ECOLOGY OF BRAIDED RIVERS

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Abstract

Braided gravel-bed rivers are widespread in temperate piedmont and mountain-valley areas. In their pristine state, braided rivers are characterized by a shifting mosaic of channels, ponds, bars, and islands, since both flow and flood pulses create a diversity of habitats with fast turnover rates. Large wood has a major role in determining the geomorphology and ecological functioning of these rivers. Braided river habitats are colonized by a diverse fauna and flora adapted to their dynamic nature including a significant proportion of highly endangered species. Animals exhibit high mobility, short and asynchronic life cycles, and ethological and phenological plasticity. Braided gravel-bed rivers also offer various categories of refugia such as shore areas, hypogeic and hyporheic habitats that are pivotal for maintaining diversity in the face of frequent disturbances. Today, however, most gravel-bed rivers bear little resemblance to their highly dynamic natural state due to anthropogenic modifications, and most braided rivers have been converted into incised single-thread channels. Gravel bars and vegetated islands are among the most endangered landscape elements worldwide. They are very sensitive to channelization, gravel extraction, and flow regulation. Therefore, more than for most other ecosystems, restoring braided rivers and their landscape elements means restoring their underlying hydrogeomorphic dynamics.

1. Introduction

Natural rivers are dynamic, and physically and biologically complex (Tockner & Stanford, 2002). They are characterized by a set of fluvial styles including straight, braided, wandering, and meandering channels (Richards et al., 2002). Conditions which promote braided channel formation include (i) an abundant supply of sediment, (ii) rapid and frequent variations in water discharge, and (iii) erodable banks of non-cohesive material (Church & Jones, 1992).

Braided gravel-bed rivers were once widespread in temperate piedmont and mountain-valley areas, primarily in regions containing young, eroding mountains (e.g. Alaska, Canada, New Zealand, the Himalayas, European and Japanese Alps; Fig. 1a). Today, most gravel-bed rivers bear little resemblance to their highly dynamic natural state. A recent survey of all Austrian rivers with a catchment area of >500 km^2 showed that formerly braided sections have been particularly affected by channelisation and flow regulation (Muhar et al., 1998), with 25% of confined river sections, but only 1% of braided sections, remaining intact. Braided rivers are among the most endangered ecosystems (Sadler et al., 2004). However, in Europe, Japan and in most parts of the USA, remaining braided rivers are among the very limited areas - in otherwise highly managed landscapes - where natural large-scale disturbances still are allowed to occur. Therefore, they serve as excellent model systems to study the relationship between multiple disturbances (floods, droughts) and ecology and to elaborate upon the complex relationship between habitat complexity and biodiversity. Braided rivers are also key areas for conservation and restoration since they provide habitat for a highly endangered fauna and flora (Tockner et al., 2003; Sadler et al., 2004). The understanding of their natural complexity and dynamics, however, forms the prerequisite for developing sustainable management schemes (Ward et al., 2001).

Though geomorphic knowledge of braided rivers is quite abundant (e.g. Billi et al., 1992; Best & Bristow, 1993; Richards et al., 2002; and references therein), only scattered

information is available on their ecology (Plachter & Reich, 1998; Karrenberg et al., 2002; Robinson et al., 2002; Ward et al., 2002). In this paper we provide a general introduction to the ecology of braided rivers, primarily to those with gravel beds. Braided sand-bed rivers such as the famous Brahmaputra-Jamuna network are not included, although environmental conditions and ecological properties are supposed to be similar to gravel-bed rivers.

We start with a brief description of the specific environmental conditions of braided rivers. This is followed by an overview of their fauna and flora, and how species are able to cope with the hostile conditions of highly dynamic systems. Then, we discuss the importance of vegetated islands and parafluvial ponds in maintaining biodiversity, and we focus on shoreline communities and on the complex trophic linkages across the aquatic and terrestrial boundary. Finally, we provide some perspectives for future research on braided rivers. We frequently refer to the Tagliamento River in NE Italy, the largest remaining active gravel-bed river in Central Europe (Fig. 1b). On this river, an ongoing transdisciplinary research project integrates hydrology, geomorphology and ecology in order to understand the complexity and diversity of an Alpine braided river corridor (Ward et al., 1999b; Gurnell et al., 2001; Tockner et al., 2003; Francis et al., this volume).

2. The environmental template of braided rivers

Braided rivers consist of multiple channels with bars and islands and often with poorly defined banks of non-cohesive sedimentary materials. Cut and fill alluviation, channel avulsion, and production, entrainment and deposition of large wood (LW), coupled with ground- and surface-water interactions, create a complex and dynamic array of aquatic, amphibious, and terrestrial landscape elements, which can be referred to as the shifting habitat mosaic (SHM) (Stanford, 1998; Poole et al., 2002; Ward et al., 2002; Lorang et al., 2004).

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The SHM is composed of habitats, ecotones, and gradients that possess biotic distributions and biogeochemical cycles that change in response to fluvial processes. This mosaic allows many species to co-exist in the riverine landscape (Ward et al., 1999a; Robinson et al., 2002; Tockner & Stanford, 2002).

Habitat turnover

Frequently disturbed ecosystems with strong disturbance regimes such as braided rivers experience rapid turnover rates of the abiotic and the biotic components. This can create, for example, a high percentage of pioneer vegetation stages on freshly deposited sediments (e.g. Hughes, 1997). While the minimum age of the oldest floodplain sites on braided rivers, as a surrogate for turnover time, is often 100+ years, habitats in the active braided tract are very young in comparison. Along the Tagliamento River, Italy, ~60% of the aquatic area and 30% of vegetated islands were observed to have been restructured in just 2.5 years (Van der Nat et al., 2003b). The maximum age of vegetated islands was ~20 years (Kollmann et al., 1999). Parafluvial ponds and backwaters were the youngest habitats, with half-life expectancies of <7 months. The degree of habitat change was determined by flood magnitude, time since the last flood, and the presence of large wood and vegetated islands. The presence of vegetated islands led to an average increase in habitat age by providing more stable habitats (Gurnell & Petts, 2002). Overall, flood dynamics reconfigured the spatial environment, although the composition and diversity of aquatic habitats remained constant (Arscott et al. 2002). These high spatiotemporal dynamics conform very well to the shifting habitat steady-state concept proposed by Bormann and Likens (1979) and make braided rivers unique among terrestrial and aquatic ecosystems.

Expansion and contraction dynamics

Riverine floodplains are increasingly recognized as expanding, contracting, and fragmenting ecosystems (Stanley et al., 1997; Malard et al., 1999; Tockner et al., 2000). The extent, composition, and configuration of aquatic and terrestrial habitats vary in response to the pulsing of discharge. For example, in the braided Ohau River in New Zealand a gradual increase in flow from 26 to 507 m^3 s^{-1} generated additional channels with the same characteristics as those existing at lower discharge, and the total number of channels at a cross-section remained constant (Mosley, 1982). This process had major implications for instream uses such as salmonid spawning because the area suitable for spawning remained constant over a wide range of flows. In this respect a braided river was considered morphologically more stable than a single-thread river.

In the Val Roseg floodplain, a braided pro-glacial river, a distinct shift of individual water sources (groundwater, snowmelt water and glacial water) creates a complex mosaic of clear and turbid water patches during the seasonal expansion and contraction cycle (Malard et al., 1999). The annual flow pulse is highly predictable and exhibits a unimodal pattern (Ward & Uehlinger, 2003). Only a small proportion of the total channel network (ca. 2.4 km of the 25km channels) maintains benign environmental conditions (permanent flow, high substrate stability, low turbidity, and relatively high temperature). Periods of benign environmental conditions are restricted to short periods in spring and autumn ("ecological windows of opportunity" *sensu* Ward & Uehlinger, 2003). These ecological windows are crucial for instream primary production, growth of benthic organisms, and maintaining species diversity (e.g. Burgherr et al., 2002). For high alpine areas future climate change scenarios predict an increase of streams with snowmelt- and rain-dominated flow regimes (Ward & Uehlinger, 2003). Concomitantly, there will be major shifts in the timing and duration of the occurrence of "ecological windows". In contrast to pro-glacial ecosystems, most braided rivers show polymodal inundation patterns. The Tagliamento River, for example, exhibits a flashy flow regime with frequent dry-wet cycles and a linear relationship between water level and

inundated area (Van der Nat et al., 2002). On this river, inundation is primarily by lateral overspill of water from the main channel and by upwelling of alluvial groundwater.

