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BIODIVERSITY OF FLOODPLAIN RIVER ECOSYSTEMS: ECOTONES AND CONNECTIVITY[1]

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ABSTRACT

A high level of spatio-temporal heterogeneity makes riverine floodplains among the most species-rich environments known. Fluvial dynamics from flooding play a major role in maintaining a diversity of lentic, lotic and semi-aquatic habitat types, each represented by a diversity of successional stages. Ecotones (transition zones between adjacent patches) and connectivity (the strength of interactions across ecotones) are structural and functional elements that result from and contribute to the spatio-temporal dynamics of riverine ecosystems. In floodplain rivers, ecotones and their adjoining patches are arrayed in hierarchical series across a range of scales. At a coarse scale of resolution, fringing floodplains are themselves complex ecotones between river channels and uplands. At finer scales, patches of various types and sizes form habitat and microhabitat diversity patterns. A broad spatio-temporal perspective, including patterns and processes across scales, is needed in order to gain insight into riverine biodiversity. We propose a hierarchical framework for examining diversity patterns in floodplain rivers.

Various river management schemes disrupt the interactions that structure ecotones and alter the connectivity across transition zones. Such disruptions occur both within and between hierarchical levels, invariably leading to reductions in biodiversity. Species richness data from the connected and disconnected floodplains of the Austrian Danube illustrate this clearly. In much of the world, species-rich riverine/floodplain environments exist only as isolated fragments across the landscape. In many large rivers, these islands of biodiversity are endangered ecosystems. The fluvial dynamics that formed them have been severely altered. Without ecologically sound restoration of disturbance regimes and connectivity, these remnants of biodiversity will proceed on unidirectional trajectories toward senescence, without rejuvenation. Principles of ecosystem management are necessary to sustain biodiversity in fragmented riverine floodplains. Copyright © 1999 John Wiley & Sons, Ltd.

KEY WORDS: biodiversity; disturbance; connectivity; ecotones; floodplains; hierarchy; river regulation; succession

INTRODUCTION

Species diversity is a synthetic concept that is inextricably linked to other ecological constructs such as succession, ecotones and connectivity, and draws upon related disciplines such as biogeography, genetics and evolution. The more recent concept of *biodiversity*, represents an even broader and more integrative perspective (Huston, 1994; Schulze and Mooney, 1994; Rosenzweig, 1995) and a heightened concern for threats to gene pools, species and habitats on a global scale (Wilson, 1992; Ricklefs and Schluter, 1993; Mooney *et al*., 1996). As emphasized by Noss (1990), conservation of biodiversity involves 'more than just species diversity or endangered species'. Biodiversity is clearly a scalar phenomenon that is amenable to a hierarchical approach.

This paper begins by briefly discussing biodiversity as a general ecological concept and the theoretical constructs that have been developed to explain patterns observed in nature. Against this background, biodiversity is examined in the context of floodplain river ecosystems, with special emphasis on the roles of ecotones and connectivity at the habitat and landscape scales. A hierarchical framework is proposed for examining diversity patterns in floodplain rivers. River regulation is perceived as an alteration of the

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natural fluvial dynamics that sustain habitat heterogeneity and a diversity of successional stages across the riverine landscape. Species richness data from connected and disconnected floodplains of the Austrian Danube are analyzed. Finally, biodiversity as a management objective that provides an opportunity to apply ecological principles in holistic river conservation and restoration practices is discussed.

BIODIVERSITY AS AN ECOLOGICAL CONCEPT

Components of biodiversity

Biodiversity is much more than species diversity and genetic diversity. It also includes functional (process) diversity and, in the broadest sense, even habitat diversity is encompassed within biodiversity. Noss (1990) builds upon the three primary ecosystem attributes of Franklin (1988)—composition, structure and function—to develop a hierarchical framework of biodiversity across four levels of organization (Table I). Floodplain rivers are especially amenable to a hierarchical approach for examining biodiversity, as will be demonstrated subsequently.

Understanding the factors that structure diversity patterns of local species assemblages requires knowledge of processes that determine species richness at the regional level and the rates of spatial turnover of species (Caley and Schluter, 1997). Gamma diversity, the total number of species in a region, is a function of the number of species per habitat (alpha diversity), the number of habitats (habitat diversity), and the turnover of species between habitats (beta diversity). Beta diversity may be calculated simply as the inverse of the mean number of habitats occupied by each species occurring in the region (1/mean number of habitats per species). Consideration of beta diversity enables one to distinguish between the separate contributions of habitat heterogeneity and species' characteristics (habitat breadth) to the total species diversity of a region (Ricklefs and Schluter, 1993). The 'region' under consideration (gamma diversity) can be defined for different scales (e.g. catchment, floodplain or floodplain transect), thereby partitioning habitat breadth from habitat heterogeneity at different hierarchical levels. In some respects, beta diversity is also a measure of the degree of connectivity between habitats. We propose that beta diversity, the turnover of species between habitats, can provide a new perspective for understanding biodiversity in floodplain rivers and the influence of river regulation on biodiversity patterns.

