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Connectivity and biocomplexity in waterbodies of riverine floodplains

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SUMMARY

1. In river corridors, water plays a key role in connecting various landscape patches. This 'hydrological connectivity' operates on the four dimensions of fluvial hydrosystems: longitudinal, lateral, vertical, and temporal. The present review focuses on: (1) lateral connectivity that links the main course of a river with floodplain waterbodies; and (2) vertical connectivity, the exchanges between the surface and groundwater via infiltration into the alluvial aquifer and exfiltration of phreatic water from the hillslope aquifer.
2. The biocomplexity of fluvial hydrosystems results from interactions between processes operating at various spatial and temporal scales. Differences in the nature and intensity of hydrological connectivity contribute to the spatial heterogeneity of riverine floodplains, which results in high alpha, beta and gamma diversity. Differences in connectivity also provide complementary habitats that are required for the parts of life cycles and life-cycles of some species. Hydrological connectivity also produces antagonistic effects, even within the same waterbody.
3. Two temporal scales are distinguished in connectivity dynamics. River level fluctuations within years lead to a pulsing connectivity that drives the functioning of floodplain ecosystems, namely the exchange of organic matter and inorganic nutrients and the shift between production and transport phases. On the scale of decades to centuries, the interactions between various processes increase the biocomplexity of floodplains; for example, river dynamics, which create highly connected waterbodies, compensate for succession that tends towards disconnection. Alternatively, river-bed incision leads to the reduction of fluvial dynamics and to the disconnection of waterbodies, although river incision may increase vertical connectivity where waterbodies are supplied by the hillslope aquifer.

Keywords: biodiversity, flood disturbance, groundwater, river dynamics, succession

Introduction

River corridors have been recognised as linear landscapes in which water flows play a key role in connecting various landscape patches (Junk, Bayley & Sparks, 1989; Malanson, 1993; Ward, 1998). This 'hydrological connectivity' operates on the four dimensions of fluvial hydrosystems: longitudinal, lateral, vertical, and temporal (Amoros, Roux & Reygrobellet, 1987b; Ward, 1989). The exchanges resulting from connections on the longitudinal dimension (upstream–downstream gradient) were emphasised by the River Continuum Concept (Vannote *et al.*, 1980) and subsequent conceptual frameworks such as the Serial Discontinuity Concept (Ward & Stanford, 1995a). In the present paper, lateral connectivity refers to the permanent and episodic links between the main course of a river and the various waterbodies lying in the alluvial floodplain (Amoros & Roux, 1988; Ward & Stanford, 1995b). Vertical connectivity includes exchanges between the

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surface and groundwater via infiltration into the alluvial aquifer (seepage) and the exfiltration of phreatic water from the hillslope aquifer (Danielopol & Marmonier, 1992; Stanford & Ward, 1993). The temporal dimension relates to changes occurring on both annual (hydrological phases, unpredictable fluctuations within and between years) and historical scales (decades to centuries) (Sedell & Froggatt, 1984; Bravard, Amoros & Pautou, 1986; Petts, Moller & Roux, 1989).

The concept of fluvial hydrosystem is based on the prominent functions of water through: (1) the hydrological connectivity responsible for exchanges between landscape patches, and (2) the kinetic energy of running water responsible for the fluvial dynamics. Interactions between these two water functions are a major source of complexity in riverine landscapes, as hydrological connectivity depends on fluvial dynamics (e.g. patches connecting during river floods, erosion giving rise to new channels that permanently connect some patches), whereas fluvial dynamics are favoured by hydrological connectivity (e.g. connections that permit the passage of running water to maintain its velocity and thereby its eroding force).

In the present paper, we focus on the lateral dimension, specifically on the aquatic patches of the landscape, i.e. the 'riverscape' *sensu* Malard, Tockner & Ward (2000). The most upstream headwaters and the downstream delta regions are not addressed here. The relationship between hydrological connectivity and biocomplexity depends on the exchange of living organisms and gene flow through extinction and colonisation processes, and also on community composition and dynamics resulting from other processes such as natural disturbance, ecological succession, modification of habitat conditions, and nutrient and food supply. We begin by reviewing the spatial heterogeneity of floodplain waterbodies and consequences on the α, β and γ diversity of different taxonomic groups. We then briefly address the role of connectivity in providing access to complementary habitats for species requiring more than one habitat type during their life cycles. In the third section of this paper, we propose an explanation for the conflicting results of different studies, some of which report positive relationships between connectivity and a given parameter, whereas others report negative relationships. The final section examines connectivity dynamics over two time scales, the seasonal/annual flow pulses that determine the exchanges of nutrients, organic matter and living organisms between the diverse waterbodies of the floodplain, and the long-term phenomena (decades to centuries) involving ecological succession, channel migration, and river bed incision. In addition, major interactions between the processes operating at different spatial and temporal scales are discussed in relation to management and restoration.

