OPINION PAPER

Floods increase similarity among aquatic habitats in river-floodplain systems

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Abstract During low water levels, habitats in river-floodplain systems are isolated from each other and from the main river. Oppositely, floods tend to connect water bodies with distinct hydrological characteristics and, as a result, ecological processes and biological communities tend to be more similar among the distinct habitats that comprise a river-floodplain system. Based on a literature review and also using unpublished data obtained in tropical floodplains, the aim of this paper is to highlight the effects of floods as a process that reduce spatial variability. The usual negative relationship between the coefficient of variation of any ecological indicator (e.g., chlorophyll-*a* or total phosphorus) and water level is the main result demonstrating a reduction in spatial variability due to floods. Considering physical, chemical or biotic data gathered in distinct habitats within the floodplain, this pattern was found in temperate and tropical regions, subjected to distinct levels of anthropogenic impacts, and at different spatial extents. The main mechanism that accounts for this pattern may be stated as follow. During low water level, the biological communities of each habitat in the floodplain (e.g., lagoons, backwater, streams) follow distinct temporal trajectories due to the effects of local driving forces (e.g., an efficient predator trapped in a lagoon but not in another). Management plans and biodiversity conservation in river floodplain systems will benefit by considering the effects of flood homogenization and increased connectivity peculiar to these unique ecosystems.

Keywords Flood pulse · River-floodplain systems · Biodiversity

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Introduction

Hydrological regime is considered the key factor driving ecological functioning and biodiversity patterns in river floodplain systems (RFSs) (Junk et al., 1989; Neiff, 1990; Bunn & Arthington, 2002). Due to the dramatic rates of river regulation and habitat degradation worldwide (e.g., Agostinho

et al., 2000; Tockner et al., 2000a, b), investigations concerning how hydrological regimes affect attributes of floodplain systems, especially biodiversity, have become a central issue for river management in the last years.

Many RFSs have been studied intensively in the last two decades (see, for example Gopal et al., 2000; 2001) and different causal relationships between hydrology and ecosystem attributes have been proposed. Nevertheless, few patterns, that can be generalized for a wide variety of systems, at different latitudes and scales, were proposed (e.g., Carvalho et al., 2001; Ward & Tockner, 2001). In addition, the processes regulating biodiversity in these systems are not still well understood (Neiff, 2001).

The relationship between water level and landscape heterogeneity were studied in Neotropical (Furch & Junk, 1985; Hamilton & Lewis, 1990; Bozelli, 1992; Thomaz et al., 1997) and north temperate floodplains (Tockner & Ward, 1999; Tockner et al., 2000a, b; Ward & Tockner, 2001; Amoros & Bornette, 2002). In both regions, the among habitats (i.e., river channels, secondary channels and lagoons) variability of limnological variables (e.g., nitrate, conductivity, nutrients and chlorophyll-*a*) decrease with increasing water levels, suggesting that floods increase similarity among RFSs habitats. We consider this a good candidate to be a general pattern for RFSs.

In this paper we show an increase in homogeneity between river channel and a diverse array of floodplain aquatic habitats during floods through analyses of physical, chemical and biological data from Neo-tropical and temperate floodplains. Both empirical data and literature values are part of this analysis. Our goal is to show that the increase in habitat similarity during floods (or "flood homogenization") can be considered a general pattern in RFSs. In addition, we consider the probable causes of this pattern and its consequences on attributes of RFSs, especially biodiversity maintenance. We believe that our theoretical framework will have high potential for the management and conservation of RFSs integrity.

The pattern

RFSs are characterized by high habitat heterogeneity (e.g., Junk et al., 1989; Tockner et al., 2000a, b;

Drago et al., 2004). Besides several ecotonal habitats, which are found in the aquatic terrestrial transition zone (ATTZ) (Junk et al., 1989), RFSs have a wide variety of aquatic habitats, such as temporal and permanent lagoons, channels, backwaters, shallow lakes, sloughs, and the main river channel. The diversity of those habitats is of key importance for maintenance of high biological diversity in the system as a whole (i.e., gamma diversity).

