Linking hydro-morphology with invertebrate ecology in diverse morphological units of a large river-floodplain system

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Abstract Interdisciplinary research in the fields of ecohydrology and ecogeomorphology is becoming increasingly important as a way to understand how biological and physical processes interact with each other in river systems. The objectives of the current study were 1) to determine changes in invertebrate community due to hydrological stages, 2) to link local physical features [flow configuration, sediment composition and morphological feature) with the ecological structure between and within dissimilar morphological units (meander and confluence), and 3) to determine the existence and the origin of bed hydro-geomorphic patches, determining their ecological structure. Results were discussed in the frame of prevailing ecological models and concepts. The study site extends over a floodplain area of the large Paraná River (Argentina), including minor and major secondary channels as well as the main channel. Overall results suggested that hydrodynamics was the driving force determining distribution patterns of benthic assemblages in the flood-plain. However, while the invertebrates living in minor secondary channels seem to benefit from flooding, this hydrological phase had the opposite effect on organisms from the main and major secondary channels. We also found a clear linkage between physical features and invertebrate ecology, which caused a dissimilar fauna structure between and within the meander and the confluence. Furthermore, several sandy-patches were recorded in the confluence. These patches were colonized by the particular benthic assemblage recorded in the main channel, supported the view of rivers as patchy discontinua, under uncertain ecological equilibrium.

1. Introduction

An increasing number of interdisciplinary fields such as ecogeomorphology and ecohydrology are rapidly evolving, both focusing on the relationship between biological communities and geomorphologic and hydrologic processes [*Allen et al.*, 2014]. This is evidenced by the growth in the number of articles published, the founding of new interdisciplinary journals, and the development of concepts in freshwater ecology based on that interdisciplinary approach. In this sense, several meaningful river concepts have been centred on the linkage between ecology, hydrology and geomorphology. For example, the well known Flood Pulse Concept (FPC) [*Junk et al.*, 1989], the Patch Dynamics Concept (PDC) [*Townsend*, 1989], the Hierarchical Patch Dynamics (HPD) [*Poole*, 2002], the Network Dynamics Hypothesis [*Benda et al.*, 2004], among others. A significant attempt to synthesize river ecosystem concepts is the Riverine Ecosystem Synthesis (RES) by *Thorp et al.* [2006, 2008]. These authors conceptualize rivers as arrays of large hydro-geomorphic patches (e.g., sandy-patches) formed by catchment geomorphology and climate. These hydro-geomorphic patches are given by local shifts in geomorphic and hydraulic conditions and typically support unique assemblages of species, contributing greatly to riverine diversity [*Gray and Harding*, 2007]. *Matthaei and Townsend* [2000], in turn, showed that floods can induce a mosaic of disturbance with some patches experiencing scour and others, deposition, while others remain unchanged. Recently, *Humphries et al.* [2014] have proposed the River Wave Concept (RWC) as a model that synthesizes the existing concepts into a simple but holistic way.

Analyzing such concepts briefly, it is noticeable that they are embedded in ecogeomorphology and ecohydrology fields, also based on empirical data across relatively small river networks (except the FPC). Only few studies

carried out in large lowland rivers in the world support the principles of those concepts [e.g., *Hoeinghaus et al.*, 2007], evidencing the need for further studies with empirical data from those kind of environments.

Taking the above mentioned into account, we selected a sector of a large river-floodplain system (Paraná River) to carry out our study, establishing three specific objectives:

1. to determine changes in invertebrate community comparing two diverse hydrological situations (temporal scale) in a minor secondary channel.
2. to link physical features (local flow configuration, hydrological stages, sediment composition and morphological features) with ecological attributes (invertebrate diversity, evenness and number of species) in order to establish differences and similarities between and within a meander and a confluence (morphological units).
3. to verify the existence, and to infer the origin, of bed hydro-geomorphic patches in a minor floodplain channel and to describe the assemblage of species inhabiting them.

The results were discussed within the frame of the above-mentioned ecological concepts and theories, particularly those based on ecogeomorphological and ecohydrological interrelationships.

2. Methodology

2.1. Sampling Area

The study area was located in the floodplain of the Paraná River, Santa Fe province, Argentina (31° 43′ 20″ S; 60° 44′ 40″ W). The Paraná River is ranked ninth among the largest rivers in the world according to its mean annual discharge to the ocean (18,000 m^3 s^{-1}), and is therefore classified as a "mega-river" by *Latrubesse* [2008]. This mega-river has an anabranching main channel in the middle course, sandy bottom sediments and exposed sandy bars [*Latrubesse*, 2008]. In order to achieve objective 1, we selected and sampled a minor secondary channel placed in the Paraná River floodplain during two diverse hydrological stages. This channel, called "Catarata stream," is a low hierarchy channel (relatively low discharge) with a mean discharge of 213 m^3 s^{-1} (own recording) and dominated by silt and clay bottom sediments (Figure 1a).

In the Catarata stream two distinctive morphological units were selected: a meander and a confluence, with the purpose of achieving objective 2. The chosen meander did show unusual characteristics and was identified as a "circular-meander" [*Andrle*, 1994] (Figures 1a and 1b). The flow pattern through this type of meander was typified by the presence of a large counter current, differing greatly from the typical river bend in which flows generally move downstream and subparallel to the channel banks throughout the bend. Likewise, deposition along the bend also does not follow the conventional pattern, but instead it occurs primarily on the concave bank in the form of a concave bank bench. Erosion was concentrated on the convex bank where no point bar deposits exist. Otherwise, the confluence also presents distinctive planform morphology. One of the channels joins the other one in a meander bend and after a bifurcation, as shown in the Figures 1a and 1c. This type of confluences has been described by *Riley and Rhoads* [2012] and *Roberts* [2004] among others. Although, both morphological units are atypical in many river systems, they occur with relative frequency in the Paraná floodplain.

The second selected location was a major channel (higher hierarchy) called "Coronda River." This is a sandy bottom river with a mean discharge of 1000–2000 m^3 s^{-1} [*Amsler et al.*, 2007] and it is in direct connection with the Paraná main channel and the Catarata stream [*Drago*, 2007, Figure 1a]. The sampling at the Coronda River was performed in front of the Catarata mouth (Figures 1a and 1d). Additionally, and only for comparison reasons, we used a data set from the Paraná River main channel previously obtained at approximately 30 km upstream of the Catarata mouth (Figures 1a and 1e). The fact that the three selected environments are well connected one to the other, and that they have dissimilar bottom composition, discharge and dimension is crucial to achieve the objectives of this study, particularly the last one.