Connectivity and spatial heterogeneity

Within a riverscape, fluvial dynamics result in shifting mosaics at two spatial scales (the floodplain scale and the scale of each waterbody). At the floodplain scale, waterbodies created by fluvial processes through lateral as well as vertical erosion, and the subsequent channel migration and abandonment, include side-arms, backwaters, cut-off braided channels, oxbow lakes, floodplain ponds and marshes (Drago, 1976; Amoros *et al.*, 1987b; Baker, Killgore & Kasul, 1991; Galat, Kubisiak & Hooker, 1997). At this scale (Fig. 1),

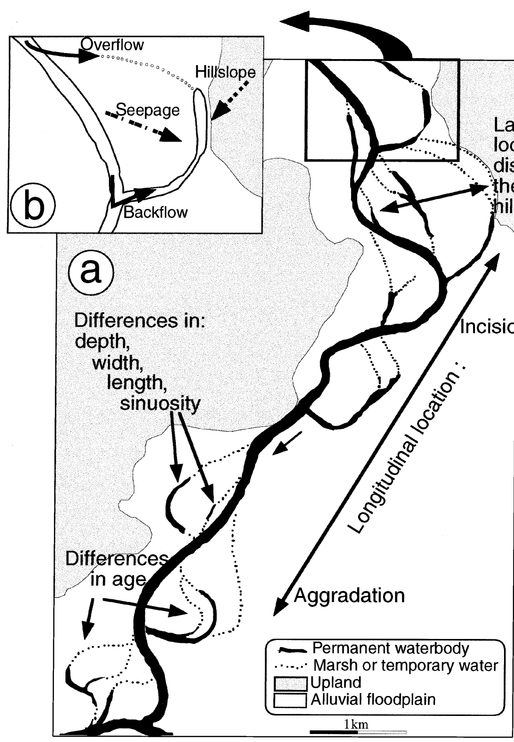

Fig. 1 Ain River, France: (a) spatial heterogeneity at the floodplain scale with indication of the main factors involved; (b) hydrological connectivity at the waterbody scale.

the diversity of biotically important habitat conditions results primarily from: (1) the distance from the patch (i.e. the floodplain waterbody) to the river; (2) the existence of permanent versus temporary connections to the river; and (3) the size and shape of the waterbody, which can be described by its length, width, depth and sinuosity. Within a floodplain, sinuosity determines the relative slope of each waterbody, which, when combined with hydraulic capacity (width × depth) determines the flow velocity and the consequent scouring potential of river overflow during floods. Fluvial dynamics can also instigate shifting mosaics at the scale of each floodplain waterbody (Kalliola & Puhakka, 1988; Henry, Bornette & Amoros, 1994; Bornette & Amoros, 1996). At the waterbody scale, patches are the small cleared-off areas resulting from vegetation removal and erosion of the substratum, as well as freshly deposited bars.

Habitat diversity resulting directly from fluvial dynamics is increased through a combination of different types of hydrological connectivity. Three kinds of hydrological connectivity may be distinguished according to the water origin: (1) river water (permanent connections at both ends, permanent connection only downstream, and temporary connection occurring only during high river stages and floods); (2) groundwater from river infiltration (seepage within the alluvial aquifer); and (3) groundwater from hillslope aquifers. Depending on these resulting spatial heterogeneity of water bodies (temporal dynamics are addressed below), four major habitat components directly influence biodiversity patterns between and within floodplain waterbodies: water temperature, suspended solids/turbidity, nutrient content, and substrata composition.

Water temperature

A great diversity in water temperature can be observed at any given time between the waterbodies of the same floodplain. In braided New Zealand rivers, Mosley (1983) measured temperatures ranging between 17.2 and 35 °C. In a lowland reach of the Tagliamento River, Tockner, Malard & Ward (2000) reported a difference of 15 °C in surface waters. This thermal diversity results from both the different origins of the water and the size of the floodplain waterbody. Waterbodies supplied by groundwater exhibit relatively constant temperatures and may serve as 'cold-water' refugia for biota in summer (Tockner *et al*. 2000), while patches supplied by surficial water experience large variations in temperature. In a floodplain of the Rhône river, Bornette, Amoros & Lamouroux (1998) measured, over an annual cycle, a mean temperature of 12.3 ± 0.6 °C in a braided side-arm supplied by groundwater versus 19.4 ± 8.6 in a side-arm supplied by the river, and 15.3 ± 5.1 in the main Rhône River. The size of a waterbody also influences its thermal condition. For example, Juget, Amoros & Gamulin (1976) measured 24.8 °C in a 100-m wide former meander of the Rhône versus 15.7 °C in a 8-m wide former braided channel surrounded by a riparian forest. The role of cold-water refugia of the waterbodies supplied by groundwater was demonstrated by Bornette, Amoros & Lamouroux (1998) who found in such waterbodies numerous species occurring nowhere else in the floodplain but often observed in colder mountainous areas or in northern regions.

Suspended solids and turbidity

The amount of suspended solids and the consequent turbidity depend mainly on the origin of the water. Groundwater is characterised by a very low suspended load while rivers transport a lot of suspended matter. The decreased water transparency reduces the macrophytes of the floodplain waterbodies and leads, in some cases, to plant burial (Rybichi & Carter, 1986; Sparks, Bayley & Kohler, 1990). The timing of connection as a result of floods is important because the effects of flooding on vegetation vary greatly between winter and summer (Junk, 1999). Phytoplankton is also negatively affected by the high content of suspended solids resulting from river overflows (Hamilton & Lewis, 1987; Köhler, 1994). At the riverscape scale, Martinet, Juget & Riera (1993),working on a floodplain of the Rhône and Heiler *et al*. (1995), studying a floodplain of the Danube demonstrated a progressively higher load of suspended solids together with a decreasing organic content with increasing connectivity to the main channel. In disconnected waterbodies, turbidity mainly depends on phytoplankton development, which is controlled by the nutrient content of the water (Fisher, 1979; Seger &

Bryan, 1981; Hein *et al*., 1999; Tockner *et al*., 1999a). Within cut-off channels still connected at their downstream end, both Juget *et al*. (1979) and Heiler *et al*. (1995) showed longitudinal gradients of turbidity decreasing with distance to the main river, as a result of river backflow.