During expansion and contraction cycles the boundary between water and land (shoreline) moves across the river-floodplain system (moving littoral *sensu* Junk et al., 1989). We can use shoreline length as an index of habitat quality and availability (Tockner & Stanford, 2002). In dynamic systems (e.g., Tagliamento River, Italy), shoreline length can be up to 25 km per river km and remains high throughout the annual cycle. In a regulated river (Danube Alluvial Zone National Park, the availability of shoreline habitats strongly fluctuates during the annual cycles of expansion and contraction. In channelised rivers (e.g., Rhône, CH) shoreline length is only about 2 km per river-km (Fig. 2). Decrease in shoreline length not only affects habitat availability for endangered communities but also impedes the exchange of matter and organisms between the river and its riparian area (see below).

Thermal heterogeneity

Temperature is a primary factor that regulates ecosystem processes and therefore structures biotic communities (Ward, 1992). Lateral and vertical heterogeneity in temperature has been recognized as an important aspect in habitat conditions along rivers (Brunke & Gonser, 1997; Arscott et al., 2001; Ebersole et al., 2003; Uehlinger et al., 2003). Across a braided reach of the Tagliamento River average daily temperature difference between the coolest and the warmest water body ranged from 4.0°C to almost 17°C; with maximum diel amplitudes within an individual water body of up to 26°C (Karaus et al., in press). A lateral thermal difference of up to 17°C on a given day corresponded to the observed difference along the entire 170-km long main river channel (Arscott et al., 2001). Water bodies in the braided river can be arranged along a gradient from low to high diel amplitudes and seasonal averages (Fig. 3). Factors that create and maintain thermal heterogeneity across the corridor include surface

connectivity to the main channel, input of alluvial and hillslope groundwater, and the presence of vegetated islands and large wood. Water bodies fed by alluvial and hillslope groundwater exhibit relatively constant thermal conditions. Shallow ponds situated in the bare gravel matrix show very distinct diel and seasonal temperature amplitudes. In particular the presence of vegetated islands and large wood leads to a decrease in the diel temperature amplitudes in floodplain ponds (Fig. 3).

For a comprehensive thermal characterization of rivers both aquatic and terrestrial habitats must be simultaneously investigated. Exposed gravel sediments may exhibit large diel temperature differences, with maximum values at the surface of up to 60°C during a hot summer day, while groundwater upwelling provides relatively constant cold water areas. Therefore, a major challenge in the near future will be the application of non-invasive methods such as infrared (IR) cameras to map thermal heterogeneity at large scales. This would allow us to identify critical spots for aquatic (cold-water refugia, spawning areas for salmonids; Toergersen et al., 1999; Baxter & Hauer, 2002) and terrestrial (shading by vegetated islands) organisms, and to monitor thermal patch dynamics (a similar phenomenon to the shifting habitat concept). Methods used so far for thermal assessment in streams and rivers are characterized by either high spatial (IR-spectroscopy; Torgersen et al., 1999) or temporal resolution (temperature loggers; e.g. Arscott et al., 2001; Uehlinger et al., 2003). However, modern IR-thermography makes detailed (high spatiotemporal resolution) and precise temperature measurements possible. IR-thermography has already been successfully used to measure temperatures of landscape elements such as rock outcrops, block glaciers, and snow fields from distances of 100m to several km (Tanner, 1999), and to estimate mammal density in wetlands (Naugle et al., 1996).

Surface and subsurface exchange processes

Braided rivers are complex above and below ground (Fig. 4). Subsurface habitats across a river-floodplain transect include the hyporheic zone beneath the channel (alluvium areas saturated in water), parafluvial zones that extend lateral to the channel (saturated areas), and unsaturated hypogeic sediments. Geomorphic heterogeneity and highly permeable substrates, particularly those composed of open framework gravels, facilitate high hydrologic connectivity. Considering different river styles, braided pattern is predicted to allow maximal subsurface-surface exchanges; therefore braided rivers are likely to present the highest diversity of surface and subsurface exchange types (Malard et al., 2002). Subsurface compartments may provide refugia for benthic organisms in unstable sites, but decrease in importance in more stable systems (Fowler & Death, 2001). As suggested by Pugsley and Hynes (1986), the hyporheic zone may offer many small-scale refugia for benthic organisms, thereby contributing to the stability (resilience) of the hydrosystem at large scale. The boundaries of the subsurface zones fluctuate in response to changes in surface water discharge and groundwater pressure. Hence, the extent of the subsurface habitats varies greatly in space and time.

Interstitial sediments act as "filters" for infiltrating surface water, and subsurface water that emerges to the surface may be of a different quality with important consequences for surface processes. A more stable temperature regime (see Fig. 3) is one of the most obvious cues for subsurface influence on surface water providing thermal refugia for stenothermic species (Arscott et al., 2001; Malard et al., 2001; Poole, 2002). Qualitatively, upwelling DOM (dissolved organic matter) is mainly biodegradable while refractory fractions seem to be physically adsorbed on sediments and the biofilm matrix (Claret et al., 1998). In addition, subsurface water that upwells is generally enriched in inorganic nitrogen and phosphorous. Therefore, upwelling water influences algae productivity, benthic assemblages, and locations of fish spawning (Brunke & Gonser, 1997; Stanford, 1998). Alluvial springbrooks, for example, provide thermal refugia for fish in addition to functioning as refugia during erosive

floods in the main channel (Baxter & Hauer, 2000). In the Nyack floodplain (Montana, USA), increased water availability (hydration) and nutrient delivery (fertilization) in upwelling areas is associated with significantly higher diversity and productivity of riparian plants compared to losing areas (Harner & Stanford, 2003). Subsurface-surface exchange also increases water residence time and enhances hydrological nutrient retention within the stream corridor. For example, in some streams the volume of the hyporheic zone exceeds that of the surface channel and may extend laterally for several kilometres in rivers with large alluvial floodplains (e.g. Stanford et al., 1994)

The significance of surface-subsurface exchanges on biodiversity is not limited to animals living beneath the surface, but may also concern surface organims. Subsurface inputs of water to the stream are often patchily distributed contributing to high spatial heterogeneity of habitat conditions in surface waters. Upwelling of subsurface water may maintain water levels or available moisture during dry periods, provides clear water as fine particles are trapped within the sediments, and adds cooler and more nutrient-rich water to the river.

While the hyporheic zone beneath the wetted channel is well known as an active component of the stream ecosystem, the unsaturated zone is a "black box", at least from the ecological point of view. However, extensive layers of unsaturated gravel, often several meters thick, are a key feature of braided rivers (hypogeic zone). If only parts of the extensive hypogeic crevasse system are accessible for riparian invertebrates it is likely to be the most extensive habitat within braided rivers (Plachter & Reich, 1998). Unsaturated sediments differ from saturated sediments in their physical characteristics. The top layer of the hyporheic zone is often clogged by fine particles and the hydraulic connectivity of unsaturated sediments is one to three orders of magnitude lower than that of saturated zones (Huggenberger et al., 1998). During the short inundation periods in high-gradient rivers sediments may remain unsaturated beneath the water surface. This unsaturated zone may be crucial for the survival

and the rapid recolonisation of terrestrial arthropods after flood and drought events. Little is known about which organisms are using these habitats and how they respond to fluctuating water tables. Dieterich (1996) exposed sediment cages at different depths within a gravel bar, and found a diverse invertebrate community comprising aquatic (oligochaeta, larvae of midges and stoneflies) and terrestrial (mites, rove beetles, ground beetles) species. High densities of terrestrial invertebrates occurred in winter, which underpins the potential role of unsaturated sediments as refuge areas during the cold season (e.g. for hibernation). Future research has to focus (i) on the physicochemical characterization (microclimate, sediment structure, organic matter content) of the unsaturated zone, (ii) on its functional role for the transformation of organic matter and nutrients (e.g. Claret et al., 1997), and (iii) on its importance as habitat and refuge areas for aquatic and, in particular, terrestrial invertebrates.