2.2. Benthic Sampling, Bottom/Suspended Load and Water Chemistry
2.2.1. Sampling Trips

Two sampling trips were carried out in the Catarata stream and one more in the Coronda River. Specific dates and hydrological conditions were selected in order to cover a certain natural variability of the system, i.e.: low-mid and flooding stage. Thus, Catarata stream sampling was conducted in August 2010 (water level: 2.96 m; Santa Fe gauging station) and April 2011 (water level: 4.79 m), while Coronda River sampling was
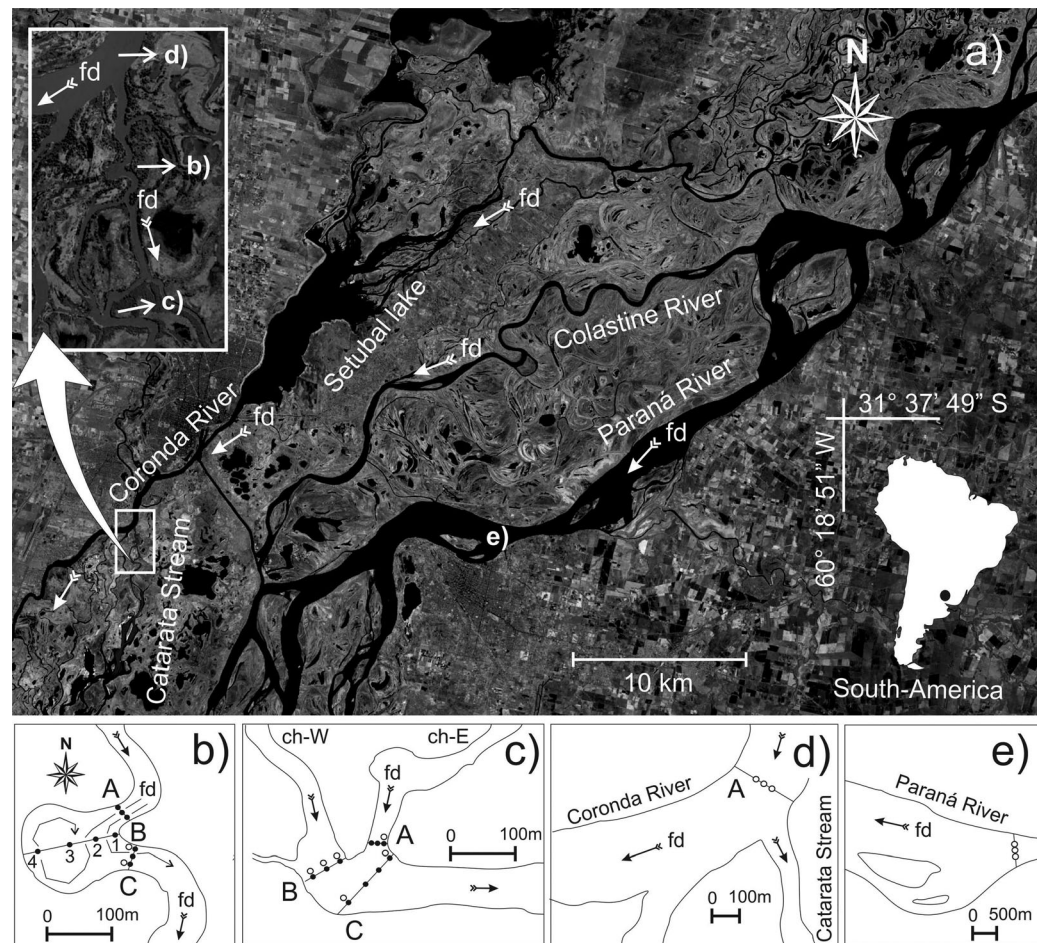
Figure 1. Map of the selected study area in the Paraná River floodplain showing location and details of sampling stations and cross sections at (a) the circular-meander and (b) the confluence in the (c) Catarata stream, (d) Coronda River, and (e) Paraná main channel. Circles stand for sampling stations dominated by silt/clay (black circles) and sand sediments (empty circles). ch-W: western channel; ch-E: eastern channel.

performed in December 2013 (water level: 3.02 m). Three cross sections were defined over each selected morphological unit at the Catarata stream, establishing 3–4 sampling stations over each cross section, depending of the local channel width (Figures 1b and 1c). Three sampling stations were selected over a cross section in the Coronda River located close to the Catarata stream mouth (Figure 1d).

Triplicate benthic sediment samples were taken at each sampling station for invertebrate counting and identification using a Tamura[TM] bottom grab (322 cm^2 surface of extraction). This grab was lowered by means of an electric winch fitted with a steel cable. A total of 129 samples were taken from the Catarata and Coronda rivers. Every benthic sample was filtered through a 200μm sieve and fixed with 5% formaldehyde in the field. The invertebrates were later hand-picked in the laboratory and stored in a 70% ethanol solution. All benthic taxa were identified and counted under upright microscope (Nikon, Eclipse E100-LED). Taxonomical determinations were made at species and genus levels using the following taxonomic keys: *Brinkhurst and Marchese* [1992] for Oligochaeta; *Paggi* [2001], *Trivinho-Strixino* [2011], *Spinelli and Wirth* [1993] for Diptera Ceratopogonidae; *Domínguez et al.* [1994] for Ephemeroptera; *Domínguez and Fernández* [2009] for other taxa.

Additional duplicate bed sediment samples for granulometric analysis (by dry sieving) were taken at the same benthic sampling sites. Suspended sediments in the water column were collected at each sampling site using a horizontal Van Dorn water sampler (2 L) at three different stratifications (near the bottom, middle water column and near to the water surface). As suspended load sediments require moving water to keep the particles above the bed, we used the suspended load as a reference measurement about

hydrological conditions. In order to characterize the water quality, the following physical and chemical variables were recorded *in situ*: transparency (Secchi disk; m), electric conductivity (μS cm^{-1}), water temperature (°C), pH and bed dissolved oxygen (mg L^{-1}), using a Hach sension TM 156 portable multiparameter (Loveland, USA).

2.2.2. Data Set

A benthic data set previously obtained in the Paraná main channel was also used in the current study. This data set was obtained in October 2005 and August 2007 during low-mid water levels by the authors of this study using identical collecting protocol (54 benthic samples in total). This information was included herein to show the ecological structure of the dominant invertebrate assemblage in the main channel, in order to make comparisons with the assemblage recorded in the Catarata stream and Coronda River. This latter was obtained by the authors of the current study.

2.3. Bathymetric and Three-Dimensional Flow

The river bed morphology was surveyed using a Raytheon single-beam echo sounder (SBES), coupled to a differential global positioning system (DGPS) deployed on a vessel. A real-time kinematic differential global positioning system (RTK DGPS) provided horizontal positions with accuracy of ~0.02 m at approximately 1 Hz. Morphological data were interpolated using standard kriging methods onto a regular grid to create bathymetric maps along the Catarata stream. Once the bathymetry data were obtained, the three-dimensional flow velocity was measured with a 1200 kHz Teledyne RDI ADCP. At each morphological unit, flow measurements were made at 3 individual cross sections, providing a detailed flow structure characteristic. In order to obtain representative values of the time-averaged three-dimensional velocities at each cross section, measurements from a series of 4 repeat transect lines were made and subsequently averaged [*Szupiany et al.*, 2007]. Velocity Mapping Toolbox according to *Parsons et al.* [2013] was used to process velocity data obtained with the ADCP. Primary (pv) and secondary (sv) flow structures around the studied units were analyzed according the Rozovskii definition, as this allows any rotation to be based upon individual verticals, rather than rotation of the whole section. The latter method essentially identifies the primary velocity direction for each profile as the depth-integrated flow vector, and the secondary currents are then obtained by the differences from this average vector within the profile. This procedure effectively identifies individual secondary planes at each vertical profile across a given section, thus allowing for identification of helical motion within a section, without distorting the secondary flow results (for more methodological details, cf. *Szupiany et al.* [2007, 2009]). By following this methodology we were able to determine discharge (m^{-3} s^{-1}), flow direction as N (to the North) and primary and secondary velocities (m s^{-1}).

The vessel position at the selected at-a-point sampling locations was attained using a Furuno GP-1650WF echo sounder (Furuno Electric Co. LTD, Nishinomiya city, Japan.) coupled to a Global Positioning System (GPS).

2.4. Statistical Analysis

As the data of macroinvertebrate density were not normally distributed, they were logarithmically transformed [$\log_{10}$ (x+1)] which resulted in normality and homogeneity of variance (Fmax) [*Sokal and Rohlf*, 1981]. One way ANOVA was conducted to determine whether there were significant differences in concentrations of suspended sand in the meander and the confluence during mid-low water and flooding stages. Furthermore ANOVA was also performed to compare benthic densities between both morphological units and hydrological stages. The post hoc Fisher's test (multiple comparison test) was applied to identify where significant differences occurred between individual groups.

In order to answer different ecological questions the Canonical Analysis of Principal coordinates (CAP) was carry out. CAPs (software v 1.0) [*Anderson*, 2004] were performed to find spatiotemporal patterns of similarity in the ecological structure (composition and relative abundance) of invertebrate assemblage at several scales [*Anderson and Willis*, 2003]. In addition, one-way Permutational Multivariate Analyses of Variance (PERMANOVA) [*Anderson*, 2001] were used to test the patterns of similarity of invertebrate assemblages among diverse biotic groups. Bray–Curtis dissimilarity index and 999 permutations [*Manly*, 1997] were used in both CAP and PERMANOVA analyses. A redundancy analysis (RDA) was performed to identify the relationships between invertebrate spatial patterns and habitat features [*ter Braak and Šmilauer*, 2002].