Nutrient content

Dissolved nutrient content of riverscape patches generally increases with connectivity to the river, which provides the patches with nutrient-rich water and sediment (Van den Brink, De Leuw & Van der Velde, 1993; Heiler *et al*., 1995; Knowlton & Jones, 1997; Schiemer, Baumgartner & Tockner, 1999). The nutrient content of the floodplain waterbodies also depends on the retention time of the water and its uptake by primary producers (Brock, Van der Velde & Van de Steeg, 1987; Tockner *et al*., 1999a), as well as on the nutrient content of groundwater supplies. Seepage from river infiltration is generally nutrient-rich (Trémolières *et al*., 1993; Tockner *et al*., 1999a), while in some locations hillslope aquifers provide nutrient-poor water (Kohler & Schiele, 1985; Carbiener *et al*., 1990; Bornette & Amoros, 1991; Dole-Olivier, 1998). In disconnected waterbodies, nutrient content also depends on surrounding land use and successionnal stage (Bornette *et al*., 1998).

Within single cut-off channels of the Rhône (Juget *et al*., 1979) and Rhine (Klein, Robach & Vanderpoorten, 1995) floodplains, longitudinal gradients in nutrient content resulted from upstream groundwater supplies mixing with river backflowing at the downstream end. Robach, Eglin & Trémolières (1993) also demonstrated, along a braided side-arm, a self-purification process leading to a 70% decrease in ammonia and a 20% decrease in phosphate content. Conversely, Klein & Carbiener (1988) and Robach *et al*. (1993) observed an increasing nutrient content in areas of frequent overflows.

Substrata

Sediment grain-size and chemical composition play an important role in macrophyte rooting and survival (Barko & Smart, 1986; Barrat-Segretain, 1996) and in providing suitable habitat conditions for benthic macroinvertebrates and lithophilous fish spawning (Balon, 1985; Obrdlik & Fuchs, 1991; Tockner, Schiemer & Ward, 1998). In floodplain waterbodies of temperate riverscapes, Rostan, Amoros & Juget (1987), Shields & Abt (1989), Schwarz, Malanson & Weirich (1996), Tockner & Bretschko (1996), Nicolas & Pont (1997) and Tockner *et al*. (1998) showed clear relationships between the grain-size and composition of the substratum and three factors: waterbody connectivity, distance from the river, and deposition conditions. In waterbodies connected at both upstream and downstream ends, the substratum usually ranges from medium to coarse-grain mineral sediment (i.e. sand, gravel or pebble), depending on the frequency of connection and scouring flow velocity. Waterbodies connected only downstream are characterised by a fine mineral sediment (clay, silt) with moderate organic content, resulting mainly from backflow inputs and deposits combined with the *in situ* production and deposition of organic matter. The sediment of disconnected waterbodies consists of deposits of autogenic organic matter.

Biodiversity

According to Whittaker (1972) three components of species diversity may be distinguished: α-diversity corresponds to within-community diversity, which may be measured as the species number within a floodplain waterbody; β-diversity corresponds to between-community diversity and is related to the rate of spatial turn-over of species (Caley & Schluter, 1997), which may be calculated as the inverse of the average number of waterbodies inhabited by each species occurring within a riverscape (Ward, Tockner & Schiemer, 1999) or as follows (Harrison, Ross & Lawton, 1992):

$$\beta = [(\gamma/\bar{\alpha}) - 1]/(N - 1) \times 100$$

where γ is the regional diversity (e.g. the total number of species within a riverscape, see below), $\bar{\alpha}$ is the mean α diversity (local diversity) and N is the number of sampled habitats within the region. β varies between 0 (complete similarity: all regional species occur in all habitats) and 100 (complete dissimilarity: each species occurring in a single habitat). Connectivity and movements between waterbodies should act as a homogenising force, thus decreasing β diversity, whereas spatial habitat heterogeneity and niche differences among species (i.e. habitat requirements of each species) should increase β diversity (Tockner, Schiemer & Baumgartner, 1999b). At the landscape scale, γ diversity is the total diversity that is a function of the within-habitat species diversity (α diversity), between-habitat species diversity (β diversity) and the habitat diversity (spatial heterogeneity of the landscape) (Ward *et al.*, 1999). Because fluvial hydrosystems may be viewed as hierarchical nested systems (Frissell, Liss & Warren, 1986; Petts & Amoros, 1996; Ward *et al.*, 1999), the total diversity (γ diversity) at a given scale becomes the within-spatial unit diversity (α diversity) at the next higher scale. Ward *et al.* (1999) documented and discussed these components of biodiversity for gastropods, amphibians and fish, at the habitat-zone level within waterbodies, to the scale of the Alps region (comparison of Danube, Rhine and Rhône Rivers) through to the floodplain waterbody types and different reaches of the Austrian Danube floodplain. Fish α diversity was found to decrease with the increasing disconnection of waterbodies, while β diversity showed the opposite pattern. In connected waterbodies the number of species differed between individual floodplains, but species composition was generally similar, including mainly rheophilous species. Disconnected waterbodies had a similar number of fish species in the floodplains, but species composition was very different, depending on local habitat conditions. Recent investigations on fish communities related to connectivity gradients in riverscapes (e.g. Baker, Killgore & Kasul, 1991; Copp, Guti & Rovny, 1994; Persat, Olivier & Pont, 1994; Nicolas & Pont, 1997; Gozlan, Mastrorillo & Dauba, 1998; Schmutz & Jungwirth, 1999; Jungwirth, Muhar & Schmutz 2000; Schiemer 2000) supported the conclusions of Ward *et al.* (1999), emphasising the role of ecological requirements and life-history strategies in fish distribution and the biodiversity of riverscapes.