3. Life in braided rivers

From an ecological perspective, braided rivers are considered as hostile environments as (i) they are very dynamic systems shaped by frequent floods and periods of water stress, (ii) their channels flow through very unproductive areas of exposed gravel and sand (low organic content), and (iii) they are characterised by high fluxes of temperature and humidity (particularly on bare gravel surfaces). Although braided rivers are extreme environments located on the descending limb of a harshness-diversity curve, they show a very high overall biodiversity, and are particularly important regionally (Burgherr et al., 2002; Robinson et al., 2002; Tockner & Stanford, 2002). The high species richness and diversity in braided rivers can be explained by small-scale habitat mosaics encompassing aquatic habitats as well as terrestrial ones, by the presence of ecotones from the freshly created shoreline to mature riverine forests, and by multiple subsurface-surface exchange areas.

Rivers and floodplains are supposed to represent the ancestral conditions for many aquatic and terrestrial species and braided rivers are expected to be important centres of biological diversification. The speciation of groundwater crustaceans is supposed to be favoured by the shifting of river channels that lead to the isolation of formerly connected channels (e.g., cyclopids in the alluvial aquifer of the braided Danube River; P. Pospisil & D. Danielopol, pers. comm). Fittkau & Reiss (1983) suggested that dynamic river-floodplain systems belong to those aquatic ecosystems where biota of lentic areas (standing water bodies) started their evolution. The temporal continuity of riverine systems and their associated disturbance regimes allowed the permanent presence of lentic water bodies throughout time, which would have facilitated such evolution. Ancient crustacean orders such as Conchostraca and Notostraca (e.g., *Chirocephalus* spp. *Lepidurs apus*) still live in river-floodplain systems. An example is *Lepidurus apus,* which has as a species existed for more than 200 million years, and it is therefore presumably the oldest living species on earth (e.g. Eder et al., 1997). In alluvial spring-brooks, several species of the 'primitive' sub-families of Diamesinae and Prodiamesinae (Diptera, Chironomidae) still occur. Similarly, the Salicaceae (willows) originally developed along dynamic rivers and subsequently began to occupy more stable habitats, although the family is still primarily associated with rivers (Karrenberg et al., 2002). Some morphological and phenological characteristics related to their life on the active zone (e.g., small seed size) are highly conservative and have not changed in response to altered selection pressures during the course of evolution (Karrenberg et al., 2002).

Aquatic and terrestrial communities

The fauna of dynamic floodplain rivers comprises a mix of obligate terrestrial species to obligate aquatic species, ranging from meiofauna in the hyporheos to mammals on vegetated islands. In braided rivers, the interplay between vertical and lateral connectivity

results in diverse plant and faunal communities (see e.g. Robinson et al., 2002; Brunke et al., 2003). Lateral hydrological connectivity, for example, can be expressed as the duration of a water body connected at the surface to the main river channel. Along the Danube River (Alluvial Zone National Park, Austria), hydrological connectivity was the main determinant that explained the distribution of aquatic organisms across a river-floodplain gradient (Fig. 5; Tockner et al., 1998; Reckendorfer et al., in press). Most species exhibited a distinct preference for a specific degree of connectivity. Based on species-specific "connectivity-preferences" one can predict the potential effect of river regulation and river-floodplain restoration on community composition. Arscott et al. (2003) illustrated how differences in habitat stability, by comparing two contrasting headwater floodplains, influenced abundance and diversity patterns of caddis flies (Trichoptera). Beta diversity (spatial species turnover) was important for Trichoptera diversity in the highly dynamic braided river, whereas alpha diversity was high in a stable forested floodplain. This means that diversity is differently organized in braided rivers compared to more stable rivers. Similarly, Castella et al. (1991) illustrated how floodplain structure and dynamics influenced the scale at which invertebrates are organized. In the regulated Rhône River between-channel heterogeneity dominated, whereas in the more dynamic Ain River within-channel diversity dominated (i.e. higher alpha diversity within individual water bodies).

Distinct spatial differentiations of aquatic communities occur at even smaller scales. Around a large bar complex along the Fraser River (BC, Canada), Church et al. (2002) identified 13 aquatic habitat types on the basis of nine physical characteristics. Each of the habitats had a quite distinct fish assemblage, with eddy pools and channel nooks having the highest species diversity and fish density. Surprisingly, this demonstrated the relatively small spatial scale at which the fundamental connection is made between the biota and the physical system that supports them. The scale was set by the very local scale at which the animals differentiate their environment and adapt their behaviour. Another critical feature of habitat

units is their limited occurrence at very high flows. At flows above 7000 $m^3 s^{-1}$ most open bar tops in Fraser River become submerged and large numbers of fish occupied the relatively slack water there. Above 9000 $m^3 s^{-1}$ (i.e. approximately mean annual flood), there were significant currents over most bar tops, and bar-edge habitats disappeared. Therefore, at these discharge levels fishes that normally occupy these units must seek refuge elsewhere. It is known that fish and benthic invertebrates that normally reside in shallow water move with changing stage (Rempel et al., 1999). Shoreline areas are obviously very important for maintaining high species diversity in braided rivers. As another example; fish such as the grayling use dead zones along shorelines as a shelter, in particular during the early life stages (Sempeski et al., 1998). Species diversity of young fish (Danube River, Austria) and shoreline birds (Tagliamento, Italy) significantly increase with the increase of shoreline complexity, expressed as shoreline length per unit river length (Reich, 1994; Wintersberger, 1996).

Braided rivers are composed of vast areas of exposed riverine sediments (ERS; gravel or sand bars, shoals). ERS are predominantly inorganic, have little vegetation and are characterized by high fluxes of temperature and humidity (Sadler et al., 2004). Despite the hostile environmental conditions, ERS are a habitat for a large number of rare invertebrates. Running spiders (Lycosidae), with a few specialists widely distributed on gravel bars (e.g., *Arctosa cinerea* and *Pardosa wagleri*), small ground beetles (Carabidae), and rove beetles (Staphylinidae) dominate the ERS community (Fig. 6). Running bugs (*Saldula* spp.) are also often present. Riparian arthropods occur in high densities along gravel shore habitats. Average density (Ind. m^{-2}) along 19 European river margins was 1-15 (max. 198) for spiders, 0.2-90 (max. 374) for ground beetles, and 0.3-50 (max. 904) for rove beetles (Schatz et al., 2002). Fine-scaled investigations on gravel bars demonstrated that Carabidae and Staphylinidae peaked at the stream edge (0-1m), spiders were more evenly distributed across a gravel bar, while ants exhibited a strong spatial and seasonal variability (Paetzold et al., 2004; Fig. 7). A high proportion of ERS species are rare and endangered, increasing the

conservation value of these landforms (Boscaini et al., 2000; Sadler et al., 2004). Many of these species will become extinct if their habitats are altered or lost as a result of human activities. The larvae of Carabidae (ground beetles) and Staphylinidae (rove beetles), for example, are very sensitive to desiccation and live in the interstices of gravel near the water line, or tunnel into sandy deposits near the surface, with their galleries being easily visible. Some of the most endangered grasshoppers depend on the presence of bare sand (*Tetrix tuerki*, *Epacromius tergestinus*) and gravel (*Bryodema tuberculata, Chorthippus pullus, Sphingonotus caerulans*). *Sphingonotus caerulans* was found by Holderegger (1999) in habitats with less than 10% plant cover, which was comparable to the values obtained by Reich (1991) for *Bryodema tuberculata*, another endangered grasshopper species on ERS. *Chorthippus pullus* and *Tetrix tuerki*, two endangered species of dynamic rivers, tolerate higher covers. Plant cover also influences the diet composition of grasshoppers: the lower the plant cover, the higher the percentage of animals in the diet so that grasshoppers act as scavengers on bare gravel but as herbivores in areas with higher vegetation cover (Holderegger, 1999).