Rare species were excluded from the CAP and RDA analyses as suggested by *Park et al.* [2006], compiling a final matrix of 55 from the 86 total species. Shannon index, evenness and abundance were estimated to compare their values at several cross sections and some particular sampling stations.

Statistical analyses were carried out using the R 3.1 software [*R Core Team*, 2012] and the MULTIV software, version 2.4.2 [*Pillar*, 2004]. For all analyses the statistical significance level was P<0.05.

3. Results

Through the bathymetric survey in the meander we detected: i) a large circular pool located at the apex of the meander bend, ii) a scour hole located on the convex side of the pool (approximately 14 m deep), originated by active erosion processes, iii) a marked shallow area located on the concave bank generated by sedimentological processes (Figure 2a).

The bathymetric map of the confluence showed the presence of two scour holes with similar depths (17 m approx.). One of these scour holes was located exactly in the junction of the eastern (ch-E) and western (ch-W) channels but the other one was placed in the west channel, very close to the confluence. The first scour hole was selected accordingly (hereinafter referred to as "confluence scour hole"), because it was formed by the hydrodynamic action at the junction of both channels. It is noteworthy to mention that both secondary channels (eastern and western; see Figure 2a) are relatively flat and shallow, particularly the eastern one, which has a 3–3.5 m average depth.

The velocity map indicated a large low-flow velocity area (depositional sector) on the concave bank of the meander, together with a reversal flow (negative velocities) over this side (Figure 2b). A large velocity depletion also occurred at the confluence, especially in the western channel. This low-velocity area involves part of the pool confluence and the western channel, where cross section B was established (Figures 1c and 2b).

An increase in both primary (pv) and secondary velocity (sv) was evident in the meander during the flooding event (Figure 3). Cross sections A and C (see Figure 1b) show a clear difference in magnitude and distribution of pv and sv, in respect of cross-section B (pool section). To be noted, the maximum pv was located on the left side of cross section A. In contrast, in cross section C the maximum pv occurred on the opposite side (right bank). As mentioned above, the lower water velocities jointly with a backwater zone were
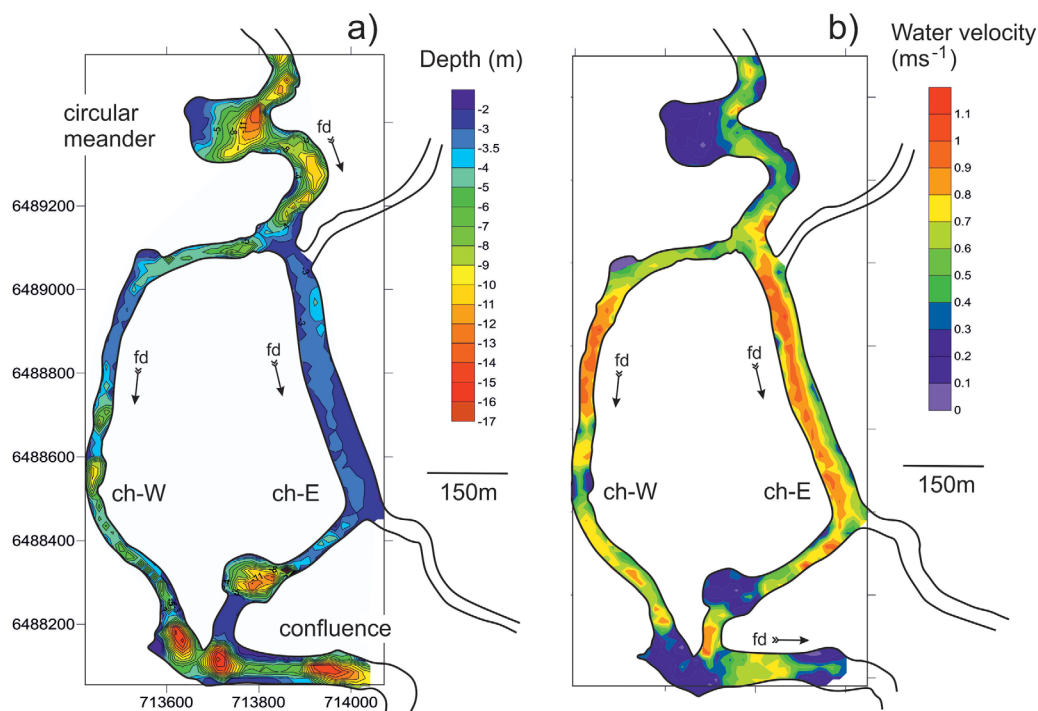

Figure 2. (a) Bathymetry and (b) mean flow velocity at the circular-meander and the confluence (Catarata stream).
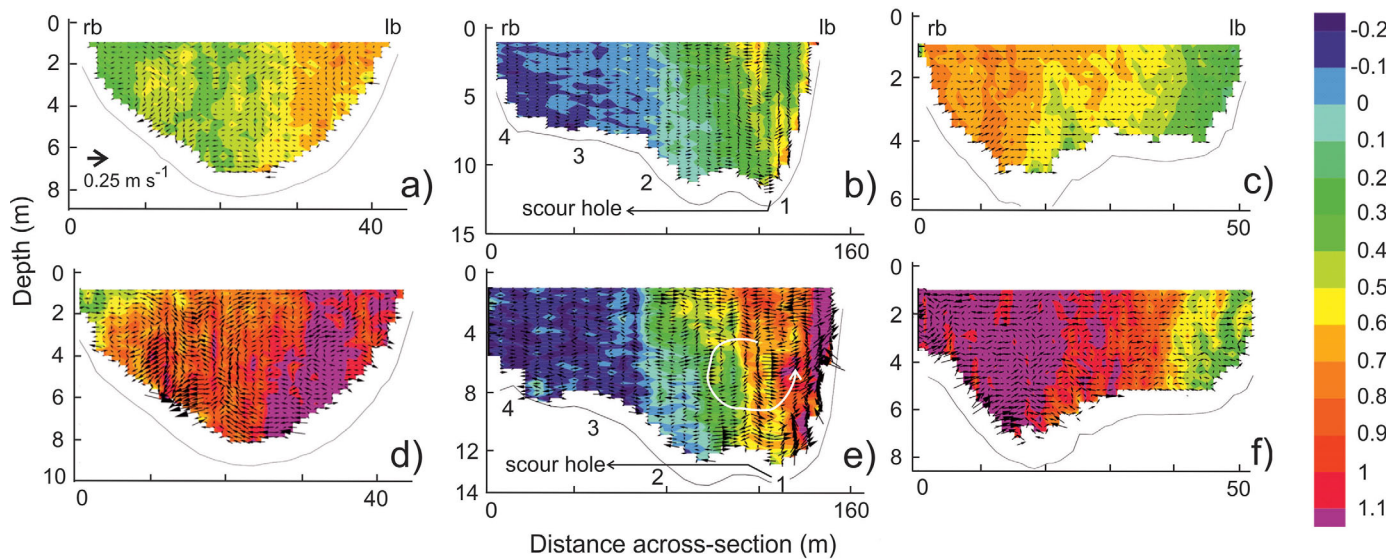
Figure 3. Primary (color scale; m s^{-1}) and secondary velocity (vector magnitude) fields in the surveyed sections of the meander during both hydrological periods. (a) cross section A in August 2010; (b) cross section B in August 2010; (c) cross section C in August 2010; (d) cross section A in April 2011; (e) cross section B in April 2011; (f) cross section C in April 2011. Where, rb: right bank; lb: left bank; white arrow: secondary recirculation cell.

recorded on the concave side (right bank). The pv over this margin was even negative (-0.2 m s^{-1}), which triggered a separation zone of recirculating flow or reflux. Moreover, a greater flow increase and disparity in flow direction was observed on the convex side of the pool (up to 1.1 m s^{-1}). As a result, two very diverse hydraulic sectors are evident (Figures 3b and 3e). The sector on the concave side was markedly enlarged, shallower, having very low (and negative) flow velocities. Indeed, these features bring on the "circular-meander" name. This phenomenon was clearly more intense during the flooding period, which resulted in severe morphological changes given by erosion over the inner bank (Figure A1 in Appendix A).

