ECOLOGICAL CONNECTIVITY IN ALLUVIAL RIVER ECOSYSTEMS AND ITS DISRUPTION BY FLOW REGULATION

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ABSTRACT
The dynamic nature of alluvial floodplain rivers is a function of flow and sediment regimes interacting with the physiographic features and vegetation cover of the landscape. During seasonal inundation, the flood pulse forms a 'moving littoral' that traverses the plain, increasing productivity and enhancing connectivity. The range of spatio-temporal connectivity between different biotopes, coupled with variable levels of natural disturbance, determine successional patterns and habitat heterogeneity that are responsible for maintaining the ecological integrity of floodplain river systems. Flow regulation by dams, often compounded by other modifications such as levee construction, normally results in reduced connectivity and altered successional trajectories in downstream reaches. Flood peaks are typically reduced by river regulation, which reduces the frequency and extent of floodplain inundation. A reduction in channel-forming flows reduces channel migration, an important phenomenon in maintaining high levels of habitat diversity across floodplains. The seasonal timing of floods may be shifted by flow regulation, with major ramifications for aquatic and terrestrial biota. Truncation of sediment transport may result in channel degradation for many kilometres downstream from a dam. Deepening of the channel lowers the water-table, which affects riparian vegetation dynamics and reduces the effective base level of tributaries, which results in rejuvenation and erosion. Ecological integrity in floodplain rivers is based in part on a diversity of water bodies with differing degrees of connectivity with the main river channel. Collectively, these water bodies occupy a wide range of successional stages, thereby forming a mosaic of habitat patches across the floodplain. This diversity is maintained by a balance between the trend toward terrestrialization and flow disturbances that renew connectivity and reset successional sequences. To counter the influence of river regulation, restoration efforts should focus on re-establishing dynamic connectivity between the channel and floodplain water bodies.

KEY WORDS alluvial rivers; ecological connectivity; floodplains; flow regulation; habitat heterogeneity; succession

INTRODUCTION
The ecological integrity of alluvial floodplain rivers is a function of ecological connectivity operating across a range of spatio-temporal scales (Antipa, 1928; Botnariuc, 1967; Amoros and Roux, 1988; Ward, 1989a; Stanford and Ward, 1993). Connectivity in this context refers mainly to exchange pathways of water, resources and organisms between the channel, the aquifer and the floodplain, although interactions with adjacent uplands must also be considered. The premise of this paper is that high connectivity, and associated habitat heterogeneity, productivity and biodiversity of floodplain river ecosystems, is maintained by natural disturbance (i.e. the flood regime and its ramifications). Anthropogenic alterations of floodplain rivers often disrupt the intensity, frequency and timing of the natural disturbance regime that is responsible for maintaining the ecological integrity of these dynamic systems.

This synthesis paper is presented in three parts: the first examines how connectivity operates across a range

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of scales to maintain the ecological integrity of floodplain river systems through dynamic interactions related to hydrology, geomorphology and successional phenomena; the second analyses how river regulation, by reducing connectivity, alters hydrological and geomorphic processes and successional trajectories; and the final part addresses ways to re-establish the connectivity/ ecological integrity of regulated floodplain river systems.

CONNECTIVITY AND ECOLOGICAL INTEGRITY

Floodplain rivers are dynamic systems, the persistence of which depends on interactions between subsystems. Floodplain ecosystems are also disturbance-dependent, relying on the kinetic energy of flooding (fluvial dynamics) to maintain connectivity. As stated by Pinay et al. (1990) in reference to plant communities, 'subsystem instability maintains the metastability of the whole riparian ecotone.'

Hydrology and geomorphology

Hydrological and geomorphic conditions interact to determine pattern and process across a range of scales. At small spatial scales, water movement patterns during seasonal flooding, for example, produce patches of aerobic and anaerobic soils on the floodplain which differ in nutrient and decomposition dynamics. Alluvial forest zonation patterns provide an example of moderate scale spatio-temporal phenomena as they represent successional stages structured by the lateral migration of the river channel across the floodplain. Large-scale topographic features of floodplains, such as terraces, were formed by processes related to glaciation/deglaciation events, sea-level changes, tectonic uplift and other long-term phenomena.