Adaptations to the braided river environment

Over evolutionary time, organisms have evolved traits that enable them to survive, exploit and even depend on disturbances. Plants and animals possess distinct morphological, physiological and ethological adaptations and exhibit high phenological plasticity (Fig. 8, Tab. 1). For example, riparian Salicaceae produce a large number of seeds that are wind-dispersed early in the year, a high seedling growth rate, rapid re-sprouting from fragments, a high investment in root systems, which anchor the plants effectively and bind together substrates, and their stems and roots are very flexible (Karrenberg et al., 2002; Fig. 8a). Likewise, the small Eurasian shrub *Myricaria germanica* (Tamaricaceae), which is entirely

confined to active zones, also exhibits vigorous re-sprouting and produces large numbers of small seeds which are wind-dispersed and have a short viability (Bill et al., 1997).

To compensate for the losses caused by the stress of the change between aquatic and terrestrial phases, animals are forced to have short and often asynchronic life cycles, high reproduction rates and great mobility (r-strategists). For example, Winterbourn (1978) found in braided river systems in New Zealand that caddisflies (Trichoptera) exhibit non-seasonal and poorly synchronized life cycles, which means that the timing of floods is less critical because mobile larvae and aerial adult stages are present throughout the year. Mobile terrestrial animals can escape flooding by migrating vertically to the canopy or by following the high-water line laterally (Adis et al., 2002; Fig. 8b). Data by Bonn & Kleinwächter (1999) demonstrate that the flight activity of Carabids increased after flood events, and that the immigrants were mainly females, which could build new colonies or subpopulations. For Staphylinids, habitats with higher inundation risks were colonized by smaller species, and the percentage of flightless species was lower than higher up the bank (Wohlgemuth-von Reiche et al., 1997). Most riparian arthropods are also adapted to survive as eggs, larvae or adults in a submerged state for some period, depending on temperature and season. The large ground beetle *Nebria picicornis* exhibits a spatial segregation of adults and larvae: the adults prefer the vicinity of the water line where food is more abundant; while the larvae live in higher grounds less exposed to flooding (Manderbach & Plachter, 1997). Investigations by Lude et al. (1999) revealed that 72% of ant colonies *(Formica selysi)* survived floods in their nests (in trapped air spaces), for up to 14 days, and they were able to re-open them again through 10-20 cm deposits of fresh sand. When water rose they were also able to form small living rafts that carried queens, larvae and eggs downstream (confirmed by experiments).

Forming metapopulations is another way to minimize the effect of stochastic disturbances on the survival of a species at the landscape level. Invertebrate populations on

gravel banks often consist of temporarily isolated subunits (e.g. the grasshopper *Bryodema tuberculata*; Stelter et al., 1997). Not only floods may lead to the extinction of subpopulations, vegetation growth may also exclude species from their habitat since several species depend on bare gravel surfaces. Hence, floods not only eliminate subpopulations but also create new bars and islands, which again can be re-colonized by pioneer species. Therefore, viable ERS populations require areas large enough to provide a balanced set of habitats of different ages (e.g. Poiani et al., 2000). Therefore, metapopulations can only be viable if large suitable habitats are available and when individuals are mobile enough to make contact with the inhabitants from other metapopulation patches. However, the ability to fly is not an indispensable supposition. Flightless females of *Bryodema tuberculata* were also able to colonize new patches by walking when separating channels went dry (Reich, 1991).

Related to metapopulation dynamics is the importance of refugia for the long-term survival of populations. Refugia are areas from which recolonisation following a disturbance event occurs and their distribution and utilisation is of critical importance for maintaining the ecological stability of systems. Therefore, the potential availability of refugia can be used as an indicator of ecosystem stability (resilience), which is the capacity of an ecosystem to respond to disturbance. Since the dominant disturbance regime is changing along the river corridor ("disturbance cascades" *sensu* Montgomery, 1999; Tab. 1), the relative importance of individual refugia changes as well. Braided gravel-bed rivers offer various categories of refugia such as shore areas, and hypogeic and hyporheic habitats that are crucial for maintaining diversity in the face of frequent disturbances. Therefore, we suggest measuring the potential availability of refugia at three different scales: (i) vertically, as the permeability of bed-sediments; (ii) laterally, as shoreline length (see Fig. 3); and longitudinally, as the relative proportion of unmodified tributaries (up to a distance of ~10km, depending on stream size) or the number of hydrogeomorphic nodes (convergence and divergence areas) within the

braided channel. This would allow an indirect assessment of the ecological stability (resilience) of braided rivers as well as the success of restoration measures.

Many species exhibit distinct phenotypic and genotypic flexibilities that allow them to successfully colonize unpredictable habitats. The common toad *Bufo b. bufo* is an abundant amphibian species of permanent forest ponds (Kuhn, 1993). However, this species can also successfully spawn in parafluvial ponds in the active zone. In contrast to stable ponds, *B. bufo* exhibits a flexible mating strategy in dynamic habitats; it spawns over extended periods depending upon the time when ponds get filled with water, and it exhibits a distinct spawning fidelity (Table 2). Recent research has demonstrated that most amphibian species are able to utilize water bodies in active zones (Tockner et al., unpubl. data). A key question is therefore whether amphibians in different river corridor areas (e.g. active zone and floodplain) form sets of different populations, that are spatially discrete, differ in size, demography, and carrying capacity, and interact via dispersal and gene flow. If so, are these populations true metapopulations? This leads to the further question: Are local populations in the active zone better adapted to the specific conditions in this zone compared to immigrants from the floodplain? All of these aspects are crucial for the development of restoration and conservation strategies for dynamic ecosystems.

Braided rivers are very dynamic systems that shift between dry and wet states at a seasonal or with a more stochastic rhythm. Depending on the organisms considered, drying or rewetting can trigger "boom" and "bust" periods (cf. Kingsford et al. 1999). Terrestrial invertebrates, for example, rapidly colonise dry habitats, benefiting from stranding and dying aquatic organisms. Unfortunately, simultaneous investigations of aquatic and terrestrial assemblages have not yet been performed.

Trophic linkages across boundaries

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Bar edges of braided rivers are inhabited by a diverse and abundant carnivorous arthropod community, primarily spiders, rove beetles, ground beetles, and ants (Plachter & Reich, 1998; Sadler et al., 2004). Large differences in productivity, together with diverse assemblages of generalist consumers, make gravel banks model systems to study spatial subsidies. Gut analyses of riparian ground beetles in a braided river (Isar, Germany) revealed a high proportion of aquatic insects in their diet (Hering & Plachter, 1996). Most recently, Paetzold et al. (2004) have proved that predation by ground dwelling arthropods is a quantitatively important pathway in the transformation of aquatic secondary production to the riparian food web. Ground beetles fed entirely on aquatic organisms; 80% of the diet of rove beetles, and ~50% of the diet of most abundant riparian spiders was of aquatic origin. Spiders and ground beetles can in turn significantly reduce the emergence of aquatic insects along the river shore, thereby controlling population dynamics of aquatic insects such as stoneflies and caddis flies (Paetzold & Tockner, in revision). Average consumption along the river edge by riparian arthropods can be as high as 40% of the total average aquatic insect emergence in the adjacent channel. Riparian arthropods along braided-river banks are generally highly mobile organisms, adapted to living in a highly dynamic environment (Plachter & Reich, 1998). Therefore, they can rapidly respond to pulsed subsidies by spatial redistributions. Mass emergence during a short, well-defined period of the year is common among aquatic insects and can be synchronized with long-term flood dynamics (Lytle & Poff, 2004). Peaks in surface drifting organisms occur during storms through accidental input of riparian invertebrates to the stream.