The amphibian communities (Morand & Joly, 1995; Tockner *et al.*, 1998, 1999b; Ward *et al.*, 1999) exhibited quite a different pattern. Their α diversity increased with the decreasing connectivity of floodplain waterbodies, whereas β diversity exhibited an opposite pattern. The capability of amphibian movements between waterbodies without hydrological connectivity acts as a homogenising factor, which decreases the β diversity between disconnected waterbodies. The high β diversity in connected waterbodies results from the high number of species-poor habitats. These patterns can be explained by fish predation, which is expected to increase with hydrological connectivity to the river and water permanency.

Opposite patterns in α diversity may even occur within a single taxonomic group. Along the lower Missouri floodplain, Bodie, Semlitsch & Renken (2000) reported peaks of freshwater turtle diversity at both ends of the connectivity gradient. The most connected, turbid and insect-poor waterbodies supported the highest proportions of lotic turtles, while the disconnected, insect rich waterbodies supported the highest proportion of lentic turtles.

Among studies on macroinvertebrate communities along connectivity gradients in riverscapes (e.g. Foeckler, Diepolder & Deichner, 1991; Obrdlik & Fuchs, 1991; Moog, Humpesch & Konar, 1995; Chwala & Waringer, 1996; Van den Brink, Van der Velde & Buijse, 1996; Tockner *et al.*, 1999b), Castella, Richardot-Coulet & Roux (1991) observed a higher α diversity in the waterbodies of the Ain floodplain, which is characterised by high fluvial dynamics (highly connected waterbodies, intermediately disturbed), but a higher β diversity in the Rhône floodplain, which has the highest number of disconnected waterbodies.

Several authors have investigated the macrophyte communities of waterbodies within floodplains in relation to their connectivity to the river (e.g. Van der Valk & Bliss, 1971; Kalliola & Puhakka, 1988; Jongman, 1992; Robach, Eglin & Tremolières, 1997; Bornette *et al.*, 1998; Vanderpoorten & Klein, 1999). Bornette, Piegay & Citterio (2001) addressed aquatic plant diversity at two hierarchical levels. They compared the macrophyte communities of the waterbodies within and between four river floodplains from the same region (catchment). Both α and β diversities appeared higher at the between-river level than at the within-river level, except for the Saône River, which is less dynamic and has lower α diversity and higher β diversity (similar to β diversity between-rivers). At between-river levels, α diversity increased with increasing slope (i.e. increasing flow velocity and thereby disturbance during unpredictable upstream-connection events) and the decreasing nutrient content of water. This result supports the hypotheses about the role of intermediate disturbance levels and productivity in enhancing biodiversity (Connell, 1978; Huston, 1979; Amoros & Bornette, 1999; Ward *et al.*, 1999). At the within-river level, the waterbodies of a floodplain on the Rhône were the only ones to exhibit a pattern similar to that described by Ward *et al.* (1999) for the Danube floodplain. The Rhône, like the Danube, has experienced a decrease in hydrological connectivity resulting from channelisation, levee construction and impoundment since the end of the 19th Century (Petts, Moller & Roux, 1989). Within three other floodplains studied by Bornette *et al.* (2001), the complex relationship between aquatic plant diversity and habitat conditions (including hydrological connectivity) resulted from the antagonistic effects of connectivity (see below).

The complexity of biodiversity patterns upon connectivity gradients in floodplain riverscapes results also from the shifting peaks of taxonomic diversity. This diversity, in turn, depends on the ecological requirements of the species, their niche breadth and their life-history strategies. For example, in the Austrian Danube riverscape, studied by Tockner *et al.* (1998), most fish species were recorded in the more connected waterbodies, while amphibians peaked in disconnected waterbodies. Benthic macroinvertebrates were species-rich in dynamically connected waterbodies, whereas macrophytes peaked in semi-disconnected waterbodies (Fig. 2).