General features of fringing floodplains. The valley of an alluvial river typically consists of the following topographic features (Leopold et al., 1964; Welcomme, 1979, 1985; Mitsch and Gosselink, 1993): (1) hillslopes forming the sides of the valley, (2) one or more levels of terraces, remnants of abandoned floodplains at higher elevations than the (3) active flood plain (inundated annually), (4) natural levees that form along the river channel from sediment deposited as the water velocity abruptly decreases when the river overtops its banks, (5) meander scrolls, the ridge and swale topography on the floodplain surface, that form a series of progressively older levees (ridges) of abandoned meander bends and the depressions (swales) between them (levees, and therefore ridges, are usually the highest points on the active floodplain and are composed of coarse, well-drained soils), (6) natural drainage channels that breach the levee, forming connections between the floodplain and the river channel and (7) permanent and temporary floodplain water bodies in various stages of hydrarch succession. During an annual flood of normal amplitude, only the tops of the highest levees and ridges are above water; the remainder of the active floodplain and the river channel are inundated by a physically continuous aquatic milieu.

Although fully cognizant of the variability in the physical environment of riverine landscapes (Church, 1992), in this paper we emphasize the common characteristics of fringing floodplain systems. For example, Wolman and Leopold (1957) reported that the floodplains of rivers flowing through diverse physiographic and climatic regions are typically inundated by channel overspill about once each year. Yet we recognize that an assumption of annual inundation for undisturbed floodplain rivers masks important variability between systems. Detailed analysis of differences across latitudinal gradients are also beyond the scope of this paper. The role of ice action, an important agent in northern rivers (e.g. Prowse, 1994), is not treated herein. Most information on the effects of flow regulation on downstream reaches is based on studies conducted at temperate latitudes, with very little data on tropical river systems (Ward and Stanford, 1993). It is not known whether the consequences of regulation on tropical rivers will, in fact, be the same as for rivers in the temperate zone.

The flood pulse. To emphasize the primary role of hydrology in structuring the floodplain biota, Junk et al. (1989) postulate that if no organic material except living animals were exchanged between floodplain and channel, no qualitative and, at most, limited quantitative changes would occur in the floodplain. Their 'flood pulse concept' provides a theoretical framework for analysing the adaptive strategies employed by organisms to exploit the wet and dry phases that alternate in a predictable annual pattern on the floodplains of large rivers. On small rivers, or in the upper reaches of large rivers, floodplains are not inundated for a sufficient length of time and the periodicity of flooding is too irregular for the evolution of adaptive strategies that are tightly coupled to the flood regime (Junk et al., 1989).
The flood pulse concept refers to the floodplain surface as the 'aquatic/terrestrial transition zone' (ATTZ) to emphasize the importance of alternating dry and wet phases in enhancing biotic diversity and productivity. Inundation of the floodplain results in a 'moving littoral' that traverses the ATTZ from the channel to the upland transition, thereby creating a dynamic edge effect. Alternating dry and wet phases increase organic matter decomposition and nutrient cycling and shorten periods of stagnation, compared with conditions in permanently inundated habitats.

The rich resources of the ATTZ are utilized by terrestrial animals during the dry phase and by aquatic animals during the wet phase (Figure 1). During the wet phase some terrestrial animals migrate to the uplands, whereas others remain on the floodplain. Those that remain are adapted to tolerate extended periods of inundation or move into the alluvial forest canopy to escape the rising water. For example, in central Amazonian floodplains, which are inundated for five to seven months of the year, terrestrial invertebrates evolved migratory and non-migratory survival strategies (Adis, 1992). Some species migrate horizontally ahead of the high water line, others migrate vertically to the forest canopy and yet others engage in migratory flights to upland forests. Most non-migrants survive the aquatic phase as dormant stages, although a few species have developed plastron respiration, enabling them to remain active under water.

Kafue Flats, a large floodplain of the Kafue River in Zambia, is flooded to a depth of up to 5 m for several months each year (Sheppe and Osborne, 1971). As water recedes, terrestrial mammals move in from the surrounding woodlands to graze on the productive grasslands that cover the floodplain during the dry phase. The Kafue lechwe (*Kobus leche kafuensis*), an ungulate endemic to the Flats, provides an example of a large terrestrial mammal that is dependent on and adapted to the floodplain (Chabwela and Ellenbroek, 1990). The grazing regime of the lechwe, the most abundant large mammal of the Flats, is closely tied to the flood cycle and is thought to be an important structuring agent for the development of plant communities on the floodplain. The complicated lekking behaviour of the lechwe is also tied to the hydroperiod.