Higher pv and sv were recorded near the surface in the eastern channel of the confluence. Velocities in this channel were considerably greater than in the western channel at both hydrological periods (0.23 to 0.43 m s^{-1} and 0.13 to 0.3 m s^{-1}; respectively). Cross section C involves the scour hole and it shows pv intensities of 0.4 m s^{-1} in 2010 and 1.0 m s^{-1} in 2011, while the sv was about 0.43 m s^{-1} in 2010 and 0.86 m s^{-1} in 2011. A secondary cell movement (see direction and magnitude of sv vectors) was also evident, while superficial flow acceleration on the left side of the pv and sv diminished toward the river bottom during the flooding water period (Figure 4). A similar trend was observed during measurements in 2010 but the flow acceleration on the surface was smaller and limited to the central part of the channel.

There was an increasing amount of suspended sand during the flooding face, denoting a higher capacity of sediment transport (Figure 5). ANOVA results confirmed this tendency (meander: P= 0.0001, F$_{(1,18)}$= 33.3; confluence: P= 0.0002, F$_{(1,18)}$= 22.4). This sand transport capacity is directly related to the potential facility to transport invertebrates in drift.

There was great dissimilarity in bed composition and water discharge between the Catarata stream and Coronda River (Table 1). Highest sand concentration was recorded in the Coronda River bottom (99% concentration), while it ranged from 36 to 70% in the Catarata stream. Note the higher sand concentration found in the confluence during the flooding event; particularly, the medium size grain. In this sense, the increasing number of sandy-patches is notable during that water stage. The mean water velocity was higher in the Coronda River. However, in the Catarata stream the maximum water velocities ranged from 1.2 to 1.9 m s^{-1}, i.e., equal to and greater than the value recorded in the Coronda River. The good water quality (given by the total dissolved solids, conductivity, dissolved O$_2$ and pH) is remarkable in both rivers (Table 1).

In the Catarata stream, the invertebrate densities were significantly higher during the flooding than during the low water stage. ANOVA result confirmed this statement (P= 0.015; F$_{(3,36)}$= 3.9). Moreover, the density recorded in the Coronda River was the highest one (P= 0.004, F$_{(1,21)}$= 10), as expected for a sandy-bottom river of the Paraná floodplain (Figure 6).
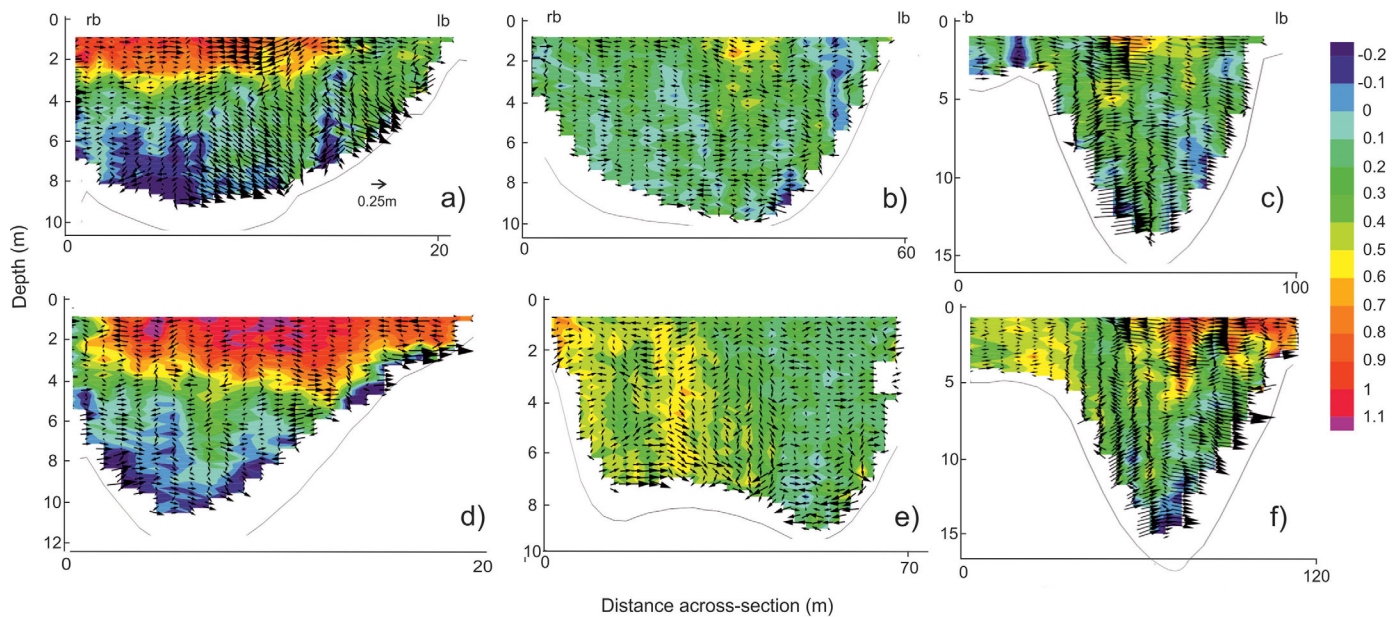
Figure 4. Primary (color scale; m s^{-1}) and transverse velocity (vector magnitude) fields in the surveyed sections of the confluence during both hydrological periods (August 2010 and April 2011). (a) cross section A in August 2010; (b) cross section B in August 2010; (c) cross section C in August 2010; (d) cross section A in April 2011; (e) cross section B in April 2011; (f) cross section in April C 2011. rb: right bank; lb: left bank.

A depletion of fauna diversity, evenness and number of species was detected during the flooding stage at both meander and confluence (Catarata stream; Table 2). However, the lowest values of these ecological attributes were recorded in the Coronda River. Additionally, diversity values, evenness and number of species found at meander cross section B were detailed at each sampling station, showing lower values at sampling-station 1 (active erosion sector).

The CAP carried out comparing benthic structure between both hydrological situations (water level: 4.79 and 3.02 m) showed a significant difference in composition and relative abundance of invertebrates (P= 0.001), evidencing the influence of the temporal scale. Significant differences between the structure of invertebrate assemblages inhabiting the confluence and the meander were also revealed (P= 0.01; Figure 7a and Table 3).

The second CAP performed, arranged by substrate composition and hydrological stages, revealed significant differences in benthic structure among groups (P< 0.05), with the exception of sandy sediments at low and high water stages where no differences were detected, suggesting that sandy-patches in the Catarata
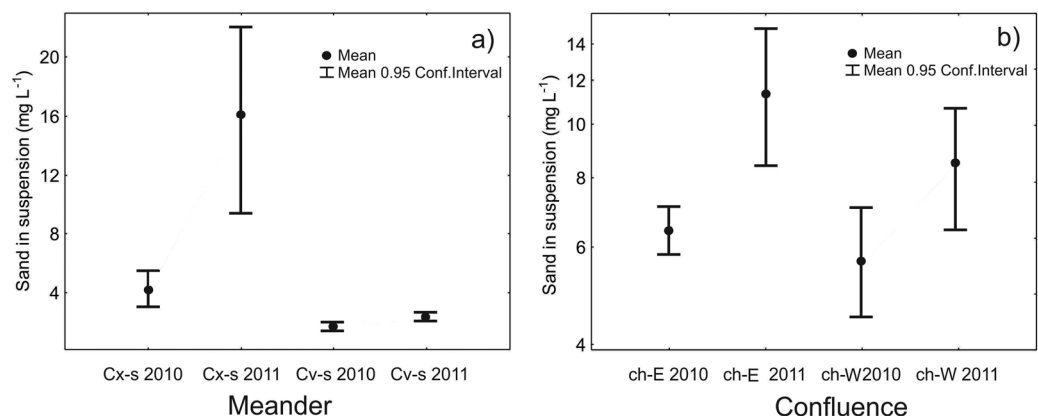

Figure 5. Suspended sand recorded (a) at the cross section B of the circular-meander during both hydrological periods, and (b) at eastern and western channels of the confluence. Cx-s: convex side of the meander pool; Cv-s: concave side of the meander pool; ch-E: eastern channel; ch-W: western channel; 2010: August 2010; 2011: April 2011.