Connectivity and complementary habitats

In addition to the biodiversity that results from the relationships between species niche breadth and spatial heterogeneity, hydrological connectivity plays a crucial role for species that require different habitat conditions during their life-cycle. Several studies have demonstrated that many fish species exhibit habitat shifts during ontogeny because of their changing requirements for flow velocity, water temperature, substrate grain-size, and food (Welcomme, 1985; Copp, 1989; Schiemer & Waidbacher, 1992; Copp *et al.*, 1994; Sempeski & Gaudin, 1995a,b,c; Muhar, 1996; Schmutz & Jungwirth, 1999; Jungwirth *et al.*, 2000; Schiemer, 2000). Fish movements between complementary habitats of the riverscape, especially to spawning and nurseries areas, are crucial for the recruitment and sustainability of fish populations. These movements greatly depend on the availability of complementary habitats within the riverscape and their hydrological connectivity.

Moreover, some waterbodies of the floodplain may serve as refugia during natural (e.g. flash floods) or anthropogenic (e.g. accidental pollution) disturbances of the main channel and thus contribute to the recovery of the river-floodplain system (Poff & Ward, 1990; Sedell, Reeves & Hauer, 1990).

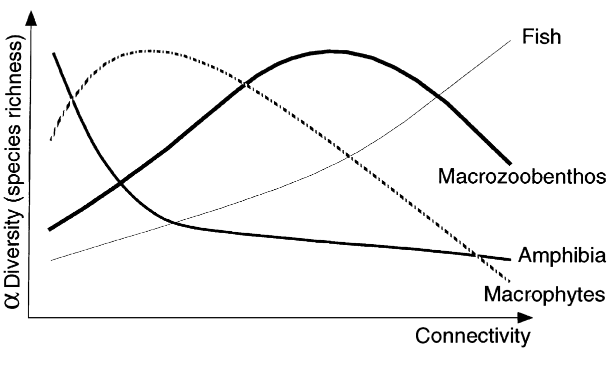

Fig. 2 Idealised α diversity patterns of different biota in relation to river connectivity in a Danube floodplain, Austria (modified from Tockner *et al.*, 1998).

Antagonistic effects of connectivity

The effects of hydrological connectivity reported in the literature sometimes appear to be contradictory. For example, Lloyd & Walker (1986) reported higher fish species diversity in waterbodies connected downstream than in disconnected ones, whereas Roberts & Ludwig (1991) observed higher fish diversity in disconnected waterbodies. A decrease in aquatic vegetation because of inputs of suspended solids that increased water turbidity was reported by Sparks *et al.* (1990). Van den Brink *et al.* (1993) also demonstrated a decrease in rooted plant communities in connected waterbodies, because of high turbidity resulting from nutrient inputs and thereby greater development of phytoplankton. Knowlton & Jones (1997), in contrast, observed higher turbidity in disconnected waterbodies resulting from high phytoplankton development in permanently standing water. These apparent contradictions arise because the effects of hydrological connectivity cannot be reduced to a simple gradient. Several phenomena interact as a result of these connections.

When a floodplain waterbody becomes connected to the river during a flash flood, flow velocity increases, breaking and uprooting aquatic plants, eroding the sediment and scouring away organic as well as mineral material. These unpredictable disturbing effects result from the flow velocity which, within a given riverscape, depends mainly on the slope of the connected waterbody. Several connected waterbodies may experience different flow velocities resulting from varying slopes because of differing sinuosities: straight (very low sinuosity) former channels (e.g. braided side-arms) may experience a very high velocity, while sinuous ones (e.g. former meanders or oxbow lakes) may only experience a rise in standing water levels without any disturbing effect on aquatic organisms (Bornette & Amoros, 1996). Very frequent connections with high flow velocity impede any settlement of aquatic plants. In accordance with the 'Intermediate Disturbance Hypothesis' (Connell, 1978), higher species diversity is expected in waterbodies that connect with intermediate frequency (Amoros & Bornette, 1999; Ward *et al*., 1999). In that case, the scouring effect of water velocity should disturb the aquatic vegetation and thereby reduce interspecific competition, allowing the co-occurrence of the maximum number of plant species. However, this maximum number also depends on: (1) the trophic status of the waterbody; (2) propagule inputs, and (3) the availability of regeneration niches required for the recruitment of colonising species.

Nutrient enrichment resulting from connectivity to the river favours the settlement and development of new plant species in cleared areas. However, species diversity declines significantly with high nutrient content, because high nutrient availability promotes phytoplankton development as well as the growth of free floating plants, both of which decrease light penetration to the bottom and thereby hinder colonisation by rooted species (Phillips, Eminson & Moss, 1978; Hough, Fornwall & Negele, 1989; Van den Brink *et al*., 1993).

River flows transport plant propagules, which may colonise the connected waterbodies (Nilsson, Gardfjell & Grelsson, 1991; Johannson, 1993; Johannson & Nilsson, 1993; Coops & Van der Velde, 1995; Cellot, Mouillot & Henry, 1998). However, to be recruited, propagules need suitable regeneration niches (*sensu* Grubb, 1977). Organically rich and flocculent sediment greatly reduce propagule establishment (Barko & Smart, 1986; Barrat-Segretain, 1996), whereas silt inputs and deposits resulting from hydrological connectivity to the river usually provide suitable regeneration niches for rooted species (Bornette *et al*., 2001). Excessive suspended solids increases water turbidity and impedes rooted species recruitment (Sparks *et al*., 1990), but free-floating species (e.g. Lemnaceae) may be recruited at the water surface if the water is sufficiently nutrient-rich. Moreover, silt input and deposition may alter both surficial and vertical connectivity dynamics through the terrestrialisation of the waterbodies and the construction of alluvial bars at their connecting ends.

