22	19 ± 23	1.9	5.0	27	3	9 ± 2	0.2	0.9
FLA-OXI	694	24	29 ± 23	3.2	8.3	0			0.0	0.0
FLA-OXO	633	35	18 ± 19	2.9	7.6	775	35	22 ± 21	6.4	26.1
FLA-SWB	119	76	2 ± 1	0.5	1.4	136	53	3 ± 9	1.1	4.6
Mainchannel	1,632	1		7.5	19.6	103	1		8.5	34.7
ATTZ	17,328	1		79.5	208.1	10,816	1		81.7	333.2
Survey area	21,797	1		100.0	261.7	12,100	1		100.0	407.7
	Sector 4					**Sector 5**				
MAN-BAR	79	31	4 ± 3	0.3	1.7	2	1		0.0	0.0
MAN-ISL	39	5	8 ± 6	0.2	0.8				0.0	0.0
MAN-SCR	607	11	55 ± 72	2.4	13.2	1,148	26	44 ± 60	2.6	26.3
FCH-LAR	236	6	39 ± 49	0.9	5.1	305	1		0.7	7.0
FCH-SMA	86	24	4 ± 4	0.3	1.9	231	54	4 ± 4	0.5	5.3
FLA-DEP	235	5	47 ± 41	0.9	5.1	5,400	78	107± 98	12.4	123.7
FLA-OXD	299	14	21 ± 23	1.2	6.5	79	4	20 ± 10	0.2	1.8
FLA-OXI	138	7	20 ± 22	0.6	3.0	60	5	12 ± 7	0.1	1.4
FLA-OXO	166	10	17 ± 9	0.7	3.6	92	5	18 ± 13	0.2	2.1
FLA-SWB	358	29	12 ± 28	1.4	7.8	161	88	2 ± 2	0.4	3.7
Mainchannel	1,173	1		4.7	25.4	381	1		0.9	8.7
ATTZ	21,434	1		86.3	464.4	35,729	1		82.2	817.9
Survey area	24,850	1		100.0	538.5	43,588	1		100.0	997.9

Functional sets:
MAN: Mainchannel set;
FCH: Floodplain channel set;
FLA: Floodplain lake set;
ATTZ: aquatic-terrestrial transition zone.

Functional units:
BAR: channel bar;
ISL: channel island;
SCR: Scroll Island;
LAR: large floodplain channel;
SMA: small floodplain channel;
DEP: depression lake;
OXD, directly connected oxbow lake
OXI, indirectly connected oxbow lake
OXO - non-connected oxbow lake;
SWB: small water body, pond.

nigra). Several bars of coarse sands were usually found immediately below the mouth of some tributaries, as in the Jaurú River and just downstream of the rocky outcrops, as in the Morro Pelado section (Fig. 3b).

4) ***Islands*** occur along most of the length of the Upper Paraguay, having originated from channel sand bars, rock outcrops and from meander scroll-bars evolution (Fig. 4). The islands were densely colonized by woody vegetation, especially of the palm species *Bactris glaucescens* and the low-growing tree *Sapium obovatum*. In the meandering and transitional sectors (Fig. 3a and c), the migration of the channel loops and subsequent neck cutoffs often formed scroll islands with floodplain forests.

5) ***Tributary confluences*** form a complex functional unit composed of the downstream-most reaches of the tributaries, a sharp transition zone at their mouths, and a shoal area on the bankline just downstream of the tributary outlet (Fig. 4). In the case of the Jaurú River, per-

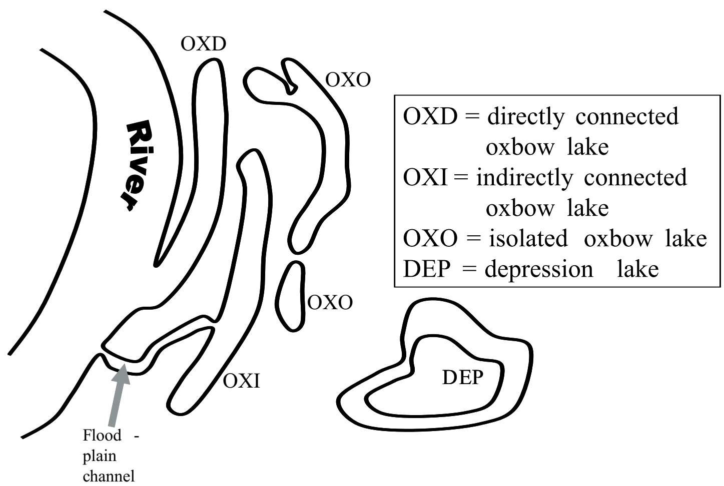


Fig. 5. The continuum of connectivity of lakes in the floodplain of the Upper Paraguay River. Exchange with the mainstem is highest in directly connected oxbow lakes OXD and lowest in remote depression lakes DEP. Between these extremes, intermediate situations may occur.