Higher similarities among aquatic habitats during floods than during non-flood periods were found in several floodplains. In its most simple form, this homogeneity was first described as the existence of high similarity in physical, chemical or biological features between the main river and the backwaters of its floodplain (e.g., Furch & Junk, 1985, in the Amazonian floodplain; Hamilton and Lewis, 1990, in the Orinoco River floodplain; and Bozelli, 1992, in the Trombetas River floodplain). It was also explicitly quantified by the first time in the Upper Paraná River floodplain, when Thomaz et al. (1997) and later Agostinho et al. (2000), recognized the "homogenization effect of floods" using multivariate analyses.

In a non-exhaustive survey in the literature (Table 1) we found several other examples that illustrate the pattern. These examples show that it was consistently repeated in different spatial extents in several ecosystems.

A first group of factors, which tend to be more similar during the flood events, are the physical and chemical factors. Among these factors, nutrients (both nitrogen and phosphorus) and conductivity have been considered in several studies (Table 1). Similarity of chlorophyll-*a* concentrations of lagoons and the river channel also increases during flood periods (Table 1).

In addition to the limnological characteristics cited previously, floods seem to decrease community turnover or beta diversity. The composition of phytoplankton, zooplankton, fish and macrophytes are less similar among habitats during low water, but they are more similar during floods. Spatial variability in planktonic richness and abundance is also lessened by flood events (Table 1).

Studies indicate that the homogenization effect of floods operate at different spatial extents. For example, at the scale of whole waterbody, different

Table 1 Data confirming the increase of similarity within and between habitats during floods recorded in several floodplains

Floodplain	Factors studied	Ecosystem/community responses
Amazon (Brazil) (pristine)	Abiotic	DOC, inorganic carbon and electrical conductivity values were more heterogeneous among stations of a same lake and between the lake and the river during low water (1)
Orinoco (Venezuela) (pristine)	Abiotic and biotic	Chemical characteristics, suspended load and plankton composition are more dissimilar among lakes during low water (2); structure of fish assemblage in lakes tend to converge as flood water enters lakes (3)
Trombetas (Brazil) (subject to impact by bauxite tailings)	Abiotic and biotic	Limnological abiotic factors, such as phosphorus, nitrogen and chlorophyll-*a* concentrations (4), phytoplankton (5) and zooplankton (6) densities are more similar between sampling stations of a same lake and between the lake and Trombetas River during high water
Pantanal – Piraim River (Brazil) (pristine)	Abiotic	The coefficient of variation of limnological factors, such as phosphate and ammonium, obtained in different sampling stations of a inundation field are lower during inundations (7)
Pantanal – Paraguay River (Brazil) (pristine)	Abiotic	Electrical conductivity and oxygen are more similar between a lake and the river after connection (8)
Upper Paraná (Brazil) (subject to water level control by reservoirs' operation)	Abiotic and biotic	Limnological abiotic factors (e.g., phosphorus, nitrogen, chlorophyll, oxygen etc.), summarized through principal component analyses (9), and the structure of zooplankton (10) and fish (11) assemblages are more similar among lagoons and between lagoons and Paraná main channel during high waters
Middle Paraná (Argentina) (subject to low degree of water level control)	Biotic	Composition of aquatic macrophyte assemblage in different lagoons are more dissimilar during low waters (12)
Mogi Guaçu River (Brazil) (impacted by pollution and deforestation)	Abiotic and biotic	During drought period the littoral region of a lagoon differed more from the other sites, indicating a higher within lagoon heterogeneity during this period (13); similarity of the fish assemblages between lagoons were higher at the wet season (14);
Acre River (Brazil) (pristine)	Abiotic	8 limnological parameters (temperature, conductivity, total seston, ammonium, nitrate, phosphate, silicate and total pigments) out of 11 analyzed in three sampling stations of Amapá lake had higher coefficient of variation during low water period (15);
Danube (Austria) (subject to high degree of water level control)	Abiotic	Coefficient of variation of nitrate and chlorophyll obtained in different sites (between 35 and 49) are lower during high water (16)
Illinois (USA) (subject to high degree of water level control)	Biotic	Nitrification and denitrification are more variable among sites during low water periods (17)
Mississippi (USA)	Biotic	Annual floods homogenize the floodplain and promote connectivity to various degrees, allowing for fish exchanges between river and floodplain that directly affect community composition (18)

(1) Funk & Junk (1985); (2) Hamilton & Lewis (1990); (3) Lewis et al. (2000); (4) Panosso and Kubrusly (2000); (5) Huszar (2000); (6) Bozelli (1992, 2000); (7) David (2001); (8) Calheiros & Hamilton (1998); (9) Thomaz et al. (1997); (10) Bonecker et al. (1998); (11) Veríssimo (1994); (12) Neiff (1979); (13) Taniguchi et al. (2004); (14) Meschiatti et al. (2000); (15) Almeida (2000); (16) Tockner et al. (2000a, b); (17) M. Lemke (unpublished data); (18) Miranda (2005)

sampling sites at the same lagoon tend to be more similar during periods of high water (e.g., in the Pantanal and Batata Lake – Table 1). At a broader spatial extent, different lagoons of a same floodplain and the lagoons of a floodplain and their main river (e.g., Orinoco, Paraná, Amazon, Danube – Table 1) tend to be more similar during high water periods.