Connectivity dynamics

Short-term dynamics

Floodplain waterbodies are either permanently (over short time scales, such as months or years) connected to the river, or separated from it by alluvial deposits resulting from natural levees, artificial levees or embankments. As each disconnecting element has a given elevation, it can be overflowed when the river level reaches a certain stage. Consequently, some low-elevation alluvial bars deposited at the ends of former braided side-arms, may be frequently overflowed during small increases in river discharge below bankfull stages, while highly elevated constructed levees may rarely be overflowed (e.g. decennial, centennial or even less frequent flood). Recently, Tockner *et al*. (2000) have proposed to extend the Flood Pulse Concept (Junk, Bayley & Sparks, 1989) to take into account the pulsing of river discharge below bankfull that determines the degree of hydrological connectivity and its ecological consequences.

In addition to these changes in surface connectivity, any variation in river level leads to a subsequent change in the water table of the alluvial aquifer, which, through its influence on the hillslope aquifer, may modify the groundwater supply (Fig. 3). During low water stages in the main river (phase A, Fig. 3), floodplain waterbodies may only be connected to the hillslope aquifer. During high water river stages (phase B, Fig. 3), the river infiltrating the alluvial aquifer elevates the water level within the waterbody, thereby reducing groundwater supplies from the hillslope aquifer. During phase B, waterbodies that are connected downstream to the river may also

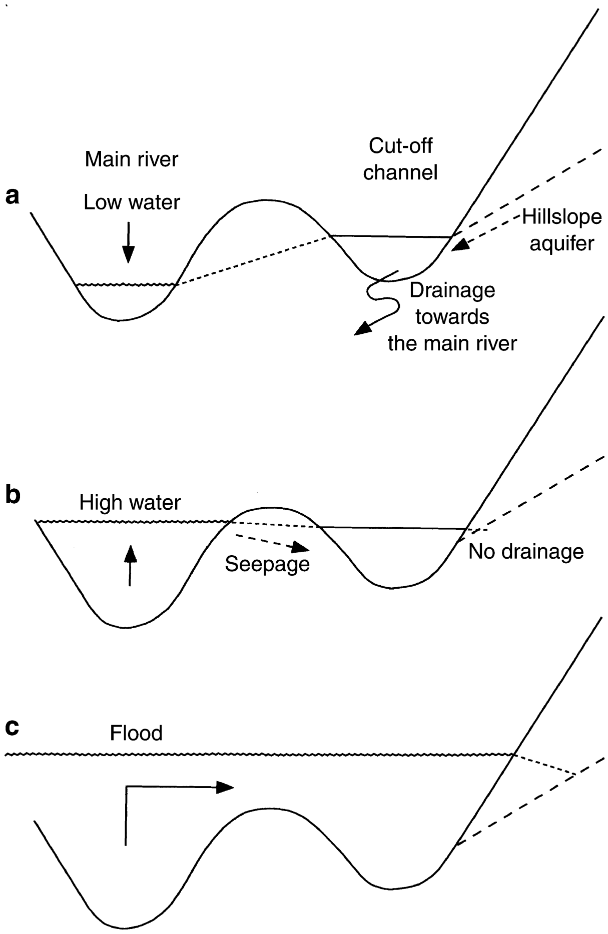

Fig. 3 Schematic illustration of the short-term dynamics of hydrological connectivity in relation to river stages: (a) (low-water stage), the floodplain waterbodies may be supplied by a hillslope aquifer; (b) (high-water stage), the floodplain waterbodies are supplied by river infiltration into the alluvial aquifer and possibly by river backflow through a downstream connection; (c) (flood), the floodplain waterbodies are supplied by overbank flow.

experience river backflow. During river floods (phase C, Fig. 3), waterbodies are supplied by overbank flow. Depending on their location within the floodplain (distance to the river, local topography), certain waterbodies experience only phase A (hillslope groundwater supply) or phases A and B (seepage supply) (Bornette *et al.*, 1998). In the floodplain of Upper Rhine Carbiener *et al.* (1990) reported that in some cases, the upstream part of a given side-arm may experience only phase A, the middle part phases A and B, whereas the downstream part may experience all three phases. In a floodplain of the Upper-Rhône Juget *et al.* (1979) demonstrated an increase in nutrient content from phase A (supplied by nutrient-poor hillslope groundwater) to phase C. In an Austrian Danube floodplain, phase A [called the 'disconnection phase' by Tockner *et al.* (1999a) because they observed no vertical connection to a hillslope aquifer] is also characterised by a decrease in nutrient content, which in this case is explained by material sedimentation, nutrient uptake and grazing. Whether or not a waterbody is supplied by nutrient-poor hillslope groundwater, phase A appears as a low or medium production phase (Ertl, 1985; Furch & Junk, 1993; Hein, Schagerl & Heiler, 1996; Tockner *et al.*, 1999a). Phase B is a high planktonic production phase as the increasing seepage inflow provides high nutrient input, which combined with high water transparency and relatively long residence times, favours phytoplankton development (Forsberg, Devol & Richey, 1988; Van den Brink *et al.*, 1993; Riedler & Schagerl, 1998; Hein *et al.*, 1999; Tockner *et al.*, 1999a). During phase C, river overflows may scour away a large part of the organic material produced during the previous phases, depending on the slope of the waterbody and hence the flow velocity (Amoros, Gibert & Greenwood, 1996). Consequently, Tockner *et al.* (1999a) defined phase C as the 'transport phase'.