manent deposition of coarse sand and large woody detritus in the mouth area has led to the development of a new channel by avulsion and the origin of a lake in the abandoned channel. Particular deep mesohabitats named scour holes (Paola 1997) were detected in the junctions between floodplain channels or in the confluence of floodplain channels with the main river stem (Fig. 4). During the field trip, we measured scour hole depths between 5 and 8 m. Long-term observations under similar conditions showed that these habitats contain coarse sediments during the high-water phases, while fine sand and silty-clayey sediments accumulate rapidly during low-water phases (Drago 1990; Drago *et al.* 2003).

6) ***Floating substrata***. Floating macrophyte mats developing in floodplain lakes show different seral stages from monodominant, thin-layered mats (locally named *camalotes* or *baceiros*, da Silva, 1984; Pott, Pott, 2000), to dense and diverse floating islands with considerable organic matter accumulation (*batumes*, da Silva 1984; Pott, Pott 2003; Nunes da Cunha *et al.* 1996; Table II). They drift from floodplain lakes to the main channel, therefore they cannot be attributed to either functional set. During rising water levels, large mats of free-floating aquatic macrophytes were observed to be carried away to the main stem (see discussion).

B) **Functional units of the floodplain channel functional set**

7) ***Central strip*** and 8) ***bank strip*** of large and permanent secondary channels have functional units and mesohabitats similar to those described for the main channel unit.

9) ***Smaller floodplain channels*** provide a wide array of physical habitats owing to their highly variable annual flow. In spite of the extremely gentle slope of the floodplain, water velocities of over 1 m s^{-1} were measured in some deeply incised alluvial channels which are preferred foraging sites of swift-swimming predatory fish, such as *Salminus maxillosus* (dourado) and *Pseudoplatystoma corruscans* (Pintado, Wantzen, unpubl.). The other hydrological extreme is given by shallow floodplain channels which can cease flow during the dry season. Various aquatic organisms which are adapted to temporary desiccation such as the lungfish (*Lepidosiren paradoxa*), trichodactylid crabs, various bivalves (*e.g.*, *Mycetopoda* sp., *Anodontites trapesialis*) and ampullariid snails were found here.

We observed that floodplain channels (locally called *corixos*) carry a considerable load of high-quality organic matter (fresh coarse particulate organic matter and plankton) between the main channel and adjacent floodplain water bodies. Cast net samplings revealed that they are key habitats for a high fish diversity (Machado, unpublished data). The density of benthic invertebrate filter feeders such as *Anodontites trapesialis* or collector gatherer as *Campsurus* sp. in these streams is about 10 times higher than in the shallow shoreline belts of the lakes which they connect (Wantzen, Butakka, unpubl.).

C) **Functional units of the floodplain lake functional set**

10) ***Oxbow lakes*** are former river channels that have been isolated by the cutoff of the meander loops. Their connectivity to the main channel gradually changes from a direct mouth at the downstream end during the early stage of development to indirect when the connection is closed by siltation or by shifting of the main channel (Fig. 5). In sector 3, main channel reaches had been abandoned and formed a series of oxbow lakes on the east side of the present main stem (Fig. 3b). Most lakes of the Upper Paraguay floodplain typically have at least two zones overgrown by aquatic plants, an inner ring generally consisting of floating macrophytes (*Eichhornia crassipes*, *E. azurea*, *Salvinia auriculata*, *Pistia*

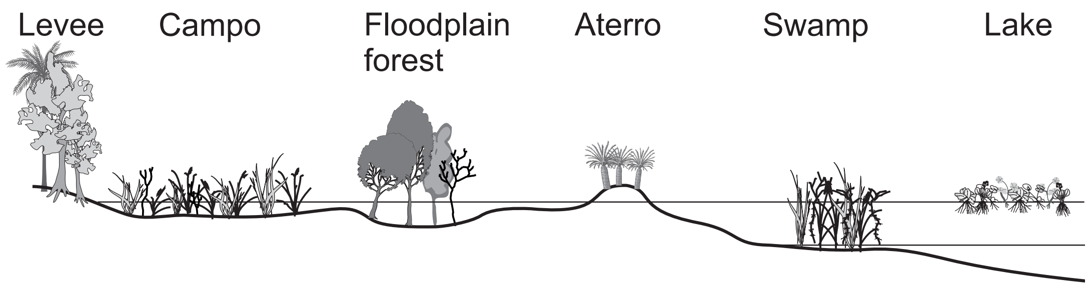


Fig. 6. The Aquatic-Terrestrial Transition Zone ATTZ) and the floodplain lake functional set of the Upper Paraguay. Levees and man-made islands ("aterros") become inundated only occasionally.