Aquatic animals colonize the ATTZ during the wet phase to take advantage of the high productivity and diverse habitat conditions. Movements of fishes associated with floodplain rivers exhibit highly diverse patterns, many facets of which are poorly understood (reviewed by Welcomme, 1985). Nonetheless, most fish species are in one of the following three main categories, based on movement patterns: (1) those that...
complete all life stages within the river channel; (2) those that reside in the river channel during the dry season and on the floodplain surface (ATTZ) during the wet phase (flood-dependent fishes); and (3) those that reside in lentic water bodies of the floodplain during the dry phase and on the ATTZ during the wet phase. Few fishes associated with floodplain rivers use main channel habitats exclusively (Junk et al., 1989) and this first category will not be considered further.

Flood-dependent fishes are highly adapted to exploit the predictable flood pulse, using the river channel as a dry season/winter refuge and for longitudinal migration (potamodromy). Adaptations are most pronounced in the tropics, partly because the flood pulse of most large temperate rivers has been modified by river engineering works. Maturation of reproductive products is synchronized with the flooding regime, which ensures that suitable spawning conditions are present and that adequate food and shelter are available for young fishes (Heeg and Breen, 1982). Plant detritus and dung that accumulated during the dry phase and the influx of riverborne nutrients provide immediate sources of organic matter and stimulate aquatic productivity. As the ‘moving littoral’ traverses the floodplain, cover for young fishes is provided by recently submerged terrestrial vegetation and the rapidly developing aquatic macrophytes. Shallow water habitats with high temperatures optimize the growth rates of young fishes while reducing predation by large fishes. The cover from inundated terrestrial and developing aquatic plants provides protection from terrestrial predators. The forest canopy contributes an array of organic detritus (leaves, fruits, seeds) and organisms (mainly terrestrial arthropods) to the inundated floodplain (Goulding, 1980). There is evidence for a coevolutionary relationship whereby the trees provide food for the fishes and rely on them for seed dispersal.

At the end of the wet phase, juvenile and adult fishes return to the river channel in a predictable sequence based on body size, age class, food habits and species-specific differences in low oxygen tolerance. Heavy predation losses of prey species and juveniles occur at the mouths of drainage channels where predators congregate. Flood-dependent fishes are not adapted to the stagnant conditions that prevail in many floodplain water bodies during the dry phase. Those that fail to migrate to the river channel at the end of the wet phase perish.

Certain fishes, however, move from the ATTZ to standing water bodies of the floodplain as water levels subside, being adapted to survive deoxygenation and, in some instance, desiccation during the dry phase (Welcomme, 1985; Lowe-McConnell, 1987). Because of the relationships between temperature and metabolic rate/oxygen solubility, the most dramatic adaptations have evolved in tropical waters.

Many taxa of fishes have independently evolved adaptations for air breathing (Welcomme, 1985). Some species, such as lung fishes, are obligate air breathers that must surface at frequent intervals. Many additional fishes from numerous families are able to meet respiratory needs by extracting oxygen from the surface microlayer, which remains well oxygenated during periods of hypoxia (Kramer and McClure, 1982). Species able to inhabit low oxygen waters are subjected to reduced interspecific competition and predation, although frequent surface visits increase their vulnerability to aerial predators. Some air-breathing fishes are capable of limited terrestrial locomotion, allowing them to colonize isolated water bodies and to emigrate from habitats undergoing desiccation (Kramer et al., 1978; Seghers, 1978).

Very few fishes are specially adapted to endure habitat desiccation. Several species can survive for short periods in damp mud or sand, but only African lungfishes (Protopterus spp.), which secrete a slime cocoon, can aestivate as adults within a dry substratum (Welcomme, 1985). ‘Annual fishes’, known among the cypri­ nodonts of Africa and South America, maintain permanent populations in temporary ponds (Simpson, 1979; Lowe-McConnell, 1987). The life cycle is completed during the wet phase and they survive the dry phase as drought-resistant eggs. Because diapause can occur in three stages of embryogenesis, different combinations of diapause result in several developmental series, thereby ensuring that some individuals survive should precipitation temporarily fill the pond before the extended wet phase (Wourms, 1972).