Table 1. Mean Values of Abiotic Variables Measured at the Catarata Stream and Coronda River[a]

| | Sampling Location | | | | |
| | Catarata Stream | | | Coronda River | |
Variable	Cm2010	Cm2011	Cc2010	Cc2011	Co
$\bar{U}$ (m s^{-1})	0.3	0.6	0.2	0.3	0.9
U_m (m s^{-1})	1.2	1.9	0.23(A)	0.43(A)	1.2
			0.13(B)	0.3(B)	
Q (m^3 s^{-1})	118.7	305.5	87.5	240.7	~1500
Mean depth (m)	7.0	8.1	7.3	8.0	18.0
Momentum ratio*	-	-	1.8	1.6	-
Sand (%)	44.5	36.3	55.1	69.8	99.0
Silt (%)	45.9	42.2	30.2	18.2	0.4
Clay (%)	9.6	21.6	14.7	12.1	0.6
FG (%)	6.7	7.0	2.3	0.4	-
VFG (%)	4.0	3.1	0.7	0.5	-
VCS (%)**	4.6	1.9	2.1	1.4	-
CS (%)**	4.8	2.0	9.1	12.1	-
MS (%)**	16.5	12.0	25.1	53.3	-
FS (%)**	38.5	27.8	35.7	21.9	-
VFS (%)**	25.0	46.2	25.1	10.2	-
TDS (mg L^{-1})	49.0	56.4	64.7	54.5	42.2
Conductivity (μS cm^{-1})	98.1	112.5	129.8	111.0	73.0
pH	6.0	6.0	5.5	5.5	7.0
Transparency (m)	0.4	0.3	0.4	0.3	0.3
Dissolved O$_2$ (mg L^{-1})	9.2	5.4	9.2	5.4	9.6
sSs (mg L^{-1})	4.3	17.5	7.2	13.3	-
sFs (mg L^{-1})	64.7	70.1	86.9	71.5	-
sOM (mg L^{-1})	8.1	6.5	9.6	6.3	-
Sandy-patches	1.0	1.0	2.0	6.0	full

[a]Cm: Catarata meander; Cc: Catarata confluence; Co: Coronda River; A: channel A (confluence); B: channel B (confluence); $\bar{U}$: mean water velocity; U_m: maximum water velocity; Q: discharge; FG: fine gravel; VFG: very fine gravel; VCS: very coarse sand; CS: coarse sand; MS: medium sand; FS: fine sand; VFS: very fine sand; TDS: total dissolved solids; sSs: suspended sand sediments; sOM: suspended organic matter; -: no measurements; ρ: water density; (*): Mr$=\frac{\rho\bar{Q}\bar{U}|_{(A)}}{\rho\bar{Q}\bar{U}|_{(B)}}$ [*Rhoads and Kenworthy*, 1995]; (**): percentages respecting the total amount of sand in the bed sediment.

Figure 6. Total densities recorded in the Catarata stream and Coronda River. Me.2010: Catarata meander in August 2010; Me.2011: Catarata meander in April 2011; Co.2010: Catarata confluence in August 2010; Co.2011: Catarata confluence in April 2011; Coronda: Coronda River in December 2013.

stream have similar invertebrate composition and abundance (P= 0.206; Figure 7b and Table 3). The substrates considered herein were silt/clay –the dominant sediment in the Catarata stream– and sand sediment –local patches–. The authors considered those sampling stations with bed sand percentages ≥ 80% as sandy sediments.

The statistical comparison between fauna composition recorded from the sandy-patches (Catarata stream), Coronda and Paraná Rivers (database) shows no difference among benthic assemblages (P= 0.54). This result suggests, *a priori*, that sandy-patches were colonized by species coming from the Coronda and Paraná rivers (Table 3). Furthermore, at a smaller spatial scale, statistical differences were found in structure assemblage between the sampling stations located on the concave side of the meander pool (sampling stations 2, 3 and 4) and station 1, located on the convex side of the pool (P= 0.04; Table 3).

Through the RDA results we observed a clear association of *Narapa bonettoi* and *Myoretronectes paranaensis* to sandy-patches of the Catarata stream and sandy sediments of the Coronda and Paraná Rivers (see the bigger ellipse in Figure 8 and Table 4). The remaining sampling stations in the Catarata stream were basically dominated by silt/clay bed sediments and typically colonized by *Limnodrilus* sp. (*L. hoffmeisteri, L. udekemianus*) and *Pristina* sp. (*P. osborni, P. acuminata, P. americana*). *Paranadrilus descolei* was strongly associated with higher concentration of organic matter in sediments. The smaller ellipse in Figure 8 shows a particular sampling-station located in the west channel of the confluence. This sampling station had the peculiarity that almost no organism was recorded there, despite the fact that it was dominated by sandy sediments.
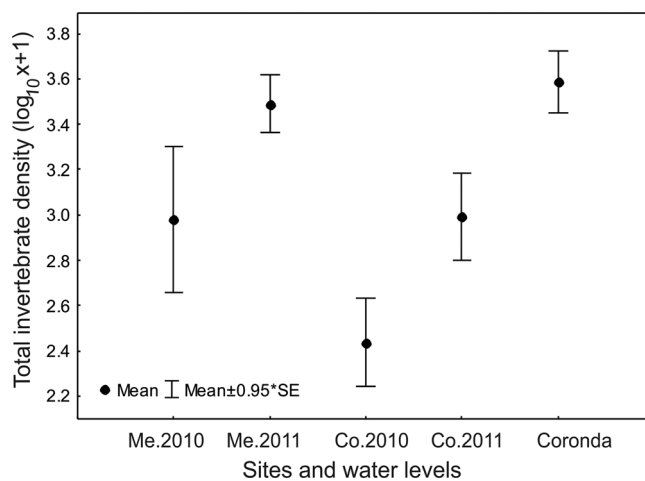
Table 2. Benthic Ecological Attributes in the Catarata Stream (Meander and Confluence) and Coronda River (N_{total} = 129 Samples)[a]

	Shannon Index (Diversity)	Evenness	Number of Species
Morphological Units			
m2010	1.01	0.63	39
m2011	0.81	0.54	32
c2010	0.91	0.65	25
c2011	0.56	0.42	21
Coronda	0.26	0.31	7
Sampling-Stations at the Meander Pool			
s-s 1	0.12	0.27	3
s-s 2-3-4	0.83	0.6	25

[a]m: meander; c: confluence; 2010: August 2010; 2011: April 2011; s-s: sampling station.

From the total data we detected two distinct assemblages of macroinvertebrates: the named "active bed assemblage," inhabiting mobile sandy sediments, and the "fine sediment assemblage," colonizing silt-clayed sediments (Table 5).