stratiotes, *Limnolobium laevigatum*, *Phyllanthus fluitans*, *Hydrocotyle ranunculoides*, *Azolla filiculoides*, *Ceratopteris pteridoides*, *Ludwigia helmintorrhiza*) and a shallower belt with rooted emergent plant species which periodically suffer drought conditions (*Aeschynomene fluminensis, Pontederia cordata*, *Polygonum ferrugineum*, *Polygonum acuminatum*, *Cyperus gardneri*, *Ludwigia leptocarpa*).

During the low water level (November 2000), the bottom sediments of the oxbow lakes which were directly connected to the river showed a horizontal gradient from fine riverine sand deposited in the slackwater zone at the mouth of the lakes to upriver ends where the sediments contained a high concentration of organic matter coming from the local vegetation.

11) ***Depression lakes***. Clustered large lakes of rounded or irregular basin shapes, originated by local tectonic subsidence were registered in sector 5. They often lacked a direct connection channel to the main river, but several of them were interconnected by narrow and meandering channels. They are progressively filled by deposition of alluvial sediments and consequent overgrowing of aquatic and palustrine plants. Both processes lead to a generation of round lake basins. The composition of their organic sediments and plants can be regarded a late successional stage of the lakes described before. The most striking feature of these lakes are the thick floating mats of plants and organic matter (da Silva 1984; Nunes da Cunha *et al.* 1996; Pott, Pott 2000). On this substrate, vegetation develops in three strata, including woody species (Pott, Pott, 2003 Table II). We measured a 1.10-m thick floating island in a lake on Taiama Island, however they may reach several meters thickness.

12) ***Ponds*** are small water bodies consisting of remnants of former large lakes, with typically developed thick muddy substrates with abundant organic debris, and water depths usually less than 1 m. In nutrient-rich, permanent floodplain ponds, large stands of *Victoria amazonica* were found near the City of Cáceres. High temperatures and low dissolved oxygen concentrations (or anoxia) are common features in ponds.

13) ***Swamps*** develop from permanent wetted floodplain areas or from terminal phases of silted lake basins. In our study area, they were characterized by the occurrence of large monodominant macrophyte stands of *Cyperus giganteus*, *Thalia geniculata*, or *Typha domingensis*. Together with these species, mixed assemblages including *Aeschynomene fluminensis*, *Polygonum ferrugineum*, *Ludwigia nervosa*, *L. leptocarpa*, *Habenaria aricaensis*, *Ipomea carnea*, *Alternanthera philoxeroides*, and *Echinodorus macrophyllus* were found. Detailed analysis of the herbaceous vegetation of these areas have been performed by Prado *et al.* (1994), Schessl (1999), and Pott, Pott (2000, 2003).

D) **Functional units of the ATTZ functional set**

14) ***Campos*** ("fields") are the local names given to the floodplain flatlands, which are shallow areas usually dominated by grasses during the dry phase and by aquatic macrophytes during the inundation phase (Fig. 6). When flooding begins, the terrestrial invertebrates migrate towards elevations (floodplain forests or levees) or float on the water surface (Adis *et al.* 2001). Many floodplain fish prey upon this terrestrial food source (Wantzen *et al.* 2002). Extensive stands of aquatic plants develop in the flooded campo, including various species of *Nymphaea*, *Ludwigia*, *Echinodorus*, *Utricularia*, *Cabomba*, and various Pontederiaceae. Periodically, dry flatlands were predominantly detected along the upper sectors of the river, while open dry areas were rare in sectors 4 and 5 even during the low water phase. The bird fauna reflected this transition by predominant occurrence of herons, ibises and other large wading birds in the upstream sectors and swimming and diving species such as cormorants (*Phalacroco-*

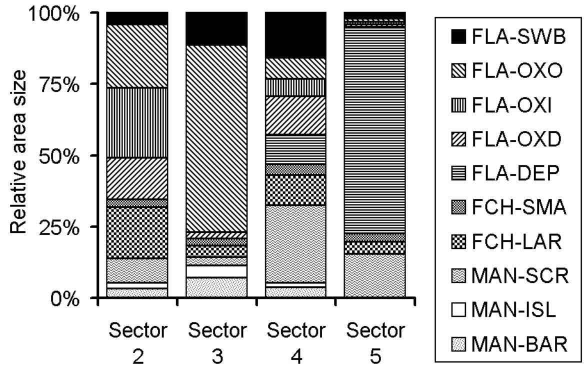


Fig. 7. Relative area size of selected functional units and sets of the Upper Paraguay River floodplain.
Functional sets:
MAN: Mainchannel set;
FCH: Floodplain channel set;
FLA: Floodplain lake set;
ATTZ: aquatic-terrestrial transition zone.
Functional units:
BAR: channel bar;
ISL: channel island;
SCR: Scroll Island;
LAR: large floodplain channel;
SMA: small floodplain channel;
DEP: depression lake;
OXD, directly connected oxbow lake
OXI, indirectly connected oxbow lake
OXO - non-connected oxbow lake;
SWB: small water body, pond.Abbreviations as in Table III.