To illustrate the occurrence of this pattern across different spatial extents we used the coefficient of variation (CV) in limnological data obtained in (i) three sampling stations at a single lake (Lake Batata) every three months during 8 years and (ii) in ten lakes and two sampling sites of Trombetas River obtained in a single year at the high and low water levels. All lakes, including Lake Batata, are in the same region (Amazon) and they are connected with the Trombetas River.

For Lake Batata, a significant negative relationship ($P < 0.05$) was observed between water level and CV values of water temperature, suspended matter, site depth, conductivity, pH and chlorophyll-*a* (Fig. 1). These results show that high water levels create more similar sites within this lake.

The same pattern was observed at a broader spatial extent, considering the data for the 10 lakes plus Trombetas River sites. Coefficients of variation estimated for dissolved organic carbon,
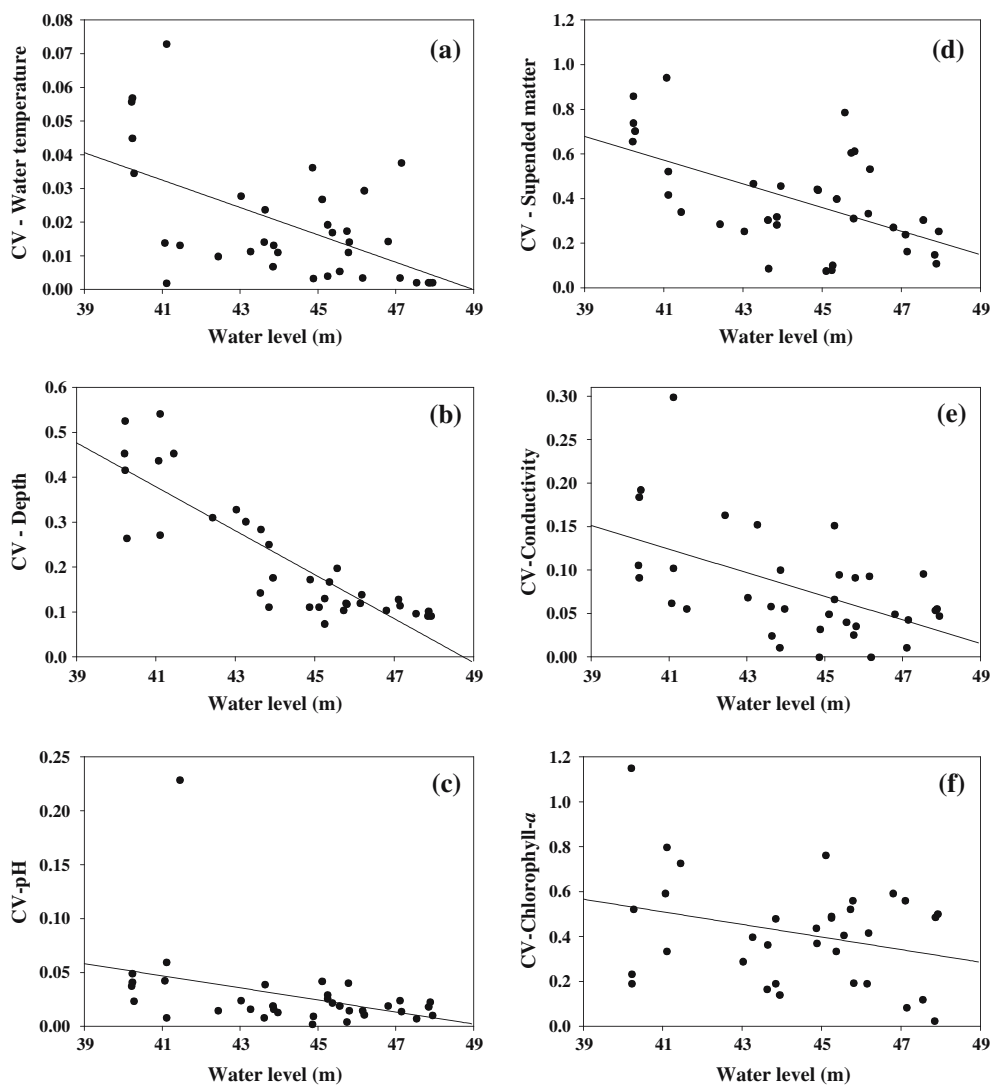