4. Discussion

4.1. Temporal Scale

Hydrologically, the wave crest in the Catarata stream was mainly characterized by a higher discharge (approximately 3 times larger than during the descending limb of the wave) and by stronger current velocities (1.5 times; Table 1). Noteworthy, during this hydrological period a significant increase in invertebrate density and suspended sediments were observed in the Catarata stream (Figures 5 and 6). As water flow is a "master variable" [*Power et al.*, 1995] that governs the fundamental nature of streams and rivers [*Hart and Finelli*, 1999], it is not surprising that the modification of flow caused by increasing water levels modifies the invertebrate density (Figure 7a). Annual flooding cycles increase invertebrate biomass and food resource making them available for higher trophic levels (e.g., fish community [*Winemiller*, 2007]) and maintaining the system in an immature but highly productive stage [*Brown et al.*, 2001; *Junk and Wantzen*, 2004]. In agreement to this, the FPC [*Junk et al.*, 1989] and RWC [*Humphries et al.*, 2014] suggest that riverine fauna benefits from flooding events, by increasing primary and secondary production and the efficient use of nutrients.

However, *Blettler et al.* [2008, 2012] and *Takeda et al.* [2001] observed an opposite tendency regarding invertebrate densities in the main channel of the Paraná River; i.e., the invertebrate density proportionally decreases during flooding events due to the intensity of bed flow conditions. According to these authors, the densities of benthic invertebrates living in the mobile bed sediments of the main channel (where the strongest bed hydraulic condition prevail), are related to discharge, hydrological level and bed hydraulics following a "bell-shaped" tendency. This indicates that there is an optimum range in the bell shaped curve; should hydrological variables increase or decrease, densities would decrease anyhow [*Amsler et al.*, 2009].

Hence, we suggest that the benthic assemblages living in minor channels of the floodplain ("fine sediment assemblage" [*Blettler et al.*, 2012, 2014]) would benefit from the highly productive flooding stage. Meanwhile, the assemblage living in the main channel ("active bed assemblage," op. cit.) is negatively affected due to the stronger bed flow conditions. Therefore, the same hydrological phenomenon would have opposite effects on invertebrates depending on the hierarchy of the inhabited lotic environments (and the texture of bed sediments).
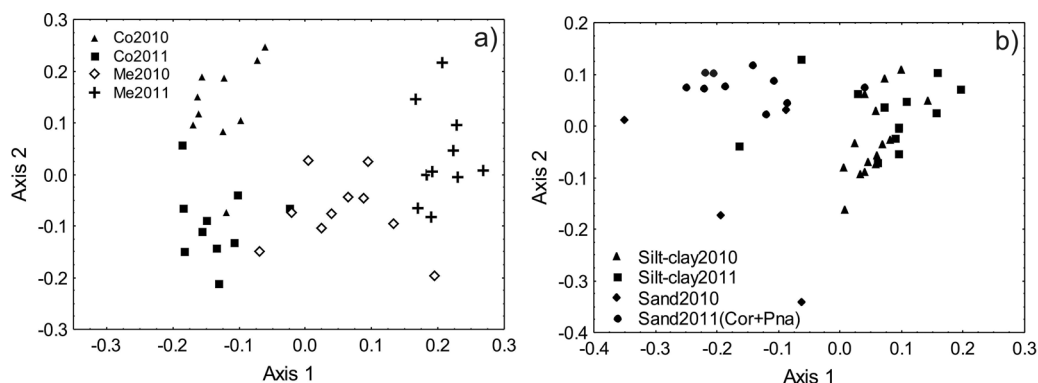

Figure 7. Ordination plot of the Canonical Analysis of Principal coordinates (CAP) showing significant differences in composition and relative abundance, taking into account (a) both morphological units and hydrological stages (Catarata stream), and (b) bed sediment composition and hydrological stages (Catarata, Coronda and Paraná Rivers). Both plots were generated with the first two principal coordinate axes from the computed results. Me: circular-meander; Co: confluence; Cor: Coronda River; Pna: Paraná River.

Table 3. PERMANOVA Results Showing Sum of Squares and P Values Among Contrast Groups[a]

Contrast Groups	Sum of Squares (Q)	P Value
Water Level and Morphological Unit (lw, hw, me, co)		
lw versus hw	0.801	0.001
lw versus me	1.090	0.002
lw versus co	1.298	0.002
hw versus me	1.201	0.002
hw versus co	1.162	0.006
me versus co	0.473	0.049
Water Level and Sediment Composition (lw, hw, sa, sc)		
lw versus sa	1.08	0.003
lw versus sc	1.482	0.001
hw versus sa	1.187	0.002
hw versus sc	1.565	0.001
sa versus sc	0.431	0.206
Sandy Patches (sCa, sCP)		
sCa versus sCP	0.204	0.543
Meander Pool Stations (1, 2, 3, 4)		
1 versus [2, 3, 4]	0.612	0.04

[a]lw= low water level (3.02 m), hw= high water level (4.79 m), me= meander, co= confluence, sa= sand composition, sc= silt and clay composition, sCa= sand composition in the Catarata stream, sCP= sand composition in the Coronda and Paraná Rivers.

4.2. Spatiotemporal Scale: Morphological Units

Dissimilar flow configuration, sedimentological composition and fauna structure were detected between both, the meander and the confluence (Table 3; Figures 2 and 7). In general terms, higher amount of bed sand (mainly medium grain size) and lower concentration of silt were found in the confluence bed (Table 1). Unlike the meander, the confluence was extensively inhabited by the "active bed assemblage" (dominated by *Narapa bonettoi*), even when the water quality was similar (optimum) at both locations. As a result, we suggest that the assemblage structure was directly linked to morphologic and hydraulic local features. This distinctive pattern occurred even when both units are separated by only 1.7 km, reducing a potential geographic influence.

At a minor spatial scale, the particular morphological features within the circular-meander, resulted in a clear differentiation of two diverse hydraulic sectors over the pool area (cross section B). The sector located on the right bank of the pool (stations 2, 3 and 4; Figure 1b) showed low water velocities and a remarkable reversal flow during both hydrological stages (even less than -0.2 m s^{-1}; Figure 3b and 5). The presence of backwaters at the pool of circular-meanders has been reported by *Andrle* [1994] and *Vietz et al.* [2012]. This sector was also characterized by the presence of many floating macrophytes dominated by *Eichhornia crassipes* and *E. azurea* (Figure A1a), which favors the formation of a thick layer of decaying organic matter on the bottom (direct observation). Contrarily, the convex side (station 1) was characterized by the presence of the thalweg track, a deep scour hole, higher flow rates (up to 1.1 m s^{-1}) and erosion processes (stronger during the flooding). Actually, the left river bank has been eroded several meters throughout some months (Figures A1a– A1d). Additionally, we detected the occurrence of a secondary recirculation cell on this side of the meander (Figures 3b and 3e). As expected, this recirculation cell was more intense and outstanding during the high-water period. In this physical context, it is noteworthy that only two bed sandy-patches were recorded in the meander. This probably occurred because on the convex side the sand remains in suspension due to the higher flow conditions (Figure 5a) while on the opposite side (backwaters) the thick layer of decaying vegetation prevented the formation of bed sandy-patches.

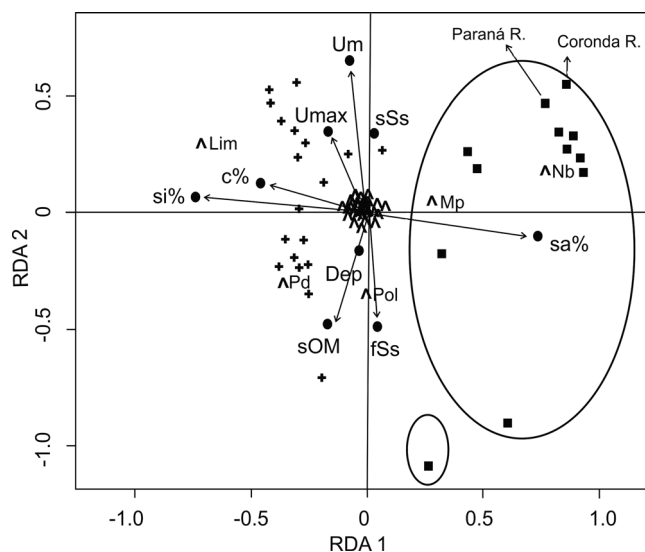The above described hydraulic configuration and geo-morphological dynamics

Figure 8. Redundancy analysis (RDA) ordination diagram showing samples and explanatory variables (habitat features). Um: mean water velocity; Umax: maximum water velocity; sa%: percentage of sand; si%: percentage of silt; c%: percentage of clay; sSs: suspended sand sediments; fSs: fine sediments in suspension: sOM: suspended organic matter; Lim: *Limnodrilus* sp.; Pr: *Pristina* sp.; Pd: *Paranadrilus descolei*; Pol: *Polypedilum*; Nb: *Narapa bonettoi*; Mp: *Myoretronectes paranaensis*; Caret symbol: benthic species; Black square: sandy-patches; Addition symbol: silt/clay sediments.