rax olivaceus) and anhingas (*Anhinga anhinga*) in the lower sections. Relatively few wetland-adapted mammal species were observed, such as capybara (*Hydrochaerus hydrochaeris*), marsh deer (*Blastocerus dichotomus*), jaguar (*Panthera onca*) and the giant otter (*Pteronura brasiliensis*).

15) ***Floodplain forests*** occurred in various regional forms. Channel islands and concave banks of meanders were colonized by pioneer woody species such as Bactris glaucescens and Sapium obovatum. In the lower reach of sector 5, extensive low-lying floodplain forest dominated by Erythrina fusca occurred along the banks of the main channel (Nunes da Cunha, unpubl.). The flatlands of sectors 2 and 3 were locally interspersed with mixed floodplain forest or monospecific stands of woody species, such as *Tabebuia aurea*, *Vochysia divergens*, *Byrsonima orbignyana*, and *Copernicia alba*. Detailed studies on this subject were performed by Dubs (1994), Pott, Pott, (2000) and Schessl (1999).

16) ***Levees*** are the highest elevations built by deposition of riverine sediments, and become inundated during the large floods. Therefore, they are important refuges for terrestrial fauna during inundation. Woody vegetation on banks and levees depends largely on soil and inundation characteristics (Nunes da Cunha, Junk 2001). In the gallery forests, we identified *Albizia niopioides, Acrocomia aculeata, Ficus gardneriana, Tabebuia heptaphylla*, *Inga* sp., *Spondias lutea*, *Cecropia* sp., and *Triplaris americana*. At dry spots, even cacti (*Cereus peruvianus*) were found. Former studies also recorded Inga vera subsp. affinis, *Alchornea castaneifolia, Banara guianensis, Combretum lanceolatum*, and *Byrsonima cydonifolia* on levées (Nunes da Cunha, unpubl.). Various bird species breed or rest in colonies on trees at the river margins, especially the wood stork (*Mycteria americana*), spoonbill (*Ajaja ajaja*), and cormorants (*Phalacrocorax olivaceus*). The palm *Scheelea phalerata* occurred on artificial elevations (aterros) made by the native population (Fig. 6). At the left margin sector 3, where the river flows on the Serra das Araras ranges, vegetation rapidly changed from floodplain species to cerrado dryland forest.

Distribution, size and diversity of functional units along the Upper Paraguay

Most of the aquatic functional units described above were discernible on the Landsat TM image and could be quantified (Fig. 7; Table III). The functional units which are closely associated with the channel meandering, such as scroll islands, point bars and oxbow lakes were registered mostly in sectors 2, 4 and 5 (Fig. 7; Table III).

The straight sector 3 was chararacterized by the occurrence of lateral and mid-channel bars in the present main channel and by isolated lakes remaining from the former channel (OXO in Table III). The westward channel migration in this area is limited by the Serra das Araras mountains (Fig. 3b), indicating an ageing process by isolation of these lakes while the floodplain is highly dynamic in sectors 2 and 5 by meander cutoffs and floodplain channel shiftings, respectively. In sectors 4 and 5, the river enters into a large alluvial plain developing an anastomosing pattern characterized by large and irregular depression lakes. In these sectors, channel bars and islands were almost lacking. Small lentic water bodies and narrow meandering floodplain channels occurred in all sectors in similar proportions (Fig. 7; Table III).

The average sizes of the functional units generally varied within one order of magnitude, *e.g.* among scroll islands (44-55 ha), oxbow lakes (12-29 ha), channel islands (7-13 ha), and bars (2-5 ha, Table III). The average width of the channel was 206 ±62 m for sector 2, 346 ±91 m for sector 3, 255±81 m for sector 4, and 87 ±32 m for sector 5, respectively, indicating moderate braiding intensity in the straight sector 3 and a large distribution of the river flow upon entering the wide Pantanal apex in sector 5. The diversity of functional units was higher in the meandering sectors 2 and 4 (Brillouin index 1.957 and 2.003) than in the straight and anastomosing sectors 2 and 5 (Brillouin index 1.562 and 1.577, respectively).