Fig. 1 Coefficients of variation (CV) estimated for the limnological variables obtained in three sampling sites of Lake Batata (Trombetas River floodplain, Amazon) plotted against water level. Each point represents the spatial CV estimated with the data obtained in these three sampling sites in the same day

dissolved phosphorus, dissolved nitrogen, conductivity, turbidity, depth, Secchi disk and suspended matter were higher during low water period (Fig. 2). Thus, lakes are more similar among themselves and with Trombetas River when they are connected.

The pattern seems to occur also in RFSs subjected to different degrees of conservation (Table 1). For example, the Pantanal, Amazon and Orinoco are representative of relatively pristine RFSs, whereas Paraná and Danube are subject to impacts associated with water level control. The homogenization effect was also observed in lakes subject to other types of impact, as is the case of Lake Batata (Trombetas River), which is highly impacted by bauxite tailings (Roland, 2000; Guenther & Bozelli, 2004).

Main mechanisms

Trying to untangle the ecological complexity of RFSs and the main mechanisms that produce the patterns found in nature are not easy tasks. Nevertheless, we present empirical evidence from several sources that suggest some explanations as
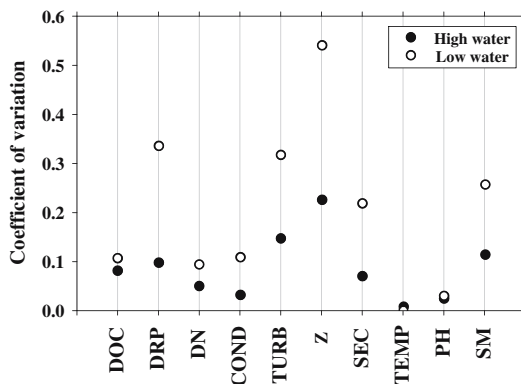

Fig. 2 Coefficients of variation estimated for selected limnological variables obtained in ten lakes in the Trombetas River floodplain and in the Trombetas River main channel (Amazon) in the high and low water periods. Each point represents the spatial CV obtained among these ten lakes and Trombetas River in one sampling period. DOC = dissolved organic carbon; DRP = dissolved reactive phosphate; DN = dissolved nitrogen; COND = conductivity; TURB = turbidity; Z = depth; SEC = Secchi disk; TEMP = temperature; PH = pH and SM = suspended matter

more plausible than others. We first hypothesize that these patterns are due to (i) increasing dissimilarities during low water levels caused by local driving forces and (ii) increasing connectivity during high water periods. We will discuss these factors separately below.

The influence of local driving forces during low waters

The floodplain aquatic habitats are isolated from each other and subject to local driving forces during low water periods (Thomaz et al., 1997; Camargo & Esteves, 1995; Tockner et al., 1999; Lewis Jr. et al., 2000; Carvalho et al., 2001). These driving forces inducing heterogeneity include: (i) water inputs from lateral tributaries and/or seepage leading to localized physical and chemical characteristics that are basin-specific; (ii) wind and animal induced sediment re-suspension, which affects water bodies according to their morphometry, and (iii) differences in ecological succession. These local forces act with different intensities in the floodplain landscape, thus creating habitats with different characteristics.

Concerning aspect (i), the water's origin determines the water temperature, turbidity and nutrient content, which greatly influence habitat heterogeneity, plant and animal recruitment, and ecosystem productivity. For example, in the Orinoco floodplain, a great heterogeneity develops at smaller scales during the dry season, when the floodplain is fragmented. This time, as can be seen from major ion data, shows a significant but variable contribution of local waters (rain and runoff) (Hamilton & Lewis, 1990). The importance of local tributaries contributions has been demonstrated in several other RFSs (Forsberg et al., 1988; Schemel et al., 2004; Souza-Filho et al., 2004; Thomaz et al., 1997). Data from the Amazon floodplain show that the percentage of local water in a lake, during low waters, depend on the ratio of drainage basin area (BA) to lake area (LA): the greater the BA: LA ratio the more river water was apparently flushed out of a lake and replaced by local water during low waters (Forsberg et al., 1988). The examples from these large basins highlight the importance of lateral tributaries as sources of variation in the floodplain

habitats and suggest that they may contribute to a large extent to increase the habitat heterogeneity during low waters in RSFs.