The efficiency of the transfer rate of energy across the aquatic-terrestrial boundary depends on a high ratio of shoreline length to stream area and the permeability of the boundary along braided banks. The alteration of riparian habitats may reduce the energy transfer between the channel and an adjacent gravel bar. Further, a decline in diversity of shoreline invertebrates is supposed to reduce the functional linkage between aquatic and

terrestrial systems, although no data are available yet. Studies along twelve (formerly) braided rivers, which differed in their degree of hydrological and morphological modification, demonstrated that river regulation altered fundamentally the entire riparian arthropod community. Channelised sections that are also impacted by hydropeaking were almost completely devoid of terrestrial arthropods (A. Paetzold & K. Tockner, unpubl. data).

Convex and concave islands

Lentic (standing) water bodies and vegetated islands are neglected habitats of braided rivers, mainly because of their absence in most extant rivers. They are very sensitive landscape elements that disappear as a consequence of river regulation, wood removal, and flow control. Today, ponds and islands are among the most endangered landscape features along river corridors (Homes et al., 1999; Gurnell & Petts, 2002; Hohensinner et al., 2004; Karaus et al., 2004). They can be used as ecosystem-level indicators of the environmental condition of river corridors.

River research has concentrated on the lotic channel. Only recently have lentic water bodies also been considered as integral habitats along river corridors (Ward et al., 2002). In particular **parafluvial ponds** - lentic water bodies within the active zone - are distinct habitats within the river mosaic. Investigation of pond heterogeneity and invertebrate diversity along the entire length of three braided Alpine river corridors exhibited peaks of parafluvial ponds in bar- and island-braided river reaches, with a maximum of 29 ponds per river-km (Karaus et al., in press). Numerous ponds were associated with vegetated islands. Indeed, the presence of vegetated islands enhanced the diversity of aquatic habitats (Arscott et al., 2000; Table 3). Ponds were absent in regulated and naturally-constrained sections along each corridor. Although covering a small proportion of the total aquatic area (<3%), ponds contributed >50% to invertebrate diversity (U. Karaus & K. Tockner, unpublished data). Each pond harboured a distinct fauna, which supports the idea that ponds have an insular nature

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("concave island") with a characteristic set of environmental properties. A high proportion of pond species were classified as rare, with a limited spatial distribution. Thermal characteristics (see Fig. 3) and water level fluctuations were the most important variables determining pond heterogeneity. Detailed investigations of aquatic invertebrates along an entire river corridor have confirmed the role of standing water bodies as foci of biodiversity (Arscott et al., in revision). Results suggested that heterogeneity in invertebrate assemblages within a habitat (e.g. a small pond) was equally as important as heterogeneity within or among reaches (i.e. lateral and longitudinal dimensions). The inclusion of lateral habitats such as backwaters and ponds also changed the interpretation of zoobenthic organization along the river continuum and illustrated that lateral habitats served as important sinks and sources for invertebrates. Overall, corridor water bodies provided redundancy and novelty (Arscott et al., in revision).

Vegetated islands are "high energy landforms" (Osterkamp, 1998). Their formation requires (1) a natural flood regime, (2) an unconstrained river corridor, (3) a sediment source, and (4) a source of large woody debris, a combination of conditions not present in highly managed river systems (Ward et al., 2002, Gurnell & Petts, 2002). For example, over 650 vegetated islands (> 0.007 ha) occur along the corridor of the Fiume Tagliamento (Tockner et al., 2003; see Fig. 1b). Islands are, however, among the first landscape elements that disappear as a consequence of river regulation. For example, only six islands remain of ca. 2000 islands historically present in the Austrian Danube. There, the construction of hydropower plants led to a decrease in gravel bars and vegetated islands by 94% and 97%, respectively (Hohensinner et al., 2004). Similarly, the response of former braided rivers in the Great Plains (USA) to upstream dam construction was channel-narrowing and a reduction in geomorphic dynamics (Friedman et al., 1996). Channel narrowing was associated with an increase in native and exotic woody riparian species colonising the former channel bed. Such increases in vegetation

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density can substantially alter channel geometry. Lateral mobility decreases, braiding intensity decreases, and channel relief increases (Gran & Paola, 2001).

Ecologically, islands are pivotal landscape elements. They represent early successional stages, are colonized by a diverse and often endangered fauna and flora, are almost devoid of invasive species, have a high perimeter-to-area ratio, serve as stepping stones for migrating organisms such as small mammals, and serve as important natural retention structures along river corridors. Nowadays, the dynamics and biodiversity of islands can only be investigated in large river beds with a whole set of islands of different size and different age. In Europe there are only a few possibilities left for such studies, as most large rivers have been modified, e.g. confined by dykes to protect arable land and housings, or used to produce hydraulic energy.

Floating organic matter links aquatic and terrestrial environments

Water movement links the riverine environments. As water moves across the river-floodplain system, it develops a hydrogeomorphic linkage that allows organisms to disperse and to transport nutrients, sediments, and organic matter. Floating organic matter links aquatic with terrestrial compartments and upstream with downstream segments of river ecosystems (both energetically and as a vector for terrestrial and aquatic organisms). Given that some animals can survive to reach a downstream shore, upstream sections may serve as a source of colonists. Also, canyons that separate alluvial valleys contain pockets of habitats that may operate as either refuges or population sinks periodically colonized by flood-borne animals.

The main driving factor in the cycling of floating organic debris and its associated fauna is the pulsing of flow. During flood events large amounts of organic material and organisms float downstream. During the decreasing limb of the hydrograph, organic material aggregates and accumulates in "dead zones" and at retention structures along shoreline

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habitats, where it forms distinct "drift lines". With an increase in the water level, deposited material becomes resuspended and transported downstream (Fig. 9). Floating organic matter serves as a major dispersal vector for aquatic and terrestrial organisms along river corridors (Tenzer, 2003). Recent results from the Tagliamento River demonstrate that coarse particulate organic matter fractions such as wood, fruits or grass are exclusively transported at the water surface. Abundance and composition of invertebrates change rapidly between transport, accumulation, and deposition phases. The number of organisms associated with floating organic debris is on average 20 times higher than that in the water column; and is primarily composed of terrestrial organisms. Many of the organisms are transported over long distances (tens of kilometres; Langhans, 2000). The removal of organic matter upstream of hydropower plants is considered to have a major impact on the ecology of river systems that significantly reduces local riparian species richness in the downstream reaches (Andersson et al., 2000). We may propose floating material as an indicator of the integrity of entire river corridors. However, basic research is required to establish and calibrate floating organic matter as an integrative indicator of connectivity along river corridors.

4. Prospect

Most braided rivers have been converted into incised single-thread channels (Surian, 1999; Piegay et al., this issue). Remaining braided rivers are under enormous pressure from channelisation, gravel exploitation, and flood control measures. During recent decades river restoration activities have increased rapidly. Although a huge amount of detailed environmental knowledge has been compiled, up to 60% of all restoration projects are still ineffective (Tockner & Stanford, 2002). The main reasons for project failure include (i) the "missing-link" between natural and social science and (ii) the lack of reference data from near-pristine ecosystems, which constrains our understanding and replication of ecosystem

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processes. More than for most other ecosystems, restoring braided rivers means restoring their underlying hydrogeomorphic dynamics. However, for the successful conservation and restoration of braided rivers we need to document how the variable physical conditions of braided rivers govern species diversity and ecosystem processes. Future research on braided rivers has to focus on the ecological importance of the unsaturated zone, groundwater - surface water interactions and their role in controlling biodiversity and bioproduction, thermal patch dynamics at varying spatial scales, the relationship between habitat age diversity and species identity and richness, adaptations and dispersal pathways in rivers, the influence of the adjacent woodland on the active zone, the importance of ponds and islands as foci for biodiversity, how ponds and islands are physically and ecologically linked, and to upscale from experiments to entire river corridors in order to identify "hot spots" and "hot windows" of process activity. In conclusion, we are convinced that braided rivers are predetermined as model ecosystems for testing general ecological concepts.