Table 4. Pearson's Correlations Among Habitat Variables and RDA Axes[a]

	RDA1	RDA2
Um (m s^{-1})	−0.07	0.63
Umax (m s^{-1})	−0.17	0.35
Depth (m)	−0.04	−0.18
Sand (%)	0.74	−0.1
Silt (%)	−0.74	0.07
Clay% (%)	−0.47	0.13
sSs (mg L^{-1})	0.03	0.35
fSs (mg L^{-1})	0.05	−0.49
sOM (gC%)	−0.18	−0.48

[a]See references in caption of the Figure 8.

had significant ecological implications. In this regard, a significant difference in benthic abundance and composition was noticed between sampling stations 2-3-4 (concave side) and the station 1 (Table 3). The backwater areas have been characterized by slow currents, silt substrates and shallow water. They are known to be very rich in food organisms and density which could contribute to the overall productivity of the whole system [*Sheaffer and Nickum*, 1986; *Buffagni et al.*, 2000]. Besides, the main ecological attributes (number of species, diversity, evenness and density) were significantly lower at the sampling station 1 (Table 2), where the dominant species was *Limnodrilus* sp (Haplotaxida, Tubificidae). Hence, a great physical heterogeneity was evident in the pool area, which has been responsible for several changes in biota. This finding is supported by *Sukhodolov et al.* [2015]. These authors associated more complex hydraulic habitats with more population densities and diversity in a meander bend.

In short, at this relatively small spatial scale (pool area) there is a noteworthy linkage among hydraulics, morphology and ecology. While this linkage has not been described previously in minor channels of large floodplain rivers, it has been reported by the HSE model [*Statzner et al.*, 1988; also see *Brooks et al.*, 2005] as well as by other authors in diverse lotic environments [e.g., *Thoms and Parsons*, 2002; *Hannah et al.*, 2004; *Vaughan et al.*, 2009; *Sukhodolov et al.*, 2015]. Besides the HSE, our results are also supported by the predictions of the RES model [*Thorp et al.*, 2006]. According to tenet 4 of the latter, diversity at the pool slackwater area should be higher since slackwaters are hydrological retention zones ("storage sectors" or "dead zones" [*Thorp and Casper*, 2002]); this was exactly our finding.

4.3. Spatiotemporal Scale: Hydro-Geomorphic Patches
4.3.1. Sandy-Patches Location
The bed sediments in the Catarata stream are mainly composed of silt and clay admixtures, greenish gray color, dark gray silt and a percentage of organic matter at different degrees of decomposition [*Iriondo and Paira*, 2007]. Otherwise, the main channel of the Paraná River and major branches such as the Coronda River, flow on a broad and thick layer of about 40 m formed by quartz sand [*Iriondo*, 2007]. Through the bathymetric mapping we found a great difference in depth (elevation) between the Coronda and Catarata beds. The bottom of the Catarata stream is located 9 m above the Coronda River, preventing the massive ingression of sand bedload transported from the Coronda River. However, a detailed analysis (sampling station by sampling station) revealed the presence of several bed sandy-patches in the Catarata stream, mainly composed of medium-size sands (Table 1). Mostly these sandy-patches were located at the cross section B of

Table 5. Density Ranges of the Dominant Taxonomic Groups Forming Both Invertebrate Assemblages

	Family	Genus	Species	Density Range (ind. m^{-2})
Active bed assemblage	Narapidae	*Narapa*	*N. bonettoi*	0–5644
	Retronectidae	*Myoretronectes*	*M. paranaensis*	0–659
	Chironomidae	*Polypedilum*	sp.	0–496
	Tripylidae	*Tobrilus*	sp.	0–48
	Otoplanidae	*Itaspiella*	*I. parana*	0–48
	Chironomidae	*Tanypodinae*	sp.	0–48
Fine sediment assemblage	Tubificidae	*Aulodrilus*	*A. pigueti*	0–2988
	Tubificidae	*Limnodrilus*	*L. hoffmeisteri*	0–2249
	Naididae	*Pristina*	*P. americana*	0–2105
	Naididae	*Paranadrilus*	*P. descolei*	0–1992
	Tubificidae	*Limnodrilus*	*L.udekemianus*	0–1198
	Naididae	*Pristina*	*P. osborni*	0–900
	Naididae	*Pristina*	*P. acuminata*	0–562
	Chironomidae	*Polypedilum*	sp.	0–512
	Naididae	*Amphichaeta*	*A. americana*	0–498
	Naididae	*Stephensoniana*	*S. trivandrana*	0–145

the confluence, increasing in number from 2 to 6 during the flooding stage. Otherwise, water velocities recorded at cross section B were considerably lower than at cross section A (Figures 2 and 4), during both hydrological periods (0.13 to 0.3 m s^{-1} and 0.23 to 0.43 m s^{-1}, respectively; Table 1).

On the other hand, the momentum ratio (Mr) was always larger than 1 indicating that the momentum flux recorded at cross section B was notoriously lower than at cross section A, during both water levels (see Table 1 and Mr equation). This fact should originate superelevation of water levels and subsequent reductions of velocities (Table 1) and hydraulic slopes at and upstream cross section B. Though water levels and slopes were not measured in this study, superelevations upstream of confluences are well known since long time ago [e.g., *Chow* [1959] nicely describes this type of effects for the confluences of the Missouri with the Kansas rivers and the Mississippi with the Ohio rivers). More recently, *Meade et al.* [1991] studied water superelevation upstream the confluences of the Amazon River with its main tributaries. Similarly, *Wang et al.* [2016] investigated the same phenomena in laboratory experiments and field measurements. In brief, the flow configuration along the western branch (low momentum fluxes, water superelevations and decreasing velocities), explains the massive sedimentation of suspended sand and the resulting patches emergence at cross section B, particularly during floods when most sand is transported. In addition, *Rhoads and Kenworthy* [1995] found that when the momentum ratio (Mr) > 1 (such was the case in the studied confluence), flow immediately downstream of the confluence resembles movement of water through a meander bend (Table 1). Under these conditions, a single large helical cell exists within the flow in the downstream channel (see Figure 4). The large helical cell lies inward of the mixing interface between the converging streams.

A similar hydraulic configuration was recorded by *Riley and Rhoads* [2012] in a relatively comparable confluence, where the development of flow stagnation was found upstream of the confluence, near the junction apex, along with deflection of the main flow by the tributary flow.

According to the RES model, those sandy-patches could be also named as micro "hydro-geomorphic patches," which result from shifts in hydrological and geomorphic conditions under different flow regimes, flow histories and stream hydraulics. Hydro-geomorphic patches are linked to the frequency, intensity and severity of discharge fluctuations [e.g., *Szczerkowska-Majchrzak et al.*, 2010; *Winemiller et al.*, 2010; *Rolls et al.*, 2012]. These patches were colonized by the above mentioned "active bed assemblage" (Table 5; Figures 7b and 8), typically recorded in the Paraná and Coronda Rivers [e.g., *Takeda et al.*, 2001; *Ezcurra de Drago et al.*, 2007]. This invertebrate assemblage lives in environments with very scarce organic matter concentrations (food) and sandy sediments [*Takeda and Fujita*, 2004]. Its species have very low biomass, resulting in poor energy resources available for higher trophic levels [*Ezcurra de Drago et al.*, 2007]. In contrast, the "fine sediment assemblage" (Table 5) has been frequently reported in many low-hierarchy channels of the Paraná floodplain and it represents a better food resource for predators belonging to higher trophic levels [*Marchese et al.*, 2002].