In addition to lateral flow, the water of floodplain habitats also originates from seepage. This water has chemical features that are quite different from that of the river channel and it affects the habitats where it emerges upwells. The groundwater is loaded with high concentrations of bioavailable solutes in the hyporheic zone and it affects the production and biodiversity of benthos and riparian vegetation. Dynamic convergence of aquifer-riverine components adds physical heterogeneity and functional complexity to floodplain landscapes and the major landscape features of alluvial floodplains include a dynamic mosaic of stream channels and wetlands fed by hyporheic flow (Standford & Ward, 1993). Results obtained in the Val Roseg floodplain (Switzerland) indicate that the concentration of nutrients have small coherence (i.e., low synchrony) in lateral water bodies due to dominance of local hydrological and/or biogeochemical processes, like groundwater upwelling (Tockner et al., 2002). It has been shown that aquatic floodplain habitats that are fed mainly by deep and shallow alluvial groundwater, hyporheic exfiltration, have high variability in terms of both substrate characteristics and faunal compositions (Brunke et al., 2003). Accordingly, Gurnell & Petts (2002) considered a variable mix of river water with surface and groundwater among the causes for vegetation heterogeneity in several European RFSs. It is expected that such increase in habitats heterogeneity, caused by hyporheic water upwelling is more accentuated during low water phases, when flow (and thus, surface connectivity) is lower. In summary, lateral tributaries and hyporheic water largely contribute to the high habitat diversity found in RFSs and such heterogeneity is maintained especially during low water periods.

The importance of wind, in combination with morphometry, (aspect ii above) was shown in the Orinoco floodplain. There an important transition occurred when the mean depth of a lake decreased to such an extent that fine sediments on the bottom of the lake were resuspended by wind-generated currents (Lewis Jr. et al., 2000). In addition to depth, effective fetch, in combination with wind velocity, was important to cause sediment resuspension during periods of isolation (Hamilton & Lewis, 1990). These internal loadings, caused by sediment resuspension, are very important in floodplain lagoons during low water periods (Carvalho et al., 2001; Thomaz et al., 1997). In fact, resuspension appears to drive plankton succession during these periods (Train & Rodrigues, 2004).

Resuspension of sediments in shallow lakes may also be caused by other factors, such as animals. In the Upper Paraná floodplain, shallow temporary lagoons (depths < 0.5 m) are subject to cattle and capybaras (the rodent *Hydrochoerus hydrochaeris*) trampling, leading to the highest values of conductivity and nutrient concentrations found among all floodplain water bodies during low water periods (Pagioro et al., 1997; Thomaz et al., 1997; Okada, 1995; Okada et al., 2003).

The morphometry of the water body affects the assemblages of large-bodied organisms. In the Orinoco RFS, the structure of fish assemblages has been largely explained by water transparency that is directly affected by lake area and depth (Rodríguez & Lewis Jr., 1997). In lagoons of the Upper Paraná RFS, depth is an important determinant of fish assemblage structure (Okada, 1995; Okada et al., 2003) and, together with littoral slope, of aquatic macrophyte assemblage structure (Santos, 2004). Floodplain lagoons vary widely in morphometry and wind exposure (fetch) and thus their physical and chemical, as well as biological characteristics are more variable during low water periods.

Another important ecological factor leading to higher dissimilarities in aquatic habitats during low waters is ecological succession (aspect iii). After isolation, each aquatic environment and even specific regions of a same environment follow their own succession whose sequence depends mainly upon the identity of the propagules transported to the water body during the last flood and on the response of these organisms to the localized environmental characteristics that will predominate in the lagoons. This individualistic (Gleasonianan) succession leads to the unique community development in each habitat subsequently creating increased dissimilarity during low waters. Thus, chance (or stochastic events ("who arrives there") may drive different ecological successions in the habitats.