4. Discussion

Similarities and differences in the distribution of functional units in the river sectors

The studied segment of the Upper Paraguay River reveals a particular articulation of the functional sectors, showing a marked meandering pattern in the first reach of the segment, which changes downriver into a straight reach followed by a transition and anastomosing stretches, respectively. The two last reaches mark the entrance of the river into the Pantanal depression. Floodplain development and occurrence of main floodplain habitats followed this pattern, with a large number of oxbows in the meandering sector, a sequence of lakes from an abandoned river channel in the straight sector, wide meanders and few oxbows in the transition and a large number of depression lakes and splitting of the main channel in the anastomosing sector. Both straightening of the channel and nearly permanent flooding in the lowermost section reduced habitat diversity.

There was a striking contrast between the relative structural homogeneity of the main channel functional units and the environmental heterogeneity of the floodplain units. This pattern has been shown for other rivers in the southern Neotropics (Marchese *et al.* 2002; Marchese, Ezcurra de Drago, 1992) and can be regarded as a common condition in large alluvial river systems (Ward *et al.* 2002). Benthic organisms which are tightly related to the hydrological and sedimentological conditions, reflect this pattern very clearly. Their diversity is much higher in the cross-sections from the mainchannel into the floodplain habitats than in the longitudinal section along the main-channel, both in the upper section of the Paraguay River (Marchese *et al.* 2005) and in the lower section (Ezcurra de Drago *et al.* 2004).

The role of superficial hydrologic connectivity in the distribution of mesohabitats

Different than rivers like the Tagliamento (Arscott *et al.* 2000), where a large part of the flood water infiltrates into the coarse-grained alluvium, the rivers of the Paraguay-Paraná hydrosystem largely rework old and very fine sediment deposits which have a very low hydrological conductivity. Drillings in the clay banks near the main channel along the studied section remained dry and revealed that there is very little subsurface water exchange. The river-groundwater interactions in the studied river corridor are still little known, however the exchange seems to be generally slow in the region (Girard *et al.* 2003). Therefore, the type and degree of superficial hydrological connectivity between the main channel and its alluvial area is a key factor in the physical, chemical and biological differences of the floodplain mesohabitats. Lakes connected by a deep channel to the parent channel showed similar physical and chemical characteristics (Marchese *et al.* 2005), and received large quantities of river-borne sediments during flooding. Earlier field studies showed that during rising water levels, fluvial sediments became transported into the still-water area of the lake (Drago *et*

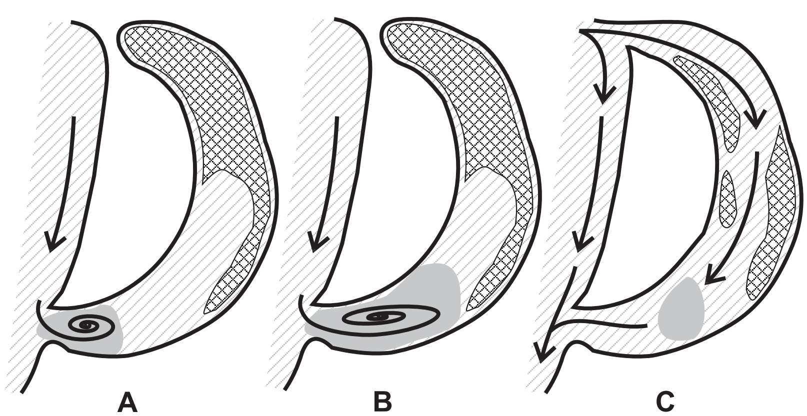


Fig. 8. Organic matter dynamics in directly connected oxbow lakes. A) Low water level: accumulation of macrophyte-derived organic matter (stippled) in the distal end of the lake and of river-derived fine particles (shaded) at its mouth. B) Rising water level: riverine deposition zone increases. C) Maximum water level: upper lake end connects to the river, and organic and fine particulate material becomes partly washed out.

al. 2003). During maximum water levels, river water flows through the upriver end, and part of the deposited organic and inorganic materials and floating macrophytes are carried away into the main channel (Fig. 8). This "flushing effect" may reduce the plant organic matter of lakes by nearly 50% (Da Silva, Esteves 1993). In extreme cases, even the bottom sediments can be scoured and the lake becomes completely cleaned by river water, sometimes exposing the old sand bed of the former channel (Drago *et al.* 2003). This process rejuvenates the lakes such that the original channel shape of the lake can be maintained for a long time span.