**Floodplain water bodies**

Alluvial floodplains contain a variety of lotic and lentic biotopes, including the river and its side channels, emergent springbrooks, tributary streams and abandoned channel segments (Figure 2). The main river and its side channels are designated ‘eupotamon’; ‘parapotamon’ refers to dead arms that retain a connection to the active channel only at their downstream end; ‘plesiopotamon’ are former braided segments that became
disconnected from the river channel; 'palaeopotamon' are former meander bends that became disconnected. This terminology was initially developed for the French Rhône in recognition of ecological differences between floodplain water bodies based on attributes such as connectivity, successional trajectory and community structure (Amoros et al., 1982; Castella et al., 1984, Copp, 1989). Floodplain water bodies are also differentially influenced by groundwater dynamics, which is reflected by hypogean faunal assemblages (Gibert et al., 1981; Marmonier et al., 1992; Stanford and Ward, 1993; Ward and Palmer, 1994), although the present paper focuses on the epigean realm.

Floodplain water bodies may be arrayed along a gradient of connectivity with the main channel or thalweg (Figure 3). Side arms of the eupotamon, which are connected with the main channel at both ends, are true
lotic segments with higher connectivity than the parapotamon, which lack unidirectional current, being connected only at the downstream end. Plesiopotamon water bodies have greater connectivity with the active channel than the palaeopotamon (oxbow lakes). Plesiopotamon are smaller, shallower habitats that rapidly undergo terrestrialization and generally occur near the active channel, whereas the palaeopotamon are larger, deeper and longer lived aquatic habitats that may be situated a great distance from the active channel. Besides distance, levees, which do not usually form on braided segments, reduce the frequency of flooding of the palaeopotamon, making them more isolated from floodplain inundation than other water bodies. As the water level rises during the flood pulse, the upstream ends of parapotamon habitats are reconnected with the active channel. With additional flood height the plesiopotamon resume a running water character. At the height of the flood all water bodies, including the palaeopotamon, are inundated. As described by Lewis et al. (1990) for the Orinoco River system, 'adjacent floodplain basins that are separate during the dry season become essentially uniform and contiguous with respect to nutrient chemistry and biological properties during the season of inundation. However, following inundation, these adjacent systems reestablish their individuality.'

Natural floodplains thus contain a broad diversity of lentic, lotic and semi-lotic habitats. Circulation patterns range from stagnant to strong unidirectional currents. Substrate conditions range from highly organic mud to coarse, highly permeable mineral deposits. Aquatic macrophytes, absent from some biotopes, in other situations form dense emergent stands, floating mats or submerged beds. The temperature regime exhibits marked changes between and within biotopes, greatly contributing to environmental heterogeneity (Ward, 1985). Springbrooks, fed by groundwater, provide summer-cool and winter-warm conditions at mid- and high latitudes and also have a longitudinal temperature gradient. Distinct spatial gradients may also occur in parapotamon habitats which receive groundwater seepage at their upstream ends (Bouvet et al., 1985). The thalweg of the eupotamon may have a different temperature than its side channels and even individual branches of a braided segment sometimes exhibit different thermal conditions. Tributaries that originate in the uplands typically have different temperatures than other lotic segments of the floodplain. Different lentic water bodies have markedly different thermal conditions as a function of size/depth, degree of shading and wind exposure. These are just a few examples of the spatio-temporal heterogeneity that structures biotic communities at the floodplain scale.

The spatio-temporal heterogeneity of floodplain river systems is, therefore, responsible for a diverse array of dynamic aquatic habitats. Habitat diversity is further enhanced by the different ages (stages of development) of the various types of water bodies. In this way, natural levels of disturbance maintain the ecological integrity of alluvial river ecosystems.

Channel inputs

In addition to fluxes of water and sediment, natural alluvial rivers are characterized by massive exchanges of organic and inorganic matter between the river channel and the floodplain. As a general rule, there is a net import of dissolved inorganic compounds to the floodplain and a net export of particulate organic matter, including living biomass elaborated on the floodplain (Gosselink et al., 1990; Mitsch and Gosselink, 1993; Sharitz and Mitsch, 1993). Exports of particulate organic matter to the channel include detritus (including episodic pulses of large wood debris), plankton, benthos, fishes and floating islands (Sudds) with associated flora and fauna (Welcomme, 1985).

Accumulations of large woody debris play a major part in structuring channel morphology (Keller and Swanson, 1979; Triska, 1984). Debris jams, by altering local current patterns, may scour the bed, increase channel width or facilitate meander cutoff. Deposition below debris jams may initiate the formation of mid-channel bars and islands. In some instances, blockage of main channels results in the formation of riparian lakes (Triska, 1984). Submerged wood provides an important habitat for aquatic organisms. For example, in a coastal plains river, submerged wood (snags) constituted 4% of the habitat surface, but supported the majority of invertebrate biomass (Benke et al., 1985). Invertebrate production on snags provided a major food source for riverine fishes.