Even considering the influence of a shared regional species pool, the magnitude of the processes that determine assemblage structures (e.g., competition and predation) will differ from lake to lake, even if we consider a similar start point (Fig. 3). If, during low water levels, we expect a high inter-habitat heterogeneity, we also can infer that, during this period, there is a low level of ''spatial predictability'' or spatial autocorrelation in the attributes analyzed. Therefore, knowing the attributes of a given lagoon will not help to predict the attributes of another lagoon near to the first. After floods (overflow), we expect a time lag until the effects of homogenization become apparent. This time lag will depend mainly on the intensity of the floods and on the rate of dispersion/migration of the different species that occur in the RFSs. Also, the increase in dissimilarity, after isolation, will be not instantaneous. This time lag will depend, among many other factors, on the intensity of drought and on the species composition that was assembled during the previous high water level period (Fig. 3).

Evidences of the different assemblage trajectories (as seem in Fig. 3) come from several taxonomic groups. For example, the rate of succession of vegetation was found to be different in several RFSs across Europe (Jarolimek et al., 2001; Gurnell & Petts, 2002). In the Middle (Neiff, 1979) and Upper Paraná RFS (Santos & Thomaz, in press), the differences in the structure of aquatic macrophyte communities observed among lagoons increased during low waters. This higher dissimilarity depended on the successional course in combination with the reproductive rate of the species and waterbody morphometry (especially depth and wind exposure; Neiff, 1979). Since floods may impede the regrowing and reestablishment of some species of aquatic macrophytes, the interval between floods is also an important determinant of succession of macrophytes in floodplain lagoons (Maltchik et al., 2004). Differences in aquatic plant cover and species composition may lead to different plankton (Cremer et al., 2004; Lansac-Tôha et al., 2004; Izaguirre et al., 2004) and fish assemblages (Pelicice et al., 2005). Thus, the effects of drought increasing the heterogeneity of plankton and fish communities may be also mediated by changes on plant communities.
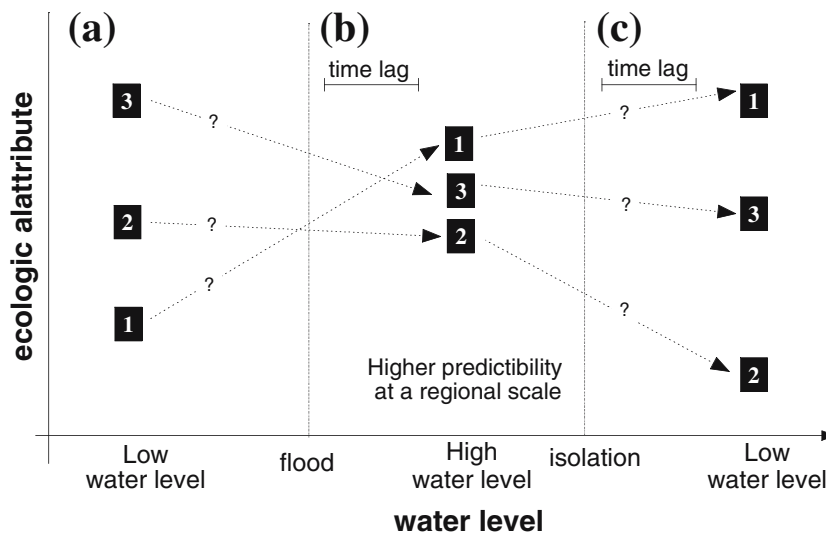

Fig. 3 Hypothesized spatial variability in floodplains along a hydrological cycle. Predicting the temporal trajectories and the mean values of the attributes for every lake in the floodplain (numbered squares) is not a simple task during low water periods (scenario a). However, the high level of spatial autocorrelation caused by floods may increase substantially our predictability capacity: knowing the attributes of a community in a given lake permits the prediction of these attributes in the other lakes (scenario b). Again, after isolation, spatial variability increases (each community may follow a distinct path) due to the local driving forces (e.g., a large number of a predator trapped in one lake but not in the others; scenario c). There is a time lag that contributes to the transitions between scenarios

For fish communities, the similarity between lagoons is low after isolation and a conspicuous difference from the original fauna was found during that period (Rodríguez & Lewis Jr., 1994; Okada et al., 2003). Biotic interactions (e.g., predation by fish and birds and competition) played a major role in these fish assemblages, leading to distinct temporal trajectories in different lagoons of a same RFS (Okada et al., 2003). In two lakes of the Orinoco RFS, the magnitude and direction of the seasonal change of the fish assemblages during the dry season were comparable across years but this temporal change was small relative to differences among lakes (Rodríguez & Lewis Jr., 1994). It shows that in lakes of this RFS there is a strong deterministic component structuring fish assemblages, but it leads to different assemblages in separated lakes. In other words, local processes operating at the habitat scale are the major determinants of the structure of biological communities during the dry season (Rodríguez & Lewis Jr., 1997).