The presence of sandy-patches is concurrent with the "river discontinua" concept (RDC) [*Poole*, 2002], since this author proposed that rivers are composed of patchy discontinua where the biota responds to local features of the fluvial landscape. Accordingly, this view of rivers as patchy discontinua was evidently supported by our results. However, this view *per se* says little about how –and from where– invertebrate arrive and colonize the sandy- patches. This fact is discussed in the next section.

4.3.2. Sandy-Patches Dynamics

As previously indicated, an increasing amount of sand in suspension was recorded in the Catarata stream during flooding (Table 1 and Figure 5). This sedimentological fact originated sandy-patches at the confluence and the succeeding colonization by the "active bed assemblage." A possible explanation for this phenomenon was that the sand, as well as the mentioned assemblage, came from the Paraná and Coronda rivers in suspension and in drift, respectively. Thus, we suggest the following sequence of events to explain the sandy-patches formation: (1) when the flow pulse of the Paraná system rises to the crest, it increases the downstream transport of sand in suspension and benthic organisms in drift, from the Paraná main channel, through the Coronda River, up to the Catarata mouth. (2) Both sand and invertebrates in suspension flow into the Catarata stream to finally be deposited at the confluence (2.6 km downstream to the mouth). (3) Then, the natural replacement of one invertebrate assemblage ("fine sediment assemblage") by the other one ("active bed assemblage") takes place. It is well-known that this lateral interaction/connection between the main channel and the floodplain is predicted by

the FPC. Nevertheless, the fauna replacement phenomenon is not a case of study commonly addressed by that concept. Actually, at this specific spatial scale of analysis, an unpredicted drop of diversity and evenness values was detected during the flooding (Table 2). Furthermore, there is no reason to suppose that the massive occurrence of sandy-patches only occurred during the flood pulse; i.e., when the water level overflows its banks. On the contrary, we suggest that this phenomenon could also occur during the flow pulse, i.e., expansion-contraction events below bankfull flooding [*Tockner et al.*, 2000]. In the current study area the reference level is 4.5 m when flow begins to flood the adjacent plain [*Abrial et al.*, 2014]. Thus, the proximity between this reference level and the maximum level recorded in this study (4.79) allows us to suppose that the Catarata stream also transports sand in suspension during the flow pulse. Therefore, we suggest that both interrelated ecological concepts ("flood pulse" and "flow pulse") better explain the recorded assemblage replacements at this specific scale (water level: 4.79 m). Observations like this, highlighted the terms "river complexity" [*Robinson et al.*, 2002] and "riverine complexity" [*Thorp et al.*, 2006, 2008], emphasizing the necessity to integrate concepts and models according to the analysis scales.

Furthermore, it is noteworthy that we recorded sandy-patches colonized by the "active bed assemblage," but they were not necessarily fully colonized. Occasionally, we also registered sandy-patches partially colonized or almost devoid of species (see the small ellipse of the Figure 8). We speculated that this colonization "in progress" can be attributed to a delay between physical and ecological processes, i.e., sediment transport in suspension and benthic dispersion in drift, due to the dominating nonequilibrium processes of this system [*Thorp et al.*, 2006]. Thus, once the sandy-patches are created, a reasonable period is required to guarantee invertebrate colonization. Hence, at this particular spatiotemporal scale the nonequilibrium processes seem to be dominant in the area. In this context, it is suitable to point out the statement by *Wu* [1999]: "equilibrium and nonequilibrium are not absolute and context-free, but relative and scale-dependent."

Finally, the overall results suggest a feasible predominance of stochastic and nonequilibrium processes which maintain the fauna in nonequilibrium state in the Catarata stream. As *Thorp et al.* [2006] proclaimed "a true equilibrial state is problematic, if not inexistent, in river networks because they are open, advective systems subject to major hydrological variations which introduce large measures of stochasticity within patches at various scales."

5. Conclusions

1. Hydrodynamics was the driving force behind the structure patterns (composition and relative abundance) of benthic assemblages in the large floodplain system. However, its effect was dissimilar in the main, major and minor channels of the floodplain. While invertebrates living in minor secondary channels seemed to benefit from the flooding, the density of those inhabiting the main and major secondary channels (stronger bed hydraulic conditions prevailing) declined.
2. A linkage between physical features (local flow configuration, hydrological stage, sediment composition and morphological characteristic) and ecological structure (invertebrate density, diversity, evenness and number of species) was detected between and within morphological units. This linkage allowed us to explain the dissimilar fauna structure detected between the meander and the confluence as well as within the pool area in the meander.
3. The ecological dynamics found in the confluence was basically given by the presence and dissipation of sandy-patches. There was an assemblage replacement detected during the flooding stage. This dynamics of sandy-patches supported the view of the river as patchy discontinua, suggesting that a true state of ecological equilibrium is uncertain, as proposed by certain ecological models (e.g., RES).

Appendix A

Morphological changes in the circular-meander were recorded all along this study. Changes were originated by erosion processes, which scoured several meters of silt and clay material on the left bank (Figure A1).
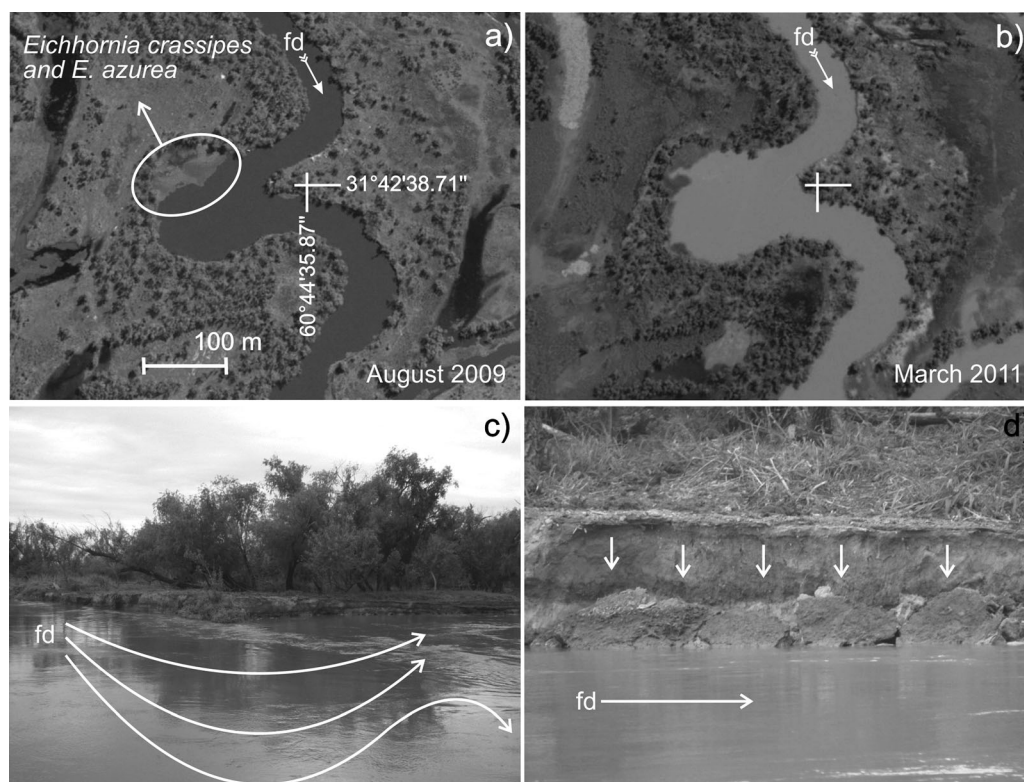
Figure A1. Selected meander bend. (a, b) satellite imagines showing the morphological erosion in the convex side of the meander bend; (c) superficial flow lines at the meander convex side; and (d) bank collapsed close to the sampling station 1.

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