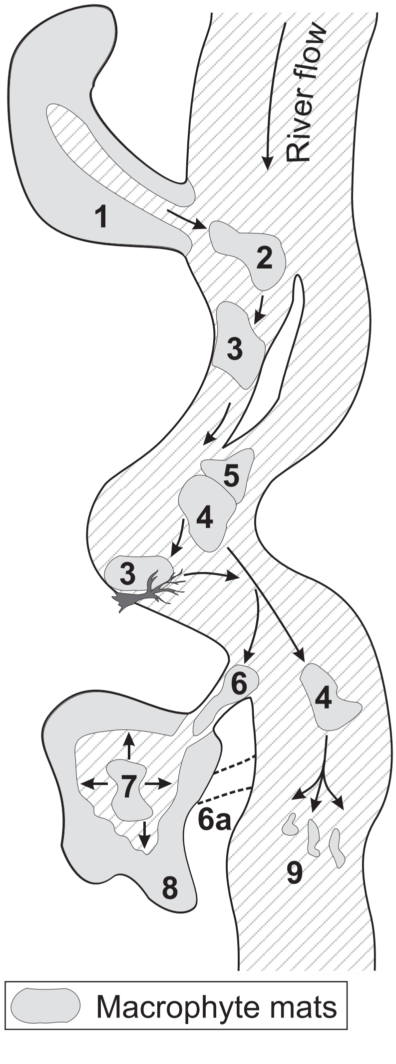


Fig. 9. Floating macrophyte mats influencing habitat structure in river-floodplain systems. 1) Development of macrophyte mats in floodplain lakes; 2) detachment and release during rising water levels, 3) storage in anabranches and at logjams, 4) downstream transport, 5) aggregation, 6) blockage of connection channels, 6a) opening of new channels by erosion, 7) wind drift in lakes, 8) decomposition, and 9) abrasion

Indirectly connected lakes receive river water through a connection channel or a channel-lake system where the suspended sediments of the inflowing water have already been settled. Due to the lack of the "flushing effect" described above, lakes of this type accumulated thick layers of macrophyte-derived organic matter on their bottoms. Decomposition processes, high water temperatures, and shading by macrophytes negatively influence the oxygen concentration during low water stages. Consequently, aquatic invertebrates were rather found in the surface-near root zone of the macrophytes than in the organic sediments. Although many floodplain fish species of the area show adaptations to hypoxic conditions (Machado, *pers. comm.*), large fish kills have been regularly observed in sector 5 and in other regions of the floodplain. This phenomenon, locally known as *dequada*, is caused by the high oxygen demand and carbon dioxide release of large amounts of decomposing organic matter (Calheiros, Hamilton 1998).

A particular role in the connectivity pattern of the Paraguay River (and probably also in other tropical rivers with large macrophyte production) is played by large macrophyte mats. The contribution of organic matter through floating macrophytes from the Pantanal to the parent river is estimated at 1.5 million tons fresh weight per year at Corumbá (Pott, Pott, 2003). Eventually, dense floating vegetation islands may block floodplain channels causing a disruption of the hydrological connectivity between the main channel and floodplain lakes (Fig. 9). However, the flow dynamics stimulates the development of new channels at the nearest low-lying point. This process causes the complex channel patterns developed in sector 5 (see 6a in Fig. 9). The blockage of the main channel of the Paraguay River has caused that a former floodplain channel, the "Bracinho", has taken over the function of the mainstem (Fig. 3c).

The role of the flood pulse, flow-pulses and multi-annual hydrological pulses

Inundation in the Paraguay river occurs in a predictive, annual timescale by a monomodal flood pulse (Junk *et al.* 1989). Flow-pulses, i.e. flooding below bankfull discharge (Puckridge *et al.* 1998; Tockner *et al.* 2000), occur only during short periods at the beginning of the flooding period. We suggest that the shape of the hydrograph, especially the slope of the rising limb, is decisive for the occurrence of different species, *e.g.* aquatic macrophytes developing from seed banks (Junk, Wantzen, 2004). The spatial extension of inundated areas varies