Table I. The hierarchical nature of biodiversity (*sensu lato*) with selected examples (greatly modified from Noss (1990))

	Composition	Structure	Function
Landscape level	Gamma diversity	Geomorphic patterns Large-scale environmental gradients Ecotones	Disturbance regimes Hydrological processes Connectivity
Community/ecosystem level	Alpha and beta diversity	Habitat heterogeneity Ecotones	Energy flow Patch dynamics Succession Connectivity
Population/species level	Frequency of occurrence Relative abundance	Microhabitat structure	Life history Metapopulation dynamics Adaptation
Genetic level	Allelic diversity	Heterozygosity Polymorphism	Gene flow Genetic drift Mutation rate

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Factors governing biodiversity

A variety of factors have been proposed as determinants of biodiversity (Ricklefs and Schluter, 1993). Over ecological time scales, most attention has been directed toward the roles of disturbance regimes, habitat heterogeneity and the resource base (productivity). A unimodal response to some of these variables has been proposed, with maximum biodiversity at some intermediate level.

The intermediate disturbance hypothesis (Connell, 1978) predicts low species diversity in habitats exposed to high levels of disturbance, where only a few highly tolerant species can survive or rapidly recolonize. According to this hypothesis, low species diversity also occurs under very low levels of disturbance, where highly competitive species can monopolize resources. Under conditions of intermediate perturbation, species diversity is maximum because a variety of taxa can tolerate the conditions, but none can completely dominate the community.

Naiman *et al.* (1988) derived a general model that predicted maximum biodiversity at some intermediate level of ecotone frequency. Biodiversity is constrained at low levels of ecotone frequency because large homogeneous patches provide little habitat for edge species. At high ecotone frequencies, substantial edge habitat is provided, but small patch size excludes interior species. Maximum biodiversity occurs where there is an 'optimal mix of patch and edge habitat'.

Here, it is postulated that biodiversity will also be at its maximum at some intermediate level of connectivity, although the authors are unaware of any definitive data to support or refute this contention. Low connectivity that prevents exchanges of matter, energy and organisms between patches should reduce biodiversity through habitat fragmentation, and excessive connectivity is expected to reduce habitat heterogeneity, with concomitant declines in biodiversity. A better understanding of the relationship between ecological connectivity and biodiversity is clearly needed for a holistic perspective of floodplain river ecosystems and the alterations induced by river regulation measures.

The dynamic equilibrium model (modified in Figure 1) of Huston (1979, 1994), that integrates the intermediate disturbance (Connell, 1978) and intermediate productivity (Grime, 1973) hypotheses, predicts that the potential number of competing species in a habitat varies according to the relationship between disturbance and productivity (resources). At high levels of disturbance, biodiversity is maximized in habitats with abundant resources (translated into a high rate of population growth), whereas at low levels of disturbance, maximum diversity is attained in habitats with sparse resources. Stated in another way, the level of 'intermediate' disturbance necessary to sustain maximum biodiversity changes as a function of resource level (i.e. population growth), with progressively greater perturbations needed to prevent competitive exclusion from being realized as resources increase. Using the terminology of Cornell and Lawton (1992), non-interactive communities, typically structured by abiotic factors, predominate in habitats with high disturbance and low resources, whereas interactive communities, with strong biotic interactions, predominate in habitats with low levels of disturbance and abundant resources.

Evidence from lotic systems

To what extent do the general concepts of biodiversity derived from studies of terrestrial and marine environments apply to running waters? This question is briefly addressed in the following paragraphs. More specific applications to floodplain river ecosystems were addressed by Décamps and Tabacchi (1994) and are reserved for later sections of the paper.

The initial proposal by Ward and Stanford (1983) that diversity patterns in lotic systems were consistent with the intermediate disturbance hypothesis of Connell (1978), presented evidence across a variety of scales in natural and regulated streams. Subsequent studies of grazing intensity by snails on algae (McCormick and Stevenson, 1989), competing species of stream insects (Hemphill and Cooper, 1983; McAuliffe, 1984; Hemphill, 1991) and stream fish (Minckley and Meffe, 1987), as well as the diversity patterns of riparian plants along river courses (Tabacchi *et al.*, 1996), provide at least partial support for the applicability of this concept to lotic ecosystems.

Hildrew and Townsend (1987) postulated that the dynamic equilibrium model could be applied to benthic communities of hard substrata in fresh waters, to predict how disturbance and productivity