The pulsing connectivity described here is important not only for the exchange of nutrients and organic matter, and therefore ecosystem processes on the landscape scale, but also for the exchange of living organisms between the diverse patches of the riverscape, which is crucial for the recruitment of numerous animal and plant species. In temperate river floodplains, the timing of episodic surficial connectivity is of paramount importance for fish reproduction, which is related to water temperature (Sparks *et al.*, 1990; Roux & Copp, 1996; Junk, 1999). The alternation of turbid water and silt inputs (during phase C), which provide sediment regeneration niches, and clear water phases during phases A and B, makes the settlement and development of rooted plant species possible (Amoros & Bornette, 1999).

Long-term dynamics

At scales ranging from decades to centuries, interactions between processes operating at diverse spatial and temporal levels increase the biocomplexity of riverscapes. Ecological succession is both a source of spatial heterogeneity and a disconnection factor. Bravard, Amoros & Pautou (1986) and Salo, Kalliola & Hakkinen (1986) showed that floodplain landscapes are mosaics of patches differing in successional stages. Such differences result from both the succession type, depending on habitat conditions (e.g. terrestrial versus aquatic, disturbance regime, origin and quality of water supply), and the stage within each succession type. The latter depends both on when the succession begins (e.g. date when a channel was cut off), and the succession rate (depending on autochthonous productivity and the rate of input and deposition of organic and mineral material).

Succession that develops at the connecting ends of floodplain waterbodies also accelerates the disconnection of these waterbodies. For example, after a meander is cut off, a decrease in flow velocity at its upstream end results in alluvial deposition that leads to the formation of an alluvial plug. The reduced water depth at this plug permits the colonisation and development of aquatic plants, which in turn constitute an obstacle to water flow, reducing the water velocity further, thus increasing alluvial deposition and so on. Such positive feedback accelerates the accretion of the alluvial plug and its terrestrialisation until shrubs and then trees can colonise. The same phenomena occur at the downstream end, when the former channel is supplied by backflowing water, experiencing a decrease in water velocity. Consequently, the terrestrialisation of the ends of former channels tends to gradually reduce the frequency of hydrological connections to the main river. However, in pristine conditions, river dynamics, through lateral erosion and main channel migration, can create new side-arms and cut-off active meanders, which become highly connected patches, where new succession can start (Amoros, Rostan & Pautou, 1987a; Kalliola, Salo & Puhakka, 1991). Piegay, Bornette & Citterio (2000) have shown that lateral migrations of the main channel of the river can also greatly modify the succession rates and, in some cases, even reverse the succession: (1) when the main channel migrates towards the downstream end of a floodplain waterbody, the erosion of the alluvial plug and the slope between the waterbody and the river increase as a result the water level is lowered within the waterbody and terrestrialisation is accelerated; (2) on the contrary, when the main channel migrates towards the upstream end of a waterbody, the erosion of the upstream alluvial plug increases the frequency of floods scouring the waterbody, thereby regressing the succession; (3) when the main channel migrates from the upstream end of a waterbody, the frequency of the scouring floods decreases, thereby permitting succession to proceed; and (4) when the main channel migrates from the downstream end of a waterbody, the length of the waterbody may increase if the downstream connection is sustained by a groundwater supply from a hillslope aquifer.

Ecological succession also tends to reduce vertical connectivity as the amount of organic matter and fine mineral (silt, clay) deposited increases with successional development (Rostan *et al*., 1987; Schwarz *et al*., 1996). These organic and fine materials gradually decrease the porosity of the coarse-grain-bed substratum, leading to a drastic reduction of groundwater exchange (Wood & Armitage, 1997). However, this clogging process may be reversed by bed erosion resulting from scouring overflows, whose occurrence depends on the maintenance of surficial connectivity (see above).

The effects of ecological succession and river dynamics interfere with those of another long-term process, river bed incision. River bed incision results from a wide variety of causes, both natural and anthropogenic, all of which generate a situation where the bedload transport capacity of the river exceeds the supply of bed material, and the river thereby deepens its channel (Galay, 1983; Petts, 1984; Erskine, 1992; Darby & Simon, 1999). Incision of the river bed leads to a lowering of the river level and subsequent lowering of the alluvial aquifer's water table. Consequently, increasing elevation differences between alluvial plugs forming at the ends of floodplain waterbodies and the mean river level, lead to a decline in surficial connectivity (Foeckler *et al*., 1991; Babinski, 1992; Bravard, Amoros & Pautou, 1997). Lowering of the alluvial aquifer's water table also leads to a decrease in vertical connectivity with regards to seepage inflow, but where the waterbodies are supplied by hillslope groundwater, the river bed incision may actually increase the connectivity with such hillslope groundwater, leading to oligotrophication of the ecosystem (Bornette & Heiler, 1994; Bornette, Amoros & Rostan, 1996). The bedload eroded in incised reaches tends to be deposited in downstream reaches where flow velocity is reduced. Therefore incising rivers show a longitudinal succession of deepening and aggrading reaches (Petts, 1984; Marston, Girel & Pautou, 1995; Darby & Simon, 1999). In aggrading reaches, the mean river level and the alluvial water table tend to rise, increasing both surficial and vertical connectivity (Bornette *et al.*, 1996; Piegay *et al.*, 2000).