Large contributions of living organisms from floodplains to river channels have been documented. During a winter flood, Wainright et al. (1992) estimated inputs of up to 4000 kg bacteria Ch⁻¹ from the floodplain.
CONNECTIVITY IN ALLUVIAL RIVERS

over a 50 km reach of a blackwater river. Bacteria elaborated on the floodplain are an important food resource for filter feeders and deposit feeders in the river channel (Meyer, 1990).

Although only a small proportion of the phytoplankton production on the floodplain of the Orinoco River is transferred to the river channel, this yield accounts for 37% of the annual transport of phytoplankton carbon (Lewis, 1988). Additional phytoplankton biomass was contributed from 'near-channel stagnant or slow-flowing areas', but the amount was not separated from that transported by the main channel.

Studies of a Venezuelan floodplain river showed how the annual hydrograph regulated which source areas provided suitable habitat for zooplankton development and controlled the export of zooplankton from source areas (Saunders and Lewis, 1988a). Zooplankton is abundant in the main channel during the dry phase when side channels develop large populations and serve as source areas. As the water level rises, zooplankton is flushed from the side channels. Following a brief pulse, populations remain low in the main channel until the river inundates the floodplain. Zooplankton transport increases as floodplain water bodies containing dense populations are inundated. The slow movement of water across the wide floodplain provides suitable conditions for the sustained development of zooplankton during the flood phase. The inundated floodplain continues to export zooplankton to the river for several months, at a time when high velocity precludes zooplankton reproduction in the main channel. This contrasts with another Venezuelan river that has a narrow floodplain with shorter hydraulic residence time, where zooplankton populations are flushed from lentic water bodies at the beginning of the flood phase and remain depleted during the period of inundation (Saunders and Lewis, 1988b).

As the water recedes and the floodplain loses its connection with the river, zooplankton remains low in the main channel until source areas are re-established in the side channels.

Studies of the Danube demonstrate much higher zooplankton abundances in backwaters than in the main channel (Vranovsky, 1974; Bothar, 1981). At times, zooplankton densities may be orders of magnitude higher in backwaters than density levels in the river. As flood waters rise, increasing the connectivity, plankton is exported to the river where it is used as food by a variety of consumers.

Benthic invertebrates are also flushed from productive floodplain water bodies during high water, thereby re-establishing functional connectivity and supplying food to channel residents (Castella et al., 1984; Eckblad et al., 1984; Friedrich and Müller, 1984; Shaeffer and Nickum, 1986a; Cellot and Bournaud, 1987; Ward, 1989b; Obrdlik and Garcia-Lozano, 1992). Large numbers of invertebrates are translocated to the channel in association with drifting plants (Bonetto, 1975; Welcomme, 1985). Both terrestrial and aquatic animals inhabit floating plants (e.g. Pistia, Eichhornia) and floating islands (Sudds). Up to 300 animals may occur on a single Pistia stratiotes plant (Rzóska, 1974) and the mat in the centre of floating meadows contains as many as 100 000 animals per square metre (Junk, 1973).

In addition to passive transport, some invertebrates actively migrate between the river and adjacent water bodies (Söderström, 1987). A well-documented example involves the mayfly Leptophlebia cupida, which emerges from floodplain marshes in Canada and flies to the river to oviposit (Hayden and Clifford, 1974). Nymphs reside in the river during autumn and winter. The initial vernal rise in water level from snowmelt runoff initiates a day-active upstream migration of nymphs along the edges of the river, up drainage channels and into floodplain marshes, where the life cycle is completed. The annual migratory pattern enables nymphs to avoid severe winter conditions in the shallow marshes and adverse spring runoff conditions in the river.

The diversity of lentic and lotic biotopes of a floodplain river system (Figure 2) provides suitable conditions for a variety of benthic communities. The eupotamon of side channels, for example, is characterized by lotic benthos that differ from those of the main channel, from those of the parapotamon and from all other floodplain water bodies. It is because of the association between biota and habitat conditions that macroinvertebrate communities may be used as 'describers' of various types of floodplain water bodies (Castella et al., 1984). This also means that invertebrates contributed to the river from the floodplain vary qualitatively and quantitatively as a function of source (habitat type), thereby providing a diversity of organic resources as temporally sequenced inputs along a continuum of connectivity.