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Brief Glossary

Adaptation. Characteristics of organisms evolved as a consequence of natural selection in its evolutionary past and/or changes in the form or behaviour of an organisms during its life as a response to environmental stimuli.

Biodiversity (or Biological Diversity). The variety of life in all its forms, levels and combinations. Includes ecosystem diversity, species diversity, and genetic diversity.

Community. Populations of different species that interact with each other in an area.

Dispersal. The spreading of individuals away from each other, e.g. of offspring from their parents and from regions of high density to regions of lower density.

Disturbance. Any relatively discrete event in space and time that disrupts ecosystem, community, or population structure and changes resources, substrate, or the physical environment.

Ecological stability. Ability of a property (e.g. population, community) of an ecosystem to return toward a steady-state equilibrium following a disturbance.

Ecosystem. The interacting system of a biological community and its environmental surroundings which together form a recognizable self-contained entity.

Food web. Representation of feeding relationships in a community that includes all the links revealed by dietary analysis.

Habitat. Place or type of place where an organism, population, or community lives.

Hydrologic connectivity. Water-mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle.

Hyporheic zone. A spatially fluctuating ecotone between the surface stream and the deep groundwater where important ecological processes and their requirements and products are

influenced at a number of scales by water movement, permeability, substrate particle size, resident biota, and the physiochemical features of the overlying stream and adjacent aquifers.

Meiofauna. Small benthic metazoans that pass through a 0.500 mm sieve and are retained on a 0.063 (or 0.045 mm) sieve. The majority of recognized phyla have meiofaunal representatives.

Metapopulation. Set of local populations within some larger area, where typically migration from one local population to at least some other patches is possible.

Productivity. The rate at which biomass is produced per unit area by any class of organisms.

Refugia. Areas from which the recolonisation after a disturbance event occurs.

Resilience. Resilience, or relative stability, is a measure of the rate at which the property or system (see stability) approaches steady state following a disturbance.

R-strategy. Ecological strategy where organisms rely on high reproductive rates for continued survival within the community. Populations of r-strategists are subject to extreme fluctuations.

Sustainability. Maintenance and/or improvement of the integrity of the life-support system on Earth.

Figure Legends:

Figure 1. A. The braided river mouth of the Kurobe River (Toyama Prefecture, Japan). Japanese rivers are steep, short and exhibit a flashy flow regime (Yoshimura et al., 2005). B. Island-braided section along the Tagliamento River (NE Italy) showing the complex mosaic of aquatic (channels, backwaters, parafluvial ponds) and terrestrial (gravel, large wood, vegetated islands) habitats. The active floodplain is ~900m wide (Photo: K. Tockner).

Figure 2: Shoreline length (km per km^2) – duration relationship in natural (Tagliamento, NE Italy), constrained (Danube, Alluvial National Park, Austria) and channelised (Rhône, Switzerland) river-floodplain systems. All flood plains are characterised by a dynamic hydrology (Van der Nat et al., 2002). The Rhone and the Tagliamento River are comparable in discharge and catchment area. In their pristine state, the Rhône and the Danube were morphologically similar to the present braided Tagliamento River.

Figure 3: Thermal heterogeneity (May until October 2001), expressed as average daily temperature and average diel amplitude, in 18 water bodies across a braided section along the Tagliamento River (NE Italy; after Karaus et al., 2004).

Figure 4: An idealised 3-D view of a braided floodplain structure, emphasising dynamic longitudinal, lateral and vertical dimensions and the role of large wood to the natural-cultural setting of the catchment (modified after Stanford, 1998).

Figure 5: Danube floodplain (Alluvial Zone National Park, Austria): Species optima (different faunal groups) and tolerance ranges across a hydrological connectivity gradient (modified after Reckendorfer et al., in press). Connectivity is expressed as the number of months with an upstream hydrological surface connection to the main channel.

Figure 6: Characteristic organisms in a braided river (from left to right): Rove beetle (*Stenus* sp., Staphylinidae), opening of a nest of the ant *Formica selysi,* and a ground beetle (*Bembidion* sp., Carabidae)(Photos: J. Zettel).

Figure 7: Tagliamento River: Abundance (mean ± SE) of Carabidae, Staphylinidae, Araneae, and Formicidae at different distances from the water's edge in June and October 2001 (modified after Paetzold et al., 2004).

Figure 8. Adaptions to the life in dynamic braided rivers. A. Shape (horizontal and vertical view) of a willow species at different water currents. Most species of Salicaceae (willows) develop highly flexible branches that do not break in fast-moving flood waters (after Vischer and Oplatka, 1998). B. The relative proportion (%) of winged individuals of populations of the groud beetle *Bembidion tetracolum* across an inundation gradient (data: Siepe, 1994).

Figure 9: Floating organic matter dynamics across aquatic-terrestrial boundaries.

Tab. 1. Fluvial style, disturbance regime, refugia, and adaptation of aquatic

macroinvertebrates along a fluvial corridor.

Location, Fluvial style	Disturbance regime	Refugia	Adaptation
Headwater Straight	Avalanches Debris flow Drying	Tributaries Hyporheic zone Substrate hetero-geneity	Drift Morphological adaptation Life cycle
Piedmont section Braided	Avulsion Cut and fill processes	Shore habitats Dead zones Large wood Hyporheic zone	Mobility Flexible life history Risk spreading
Lowland section Meandering	Inundation Lateral channel migration	Floodplain Large wood Backwater/pond	Physiologic/ethologic adaptation Diapause

Tab. 2. Different reproduction strategies of the common toad (*Bufo b. bufo*) in relation to the dynamics of river-floodplain water bodies (after Kuhn, 1993). (?): No information available.

Reproduction biology	Permanent water bodies	Temporary and dynamic floodplain water bodies
Spawning time	Early, fixed	Opportunistic
Spawning aggregation	Large (mostly)	Small
Male tactics	Search and fight	Mating calls
Selection of spawning sites	(?)	Distinct
Spawning site fidelity	Distinct	(?)

Table 3: Biocomplexity in an island- and a bar-braided flood plain (Tagliamento River, NE Italy).