Conclusion

Riverscapes include all floodplain waterbodies that are more or less connected through surface or subsurface waterways to the river, alluvial aquifer or hillslope aquifer. Riverscapes are characterised by high α, β and γ diversity as well as high diversity of life history strategies that result from the combination of complex gradients of habitat conditions and hydrological connectivity. This complexity is because of the interaction between several processes, which operate at different spatial and temporal scales (Fig. 4).

Ecological succession that progresses in the floodplain waterbodies modifies, at a decennial-to-centennial scale, the habitat conditions and species composition of each waterbody. At the riverscape scale, succession generates a mosaic of patches resulting from the co-occurrence of different successional stages caused by: (1) different initial habitat conditions (cf. river dynamics at the floodplain level); (2) different ages (cf. starting date of the succession); and (3) different successional rates related to ecosystem productivity (cf. origin of water supply) combined with the net effects of local scouring versus silting (cf. local disturbances from river dynamics) and pulsing connectivity (cf. alternation of production and transport phases). Through the development of vegetation that slows flow velocity and the production and deposition of organic matter, ecological succession also tends to reduce surface and subsurface connectivity which may act as feedback on the effects presented above.

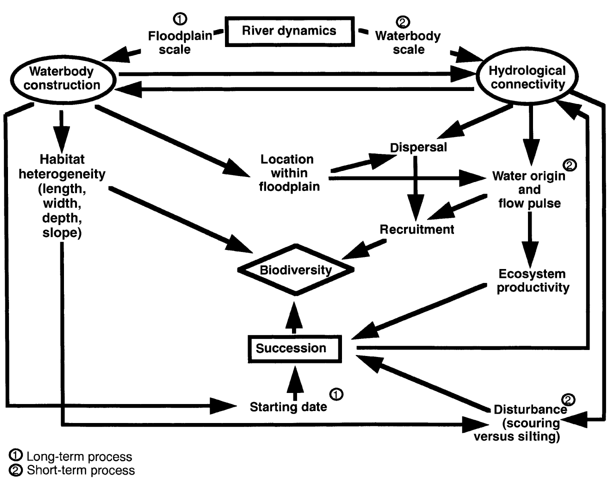

Fig. 4 Simplified diagram to illustrate biocomplexity resulting from interactions between processes operating at different spatial and temporal scales.

River dynamics through lateral erosion and long-term channel migration at the riverscape scale, destroy and generate diverse habitats that differ in their geomorphology (i.e. depth, width, length, sinuosity) and sediment grain-size. In addition to increasing habitat heterogeneity, the creation of habitats highly connected by river dynamics compensates for ecological succession at the riverscape scale. River dynamics also determine the location of each waterbody within the alluvial floodplain: its transversal location is defined by the distance between the river and any hillslope aquifer; its longitudinal location is related to any incision versus aggradation reaches (Fig. 1). Both locations highly influence surface and subsurface hydrological connectivity. River dynamics may also produce short-term, local scouring or silting effects within waterbodies – depending on their location, their surface connectivity and their geomorphology such as hydraulic capacity and slope – and can thus decrease or increase successional rates and the disconnecting effects of ecological succession. Scouring, silting and river channel migrations are greatly influenced by river bed incision, which is a long-term process depending, in turn, on catchment influences.

The origin of the water supply (river, river infiltration and seepage, hillslope aquifer) depends on the waterbody's location and its surface and subsurface hydrological connectivity. The water's origin determines the water temperature, turbidity and nutrient content, which greatly influence habitat heterogeneity, plant and animal recruitment, and ecosystem productivity.

Pulsing connectivity controls nutrient inputs and the alternation of production and transport phases.

The duration and timing of each phase is important, not only for ecosystem productivity, but also for species recruitment, which is related to thermal seasonality. Pulsing connectivity depends on the hydrological regime of the river, which is influenced by processes operating on the catchment scale, and by the local topography and sediment porosity. In the long term, pulsing connectivity is also influenced by river bed incision.

Anthropogenic impacts, including the alteration of natural flow pulses, channelisation, dredging, artificial levee construction and groundwater abstraction, reduce spatial heterogeneity as well as hydrological dynamics. Moreover, because embankments block river dynamics and impede lateral erosion (Bravard *et al.*, 1986; Amoros *et al.*, 1987a), the decline in connectivity resulting from ecological succession can no longer be compensated for by river dynamics.

Because the diversity of each taxonomic group peaks at a different position on the connectivity gradient, riverscape management and restoration strategies should not focus on a single taxonomic group, a single hierarchical level of diversity, or a single degree of connectivity, but instead on sustaining or restoring the hydro-geomorphological dynamics in order to increase spatio-temporal heterogeneity. Riverscape management and restoration strategies should be process-oriented and embedded within a holistic framework that takes into account the driving processes and their interactions, that operate at different spatial and temporal states.

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