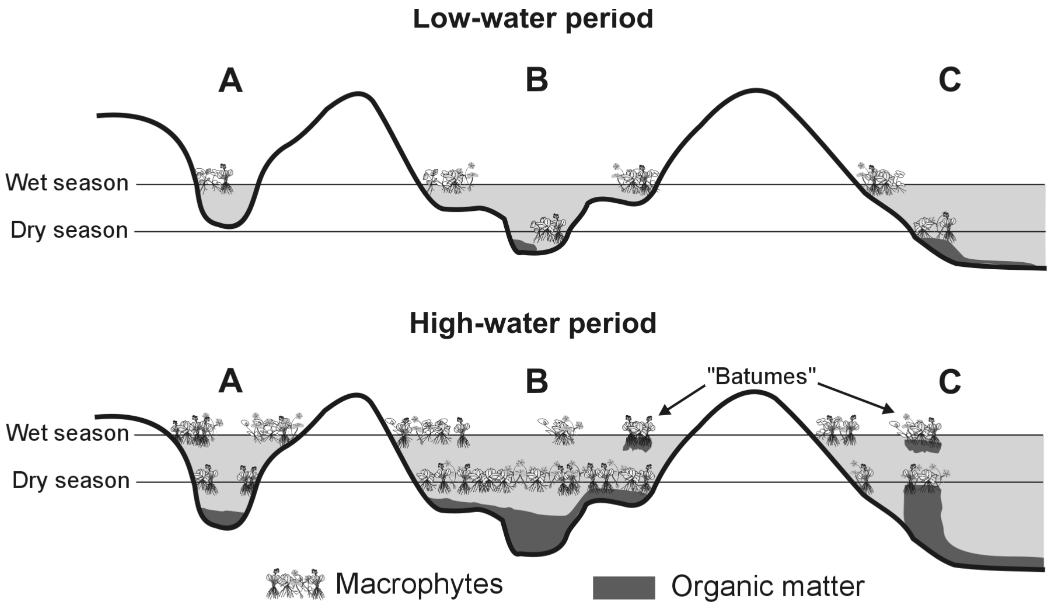


Fig. 10. Hypothetical effects of long-term water level fluctuation on the turnover of organic matter in different floodplain water bodies in the Upper Paraguay. Top: pre-1970 situation; bottom: current situation with elevated water levels. A) In temporary ponds, organic matter is decomposed while drying out. Permanent inundation leads to the development of thick organic layers. B) Shallow, largely dry depressions build up large macrophyte mats on the surface. C) In permanent lakes, the macrophyte belts become uplifted "batumes") and a second belt develops at the new margins.

in different subregions of the floodplain due to variable elevation gradients Hamilton *et al.* 1996). Furthermore, there are large interannual variations causing multi-year patterns of drier and wetter years which certainly influence the structure of the aquatic habitats. During the 1960s and early 1970s, the minimum and maximum water levels of the Paraguay River were extraordinarily low, and rose dramatically in 1973 (Fig. 2). Then, previous lake margins drowned, and their aquatic vegetation belts expanded. For example, in the Bento Gomes River, a tributary of the Paraguay (Fig. 1), a river-lake has enlarged its area approximately fivefold in the past 30 years (Nunes da Cunha *et al.* 1996). Similarly, formerly rounded depression lakes coalesced with drowned floodplain channels, forming irregular water bodies in the area east of 57°30' in the anastomosing sector (Fig. 3c). We suggest that the current sequence of years with increased average water levels has also had a conservative effect on large organic mats that developed along the lake margins before the 1970s and that some of them may have become uplifted with the rising water (Fig. 10). In Figure 3b (lower right corner), the former shorelines are indicated by the inner ring and the present shape of a large depression lake can be clearly seen. We suggest that this process is also enhanced by a current low tectonic subsidence of this alluvial area.

A generalized scheme of neotropical lowland river-floodplain systems

The near-natural condition of the Upper Paraguay River allows generalizations about floodplain dynamics of lowland rivers in the Neotropics (Fig. 11). The pulsing water regime of the river is the primary force which provokes a permanent change of the functional units. The timing and shape of the pulse can vary due to climatic variation and landscape morphology (Fig. 2; Puckridge *et al.* 1998) and strongly influence the performance of the biota (Tockner *et al.* 2000; Junk, Wantzen, 2004). The type of connectivity between aquatic habitats and the main channel usually controls the strength of its impact (Ward and Stanford, 1995; Ward *et al.* 2002; Junk, Wantzen, 2004). Local water level differences of adjacent water bodies and variable channel morphology create a complex system of hydrological connectivity, which may reduce, block, or even revert the flow between lotic and lentic alluvial environments. Biota have an additional effect on the floodplain dynamics by continuous autogenic processes such as plant succession and by occasional events such as the release of large wooden logs from bank slumping (Triska 1984; Kollmann *et al.* 1999) and floating vegetation islands from oxbows (Fig. 8). Both logs and aquatic vegetation stands represent efficient traps for fluvial sediments increasing the channel silting process and