The different types of floodplain water bodies are also characterized by specific assemblages of fishes (Welcomme, 1985; Copp, 1989). During the dry phase fish biomass is higher in backwater habitats than
in the main channel and the fish productivity of a given reach is positively correlated with the development of backwater habitats (Shaeffer and Nickum, 1986b; Amoros and Roux, 1988; Copp, 1989). Within the main channel of the Mississippi River, the highest densities of young fishes (larvae and juveniles) occurred downstream from backwater connections (Shaeffer and Nickum, 1986b). Fish biomass elaborated on the floodplain during the wet phase—that is transferred to the river by the lateral migration of flood-dependent species (as discussed in a previous section)—constitutes the major input of ichthyomass to the channel.

**Floodplain forest succession**

The important role of natural disturbance in maintaining ecological integrity at the floodplain scale is well documented (e.g. Junk et al., 1989; Duncan, 1993). The high biotic diversity of the upper Amazon basin is attributable to large-scale disturbance induced as river channels migrate back and forth across their floodplains, creating a mosaic of forest stands and successional stages (Salo et al., 1986).

The floodplain of the Manu River in upper Amazonia (Peru) provides an excellent example of the role of river channel migration in structuring alluvial forest succession (Terborgh and Petren, 1991). Channel migration across the 6 km wide floodplain simultaneously deposits alluvium on the convex side of meander bends and erodes the opposite bank. Erosion of the concave bank averaged 25 m/year on one meander bend, a migration rate of 2.5 km per century. As the forest growing on the concave bank is undercut by erosion, primary succession is initiated on beaches (point bars) formed in annual increments on the inside bends. During low water annual plants and the woody composite *Tessaria integrifolia* germinate on newly formed beaches. Many *Tessaria*, which grows to heights of 2 m or more during the first year, are carried away by the next flood, but some stems are flattened and buried by the new layer of sediment. The second year, after flood waters recede, the buried vegetative shoots attain heights of 3–4 m. They are now at a higher level further from the migrating river and can withstand the next flood. In three to five years the mature stands of *Tessaria*, 8–10 m high, are invaded by the cane *Gynerium*, which eventually overtops *Tessaria*, resulting in its demise. Seedlings of many tree species become established in *Gynerium* stands, being protected from washout by the dense cane stems which reduce current velocities during floods. Even-aged stands of *Cecropia*, the fastest growing tree, attain heights of 20 m or more, forming a cane–*Cecropia* association that is maintained for several years, but is eventually overtopped by slower growing trees. Reduced light levels eliminate the cane; *Cecropia* only lives for a few decades and so is also eliminated from the mixed forest association. A tall herb layer, dominated by *Heliconia*, forms a dense understorey that suppresses further recruitment of trees. Eventually, two slow-growing trees (*Ficus* and *Cedrella*) grows to heights of 35–40 m, forming a late successional association that persists for about a century. Succession to the mature floodplain forest phase takes from 300–500 years and is possible only on areas of the floodplain with lower than average rates of channel migration. The mature forest has high structural diversity (five vertically superimposed strata, the tallest of which exceeds 50 m), high tree diversity (> 200 species per hectare) and the highest diversity of birds and mammals. The meandering river is, therefore, an example of a natural disturbance that creates multiple successional stages and a dynamic mosaic of habitat types across the alluvial floodplain.

**REGULATED FLOODPLAIN RIVERS**

*Lost connectivity*

Flow regulation by dams disrupts the downstream river system's natural disturbance regimes (Figure 4). Reduction of flood peaks reduces the frequency, extent and duration of floodplain inundation. Reduction of channel-forming flows reduces channel migration. Truncated sediment transport (sedimentation within the impoundment) typically results in channel degradation below the dam and a concomitant lowering of the water-table. The temporal pattern of flooding is also altered by regulation, one effect of which is to desynchronize annual flow and temperature regimes (Sparks et al., 1990). These changes and others directly and indirectly influence a myriad of dynamic factors that affect habitat heterogeneity and successional trajectories and, ultimately, the ecological integrity of floodplain rivers.
Figure 4. Some implications of major hydrological changes induced by flow regulation on downstream river–floodplain systems.

Figure 5. Hydrarch succession of floodplain water bodies along two trajectories (see Figure 2).
In much of the world anthropogenic impacts have severed major interactive pathways, thereby isolating rivers from their floodplains and disrupting the dynamic patterns and processes that structure river–floodplain ecosystems. The downstream effects of flow regulation (Figure 4) are typically compounded by other modifications (e.g. channelization, levee construction) that further reduce connectivity between the river channel and the floodplain (Amoros et al., 1982; Welcomme, 1985; Bravard et al., 1986; Ward and Stanford, 1989; Brinson, 1990; Gosselink et al., 1990; Junk and Welcomme, 1990; Petts, 1990; Sparks et al., 1990; Penka et al., 1991; Stanford and Ward, 1992).