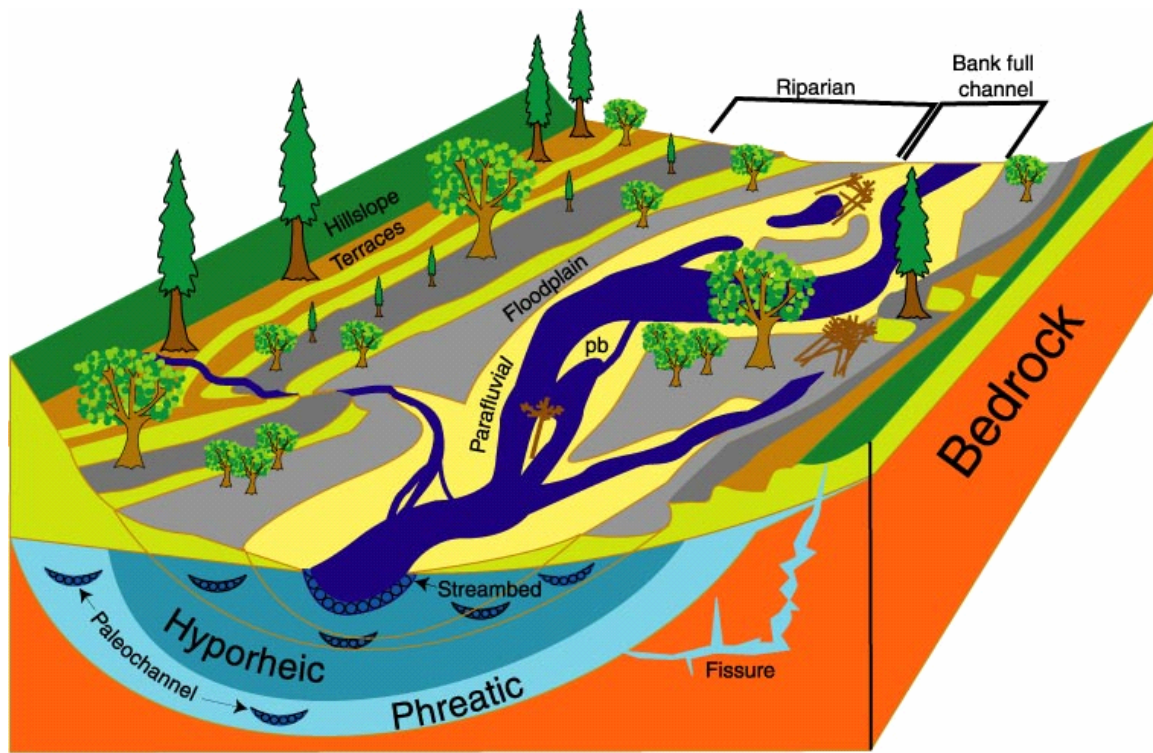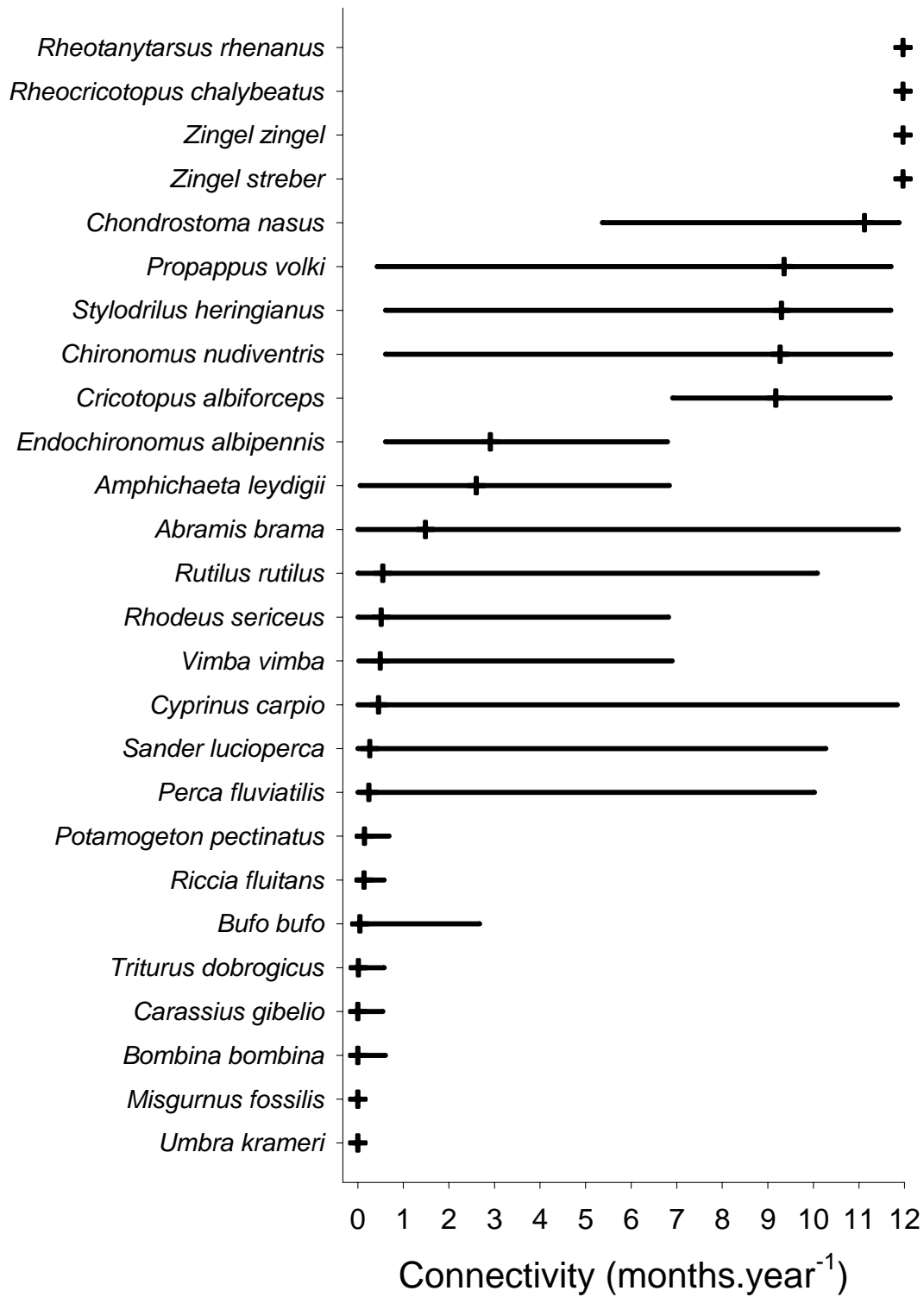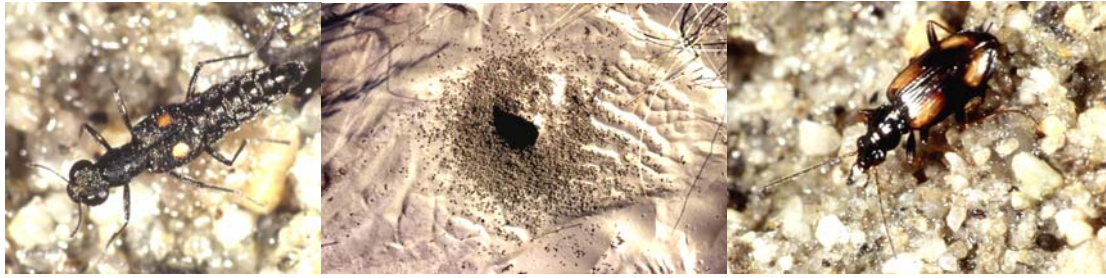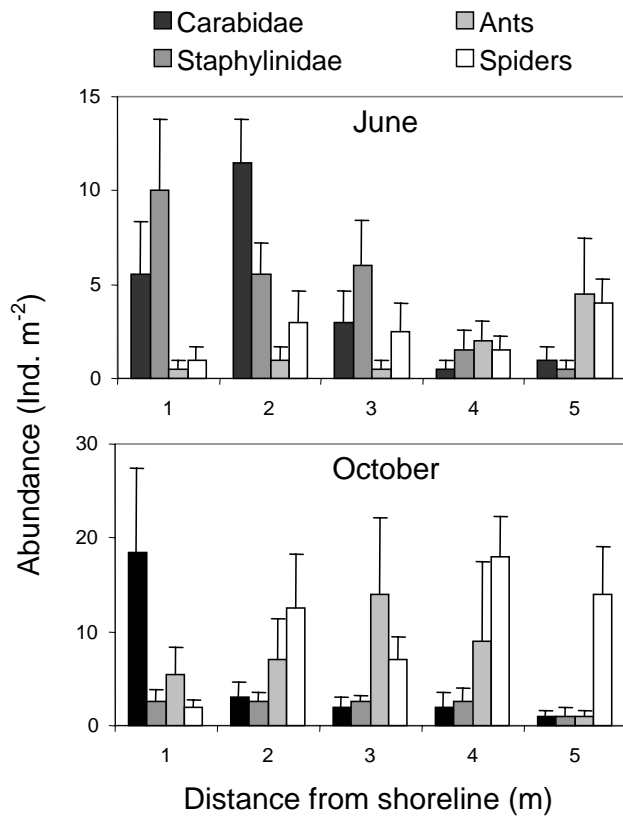|	Bar-braided	Island-braided	Reference
Width of active channel (m)	830	1000	Tockner et al. (2003)
Large wood (t ha^{-1})	15-73	102-158	Van der Nat et al. (2003a)
Channels (half-life expectancy; months)	4.1	7.7	Van der Nat et al. (2003b)
Aquatic habitat diversity (H')	1.6	2.0	Arscott et al. (2000)
Average number of ponds	7	22	Van der Nat et al. (2002)
Average shoreline length (km km^{-1})	13.7	20.9	Van der Nat et al. (2002)
Amphibian species	5	7	Klaus et al. (2002)
Carabid beetle species	34	47	Tockner et al. (2003)
Benthic invertebrates: α-diversity	30	27	Arscott et al. in revision
Benthic invertebrates: β_2-diversity	10.5	21	Arscott et al. in revision
Benthic invertebrates: γ-diversity	50	53	Arscott et al. in revision