Thus, we may also assume that different paths lead to different communities in water bodies during the low water phases, contributing to increased dissimilarities among habitats (i.e., increased beta diversity).

The influence of regional driving force (flooding) during high waters

Increase in river water level enhances the connection between the river and the floodplain aquatic habitats as well as among floodplain habitats. During high water phase, horizontal fluxes are produced from the river course to the floodplain (Neiff, 2001). This increase in connectivity enhances the exchange of water, sediments, minerals and organisms among the different habitats in the floodplain (Agostinho & Zalewski, 1995; Lewis Jr. et al., 2000; Neiff, 2001; Aspetsberger et al., 2002; Zalocar de Domitrovic, 2003; Bonecker et al., 2005). Planktonic organisms may also move freely and passively within and between aquatic habitats. For example, fish larvae have passive dispersion towards the floodplain water bodies during flood pulses (Araujo-Lima & Oliveira, 1998; Nakatani et al., 2004).

Even conspicuous spatial differences within individual lagoons (e.g., comparing areas covered with aquatic macrophytes with bared areas) may be reduced due to the homogenization effects of floods. For example, non-planktonic rotifers have been found in the pelagic zone of floodplain lagoons during high waters as a result of interaction with the littoral during these periods (José de Paggi, 1993; Bonecker & Lansac-Tôha, 1996; Garcia et al., 1998). Similarity between river channel and floodplain lagoons also increases for this group during high waters due to increased connectivity between both habitats (Bonecker et al., 1998). The importance of horizontal exchanges during floods was shown in the Upper Paraná RFS, where the highest species richness of zooplankton was found in connected lagoons, subject to greater water exchanges than isolated lagoons (Aoyagui & Bonecker, 2004).

Large-bodied organisms move passively or actively during high water periods. For example, propagules of aquatic macrophytes disperse passively (e.g., free floating species, that are common in RFSs; Thomaz et al., 2004) but fish disperse actively when the habitats are connected (Rodríguez & Lewis Jr., 1994; Agostinho & Zalewski, 1995). These examples highlight the importance of floods for passive or active exchanges of organisms and propagules among RFS water bodies.

Nevertheless, the increase in similarity between the river channel and floodplain habitats depends on overbank flooding. On the other hand, the ecosystem expansion without overbank flooding ("flow pulses", according to Tockner et al., 2000a), may lead to high similarities in the two first scales considered (within floodplain aquatic habitats and within different sites of a same lagoon) but not between these water bodies and the river channel. These predictions still need to be tested.

Possible consequences for biodiversity maintenance

Understanding the consequences of flooding for biology within a RFS, including dispersal, adaptation and ecological succession is of paramount importance to develop efficient conservation and management strategies (Ward & Tockner, 2001). In this sense, our survey in the literature may

bring important insights because they were derived largely from a variety of near natural South-American river-floodplain systems.

It has been proposed that species richness is maximized in RFSs due to the intermediate degree of three inter-related variables: disturbance (Intermediate Disturbance Hypohesis, *sensu* Connell, 1978), ecotone occurrence and hydrological connectivity (Ward & Tockner, 2001). At low connectivity, species diversity should be reduced by the absence of the fluvial dynamics that sustains a diversity of successional stages within RFSs, whereas excessive connectivity will keep all communities in pioneer stages (Ward & Tockner, 2001). Other studies have found that diversity of different groups (fish, macrophytes, macrozoobenthos and amphibians) peaks differently across the gradient of connectivity intensity (Tockner et al., 2000a).