Altered successional pathways

In the context of river–floodplain ecosystems, ‘succession’ may be considered from two very different perspectives: (1) hydrarch succession of floodplain waterbodies; and (2) alluvial forest succession.

Hydrarch succession of floodplain waterbodies (Figure 5) follows two distinct trajectories towards terrestrialization (Amoros et al., 1982; 1987b; Copp, 1989). Those that form by the abandonment of braided segments undergo relatively rapid succession dominated by allogenic processes (e.g. sedimentation), whereas those that form by the abandonment of meander loops to form oxbow lakes (palaeopotamon) undergo much slower succession dominated by autogenic processes (e.g. eutrophication). Palaeopotamon habitats exhibit lower connectivity (Figure 3), are larger, deeper, older and more distant from the active channel, on average, than plesiopotamon habitats. Terrestrialization of abandoned meanders requires centuries, in contrast with decades for abandoned braids (Amoros et al., 1987b). The autogenic pathway in Figure 5 applies to situations where entire meander loops are abandoned to form oxbow lakes. Meandering rivers also abandon smaller aquatic habitats that are dominated by allogenic processes. The predominance of allogenic or autogenic processes determines the restoration potential of floodplain water bodies, as will be discussed subsequently.

At the floodplain scale, the trend toward terrestrialization (hydrarch succession) is countered by the formation of new water bodies and by the rejuvenation of extant water bodies. Such high connectivity results in a diversity of aquatic and semi-aquatic habitats that collectively encompass a wide range of successional stages. Anthropogenic impacts that reduce fluvial dynamics generally accelerate terrestrialization and retard the formation and rejuvenation of floodplain water bodies (Figure 4). In a comparison of two floodplains of the Danube, one disconnected from the channel and the other with connectivity largely intact, Löffler (1990) documented much greater diversities of macrophytes (60 versus 20 species), zoobenthos (35 versus 16 species of molluscs) and fishes (30 versus four species) on the unaltered site. Similar results were documented for two
floodplains of the upper Rhine (active versus abandoned), where restricted fluvial dynamics on the abandoned floodplain reduced habitat heterogeneity of aquatic biotopes, thereby altering community composition and reducing diversity of macrozoobenthos (Obrdlik and Fuchs, 1991).

Flow regulation, by altering fluvial dynamics and sediment transport, induces major changes in alluvial forest succession (Johnson et al., 1976; Pautou and Décamps, 1985; Bren, 1988; Décamps et al., 1988; Johnson, 1994).

One mode of action occurs through the influence of regulation on channel migration (Figure 4). Channel stability may be perceived as a disturbance gradient from stable reaches below dams (regulated) to highly unstable reaches of severe braiding, both extremes exhibiting low levels of habitat diversity relative to actively meandering rivers (Figure 6). The stable channels of regulated rivers truncate forest successions so that the potential for high levels of habitat heterogeneity and biodiversity described in a previous section is not realized.

Changes in the hydroperiod from the channel margins to the uplands, coupled with differences in soil type and surface topography across the floodplain, contribute to spatial heterogeneity of alluvial forest composition and successional stages. Flow regulation typically reduces the frequency and extent of floodplain inundation and lowers the water-table, with major ramifications for floodplain vegetation. Productive pioneer species tend to be replaced by less productive upland species (Décamps, 1984) that are able to invade the floodplain under conditions of artificially enhanced environmental stability. In essence, the overall effect of regulation on downstream river–floodplain ecosystems is to impose equilibrium conditions on non-equilibrium communities. It is not surprising that the communities that develop after regulation are poorly adapted to the infrequent catastrophic flood resulting from 'flood control' measures.