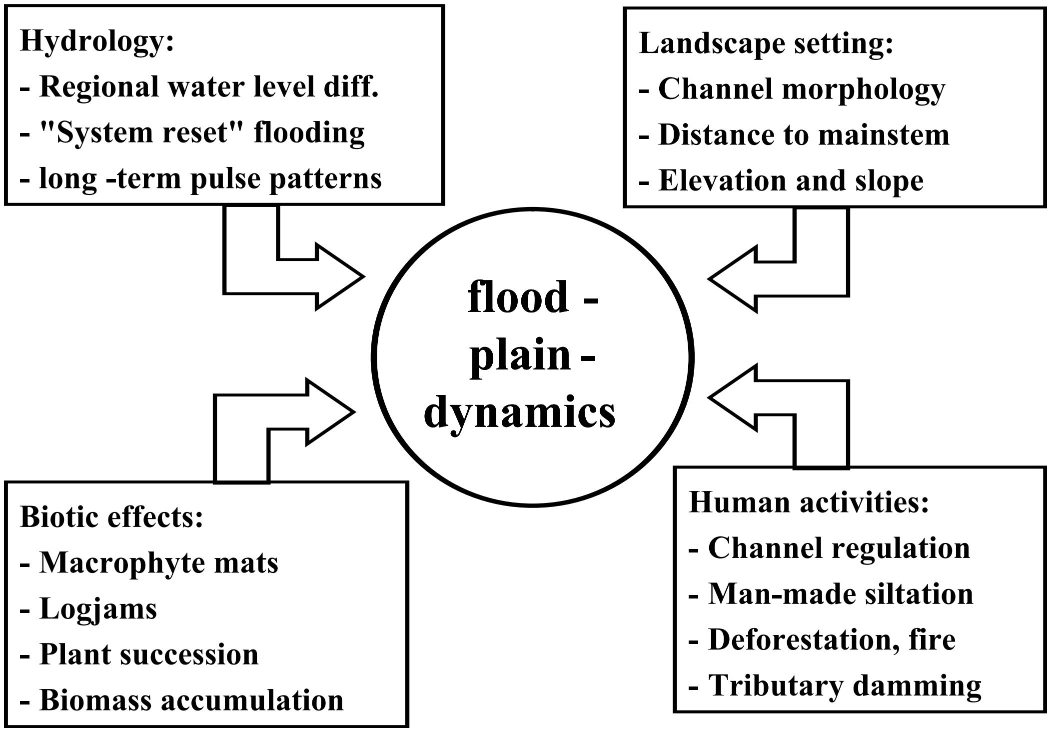


Fig. 11. Factors influencing the physical and chemical properties of aquatic habitats in floodplains. Landscape morphology and hydrological setting exert a primary control on the dynamics of the floodplain habitat structure, which become additionally influenced by biotic effects and human activities.

the development of bars and islands as well as the formation of floodplain lakes. While large woody debris are either dead trees which only represent a mechanical obstacle, or viable parts of single individuals (Kollmann *et al.* 1999), the vegetation mats "inoculate" the stranding site with a variety of species as they have a much larger potential to convey even terrestrial species. All these processes cause a high local variation within the context of the predictable annual inundation, and, consequently, increase the biocomplexity of the floodplain system (Amoros, Bornette 2002).

Conclusions

In spite of the so-far relatively good state of conservation of the Upper Paraguay River, recent man-made changes in the hydrology may have multiple, deleterious effects on the river and wetland structure (da Silva *et al.* 2001; Hamilton 2002). Large scale deforestation and mining activities in the subcatchment areas have increased sediment load of the tributaries, as in the Jaurú River (pers. obs.) and Taquari River (Hamilton *et al.* 1997). The long-debated waterway-project (hidrovia) has still not been fully abandoned and continues to threaten the Paraguay-Pantanal hydrosystem by deepening the river channel - with hazardous consequences for the floodplain size (Ponce, 1995, Hamilton 1999). Even without an approval of the project, dredging and navigation with inadequately sized barge convoys were registered (Wantzen *et al.* 1999). Moreover, several tributaries of the Pantanal main rivers have been dammed for hydroelectric power generation and plans for further exploration exist. The dams reduce flood peaks during the wet season so that the critical height for the spill-over from the channel into the floodplain is often not reached any more. On the other hand, occasional releases during the dry season cause untimely peak floods, which kill terrestrial species colonizing the sand bars, *e.g.* breeding skimmers. Our results show that both connectivity and variability of flood pulses are crucial for the habitat dynamics - and implicitely habitat diversity - in the river-floodplain-system of the Paraguay River. As most aquatic habitats are very shallow (maximum depth 2m), a lowering of the river water level would have similar consequences for most of the aquatic habitats. We consider the connection channels between permanent water bodies as the most sensitive functional unit in this system as they are a prerequisite for the exchange of aquatic biota, dissolved nutrients and suspended organic matter.

In conclusion, the maintenance of the natural variation of the flood pulse should therefore receive highest priority for landscape planning in the Upper Paraguay basin.

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