Despite these considerations, we emphasize that even if the highest diversity is reached at intermediate levels of disturbance, intensive floods (which promotes high connectivity) are important for exchange of propagules, nutrients, and organisms among habitats. Such exchanges during high waters (see Lewis Jr. et al., 2000), are mandatory to keep high biodiversity unique of RFSs. This is because the exchanges increase the probability of rare species to disperse and colonize new sites during floods. This statement is even more important if we consider that some species need specific types of habitats to succeed. For example, the successful recruitment of the tree *Calophyllum brasiliense* in the Meander forest (Amazon) requires dispersal to early successional habitats (King, 2003). It is also demonstrated that fish larvae depend on lagoons with appropriate habitat complexity to succeed (Agostinho & Zalewski, 1995; Nakatani et al., 2004).

The short-term exchanges following events of high connectivity cause, at first, a decrease in beta diversity of RFSs (the ''homogenization effect''). Nevertheless, they are key to keep long-term high species richness of floodplains (gamma diversity), complementing the role of intermediate disturbances. Consequently, it is expected that artificial flow reductions that lead to reduced connectivity, have serious deleterious effects upon long term RFS ś biodiversity. The importance of connec-

tivity has lead to its adoption as a natural guideline to design strategies for RFSs rehabilitation (Pedroli et al., 2002). It has been observed, for example, that this process has a key importance in the recover of Lake Batata (Trombetas River – Amazon) from the impact it suffered with bauxite tailings. It is caused basically by organic matter and organism inocula exchanges between the lake and the Trombetas River main channel (RL Bozelli, unpublished data).

It is well known that flow is often a principal river attribute that is changed by different watershed uses (e.g., reservoir construction, hydroways construction, levee alterations and water obstruction; Bunn & Arthington, 2002; Sheldon et al., 2002; Souza-Filho et al., 2004). Great dissimilarity of the fish assemblages among lagoons in the Upper Paraná RFS was recorded after a long period of reduced connectivity, caused by flow reduction associated with reservoir operations (Oliveira et al., 2001). These findings show that the impacts of reservoir operation upon fish assemblages are in accordance with our expectations that in the absence of floods, floodplain habitats are more heterogeneous. Although flow alteration may affect differently the groups of organisms (e.g., long lived aquatic macrophytes versus short lived phytoplankton), interruption of connectivity is deleterious to the whole biodiversity in medium or long term periods due to the reduction in propagules exchanges between habitats. In addition, prolonged low water periods may lead to maximization of competitive exclusion, leading to further local extinctions. It has been shown, for example, that in disconnected forests competitive species may dominate in the absence of floods (van Looy et al., 2004) whereas when floods occur coexistence of several species is possible (Deiller et al., 2001). Accordingly, investigations in a South Brazilian floodplain lagoon showed that the absence of dominance in aquatic macrophyte community was associated with highest number of flood events (Maltchik et al., 2005).

Flow reduction may also contribute to biological invasions by alien species that can cause extinction of native species (Bunn & Arthington, 2002; Agostinho et al., 2005). Large-scale surveys carried out in the Paraná basin showed that

introduced fish succeed in basins with high endemism and/or regulated by dams (Agostinho et al., 2005). Thus, considering that species introductions are considered one of the main causes of extinctions (Clavero & García-Berthou, 2005), the increase in exotic species following flow regulation may be considered a matter of concern for biodiversity maintenance in RFSs.

Complementarity is an important and innovative concept in conservation biology (e.g., Justus & Sarkar, 2002). Basically, it is a measure of how an area possesses species not yet found in other areas. Thus, some areas with low species richness may have high complementarity value due to the presence of rare species. Paradoxically, long droughts may increase the number of areas to be "reserved" (network length) due to the high spatial turnover in species composition during these periods. However, we suspect that the higher spatial turnover during low water periods is associated with low species richness. Thus, this innovative concept should be applied with caution to design networks of reserves in floodplain landscapes. It will be interesting to compare the spatial configuration and the length of the networks that could be generated in high and low water periods.

Perspectives

Based on several examples collected in different spatial scales and several floodplains, we suggest that the "homogenization of habitats" following floods may be considered a general pattern. The homogenization flood effect is derived from increased connectivity (regional driving force) during high waters, complemented by high isolation (when local driving forces dominate) during low waters. In this way, we suggest as future possible fields for research: (i) analyses of similarity employing multivariate methods in different periods of the flood pulse; (ii) specific studies of organisms movement across river and floodplain habitats during high waters and (iii) studies of succession dynamics and how it affects alpha and beta diversity of the floodplain habitats during low waters. Given the above links between these processes and RFSs' biodiversity, we believe that these approaches would be helpful in

conserving the unique richness of these fragile and endangered ecosystems.

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