Recruitment, establishment and survival of riparian tree species is closely tied to the hydrological regime. This has been well documented for floodplain forest corridors along prairie rivers in North America dominated by the cottonwood–willow (Populus–Salix) community (Johnson et al., 1976; Reily and Johnson, 1982; Bradley and Smith, 1986; Rood and Mahoney, 1990). Wind dispersal of seeds coincides with the recession of spring floods that form seedbeds on newly deposited alluvium of point bars. Seeds remain viable for only a few weeks. Because seedlings are poor competitors, they are successful only on recently disturbed microsites. On the river studied by Bradley and Smith (1986), successful establishment of seedlings (Populus deltoides) was correlated with years when daily maximum flows during the period of seed dispersal (June 1 to July 10) attain a stage equal to or greater than the 2-year return flood. Once established, seedlings may be uprooted by erosive flooding or killed by desiccation. Poplars are phreatophytes, the roots of which must maintain contact with the water-table. As the elevation of the point bar is raised by sediment deposition during annual floods, the surviving saplings are less likely to be adversely affected by scour. Suitable conditions for the long-term establishment of a new generation of trees does not occur annually, even in natural rivers.

In floodplains downstream from dams, floods are reduced and may not coincide with the period of seed dispersal. Reduced rates of channel migration, coupled with reduced flooding and sediment transport, decrease the formation of new areas of bare substrate required as seedbeds. Lowered water-tables from channel degradation below dams may induce drought stress, killing seedlings and older trees and reducing the growth rates of trees that survive. The pioneer cottonwood–willow forest is adversely affected, being gradually replaced by a late successional community dominated by green ash (Fraxinus pennsylvanica) that under natural conditions occurs on terraces near the edge of the floodplain (Johnson et al., 1976). Prairie rivers of North America are highly regulated by dams and the pioneer floodplain forests are in decline. The natural disturbance regime that maintains high habitat heterogeneity and biodiversity has been largely replaced by more stable conditions induced by river regulation.

A very different response was documented for the Platte River, however, where flow regulation was accompanied by woodland expansion (Johnson, 1994). River regulation transformed the Platte River from a wide braided system largely devoid of woody vegetation to a single thread channel with a dense alluvial forest corridor (Schumm, 1985). Johnson (1994) attributed the divergent response exhibited by the Platte River to its geomorphic type (braided). In contrast with the situation described for meandering prairie rivers, 'successful recruitment and expansion of Populus and Salix in braided rivers are not positively associated...
with peak-flow events but with periods of low flow' (Johnson, 1994). Flow regulation, by reducing spring flows, provided suitable conditions for seedling establishment across much of the braided channel.

RE-ESTABLISHING CONNECTIVITY

The preceding material consists of selected examples of the important part played by natural disturbance/connectivity in maintaining the ecological integrity of river–floodplain ecosystems and how river regulation may diminish that integrity. In the context of alluvial rivers, ecological integrity may be equated with the diversity of successional stages of the aquatic and riparian biotopes on the floodplain. According to this perspective, sound ecosystem management is predicated on (1) comprehensive understanding of natural systems, (2) maintaining or re-establishing natural interactive pathways and (3) reconstituting natural disturbance regimes.

It is necessary to distinguish between different levels of restoration potential or ‘degrees of reversibility’ (sensu Amoros et al., 1987a). For example, rejuvenation of a senescent palaeopotamon habitat, which developed slowly via mainly autogenic processes, would involve a massive effort compared with rejuvenation of a plesiopotamon habitat which developed by allogetic processes (see Figure 5). Relatively minor excavation may rejuvenate the plesiopotamon by reconnecting it to the flushing action of high flows.

Re-establishing connectivity between river channels and their floodplains is slowly being recognized as a viable management strategy. In the upper Rhône, parapotamon water bodies have been reconnected at the upstream ends, reconstituting their previous eupotamon stage; alluvial plugs have been removed from plesiopotamon habitats, changing them back to parapotamon (Bravard et al., 1992). On the upper Rhine, gravel is added to the channel to compensate for truncation of sediment transport by upstream impoundments, in an effort to reduce bed degradation and maintain groundwater levels (Dister et al., 1990). Because the Rhine has been isolated from its floodplain, major cities along the river are no longer protected from the 200-year flood as they were in 1955. For the purposes of flood control, it is proposed to restore quasi-natural dynamics and reconnect the near-natural floodplains of the Rhine. Purchase of alluvial floodplains along the Charles River, Massachusetts has been deemed the most effective and economical means of flood control to protect the city of Boston (Mitsch and Gosselink, 1993). Schiemer and Waidbacher (1992) have made recommendations for restoring connectivity between the channel and floodplain water bodies in anticipation of establishing an ‘Alluvial Zone National Park’ along a reach of the Austrian Danube.

Because fluvial disturbance/connectivity are the critical attributes that maintain the ecological integrity of floodplain rivers, they should serve as the focus of restoration efforts. Resource managers must become 'conservators of ecological connectivity' (Stanford and Ward, 1992).

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REFERENCES