Figure 1A

Figure 1B

Fig. 2
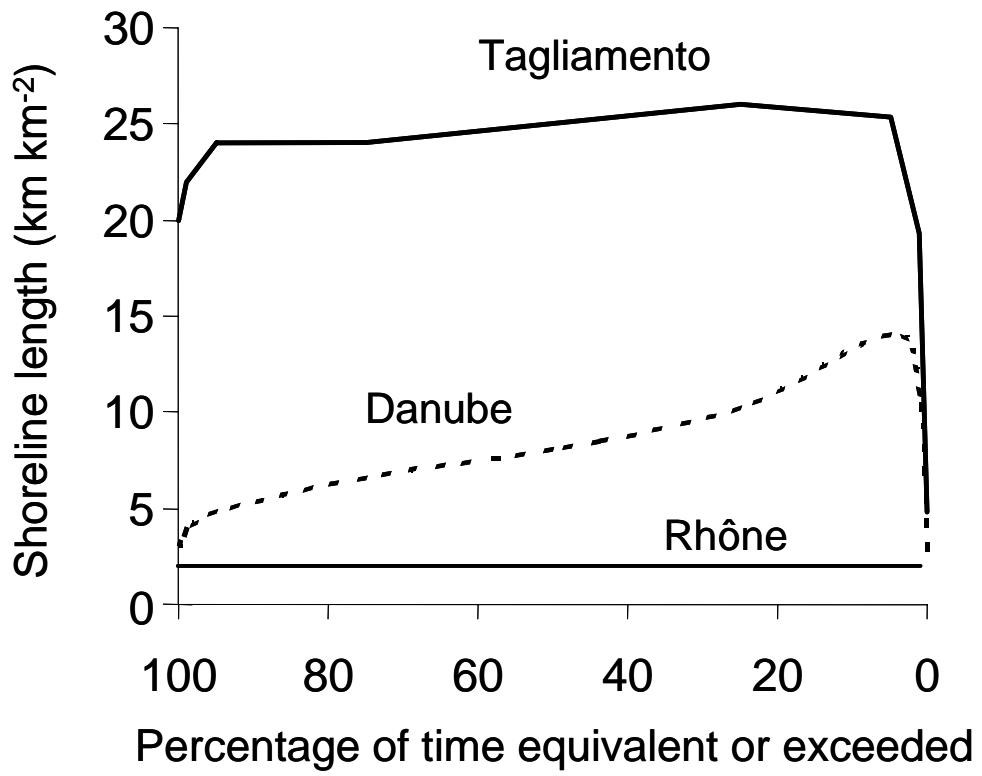
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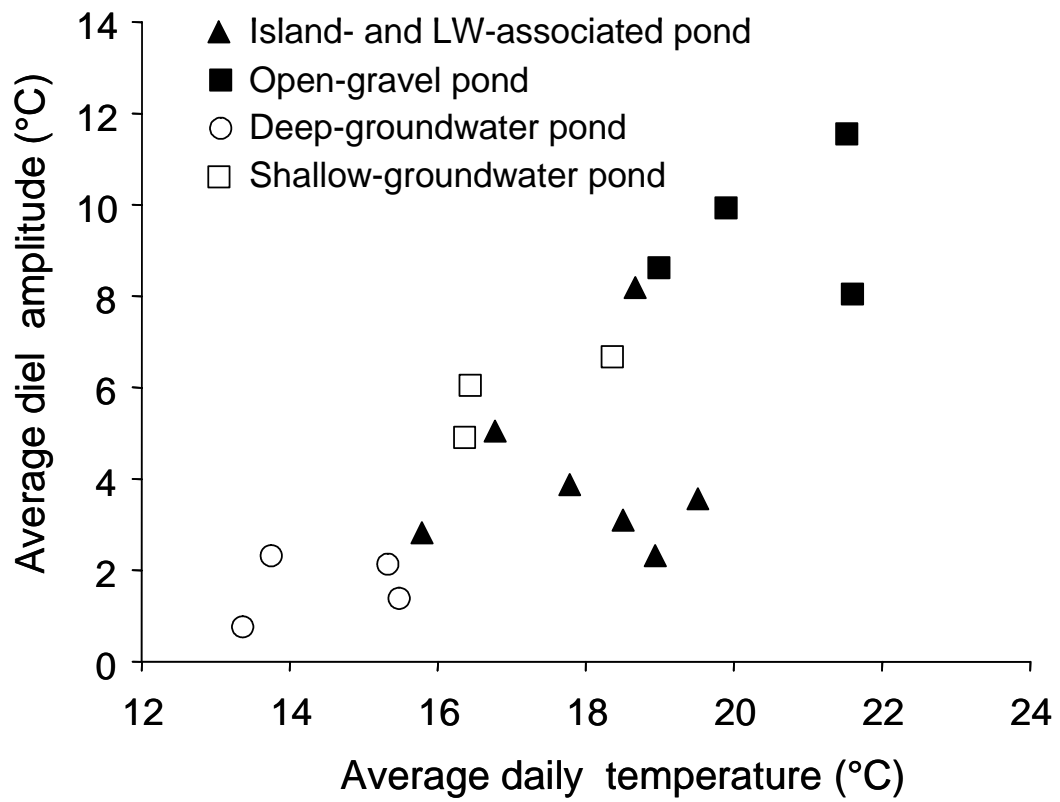
Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

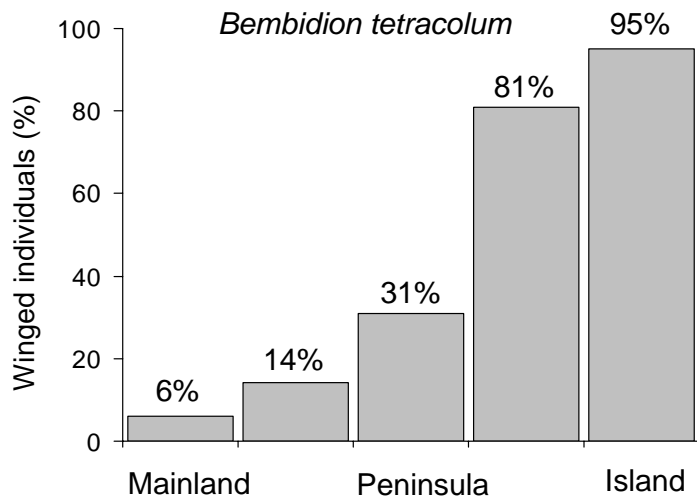A.

B.

Figure 9

Detrital dynamics across boundaries