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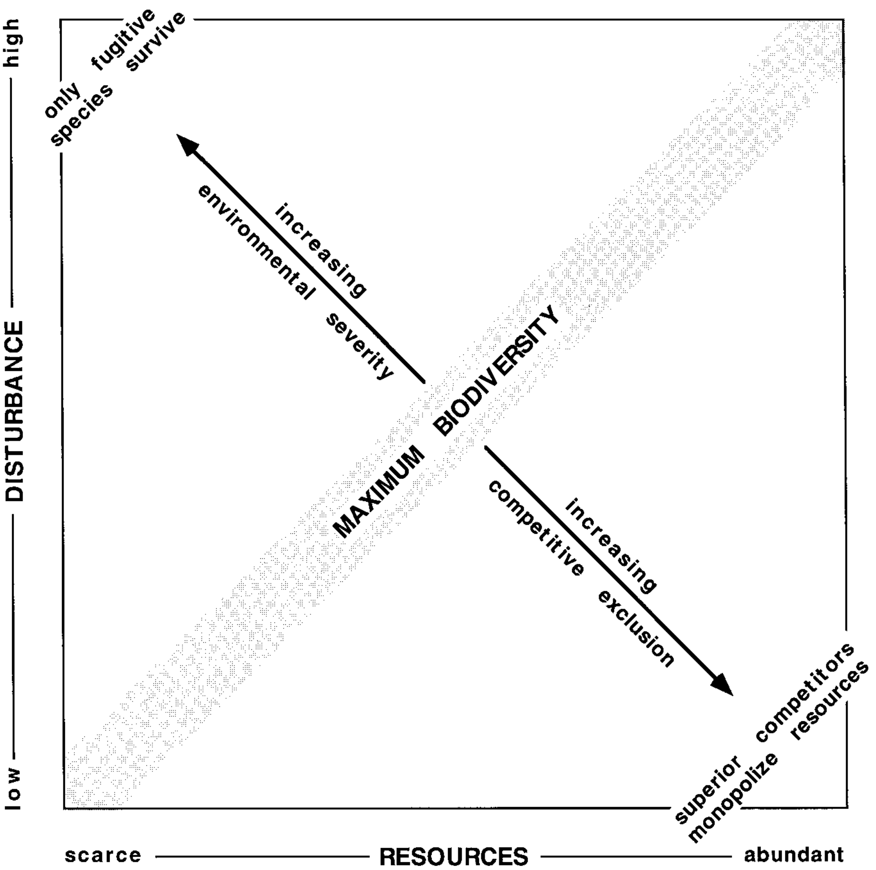

Figure 1. The hypothesized relationships between disturbance, resources and biodiversity (greatly modified from Huston (1979, 1994))

regimes structure feeding guilds and the predominance of sessile versus mobile species. Because of the overriding importance of disturbance and productivity both singly and in concert to floodplain rivers, we believe that the dynamic equilibrium model has major implications for the maintenance of biodiversity in these dynamic systems.

ECOLOGY OF FLOODPLAIN RIVERS

Floodplain rivers are disturbance-dominated ecosystems characterized by high levels of habitat diversity and biota adapted to exploit the spatio-temporal heterogeneity (Welcomme, 1979; Salo *et al.*, 1986; Copp, 1989; Junk *et al.*, 1989; Duncan, 1993; Mitsch and Gosselink, 1993; Ward and Stanford, 1995; Décamps, 1996; Petts and Amoros, 1996). The fluvial action of flooding and channel migration create a shifting mosaic of habitat patches across the riverine landscape. Ecotones, connectivity and succession play major roles in structuring the spatio-temporal heterogeneity leading to the high biodiversity that characterizes floodplain rivers (Figure 2).

Ecotones and connectivity

Ecotones and connectivity are interrelated structural and functional attributes respectively, of heterogeneous environments. Ecotones are transition zones between adjacent patches which, although differing from each other, exhibit high within-patch homogeneity. The ecotone concept has been a recurrent theme

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in ecology (Risser, 1995), with heightened interest in recent years attributable, in part, to the influence of ecotones on biodiversity (Hansen and di Castri, 1992; Lachavanne and Juge, 1997). Ecotones occur over a range of scales in floodplain rivers, forming the boundaries between land and water, between surface water and ground water, and between in-stream habitat patches (Naiman and Décamps, 1990; Ward and Wiens, 1999). This paper focuses on habitats at the floodplain scale.

In alluvial rivers, the floodplain forms a complex gradient (coarse resolution ecotone) between the river channel and the uplands, within which a variety of secondary and tertiary ecotones are embedded. These ecotones within the larger floodplain ecotone influence process (e.g. nitrogen fixation) and structure species richness patterns (Naiman *et al.*, 1988; Amoros *et al.*, 1996). A variety of ecotones occur within floodplains. The littoral zone, for example, forms ecotones between the open water of floodplain lakes and the shore. Ecotones also occur between different stands of floodplain vegetation. There are also vertical ecotones between surface water bodies and groundwater aquifers (Gibert *et al.*, 1997). All of these ecotones are characterized by relatively steep gradients (e.g. thermal, chemical and organic), thereby collectively forming a high level of environmental heterogeneity across the riverine landscape.

Connectivity may be defined as the ease with which organisms, matter or energy traverse the ecotones between adjacent ecological units. From a purely biological perspective, connectivity refers to gene flow between metapopulations and the extent to which ecotones alter dispersal, movement and migration. Connectivity also refers to the extent to which nutrients, organic matter and other substances cross ecotones. Hydrological connectivity, the transfer of water between the river channel and the floodplain and between surface and subsurface compartments, has major implications for biodiversity patterns (Welcomme, 1979; Amoros and Roux, 1988; Schiemer and Spindler, 1989; Obrdlik and Fuchs, 1991; Gibert *et al.*, 1997; Ward, 1998a). This is owing in part to the role that hydrological connectivity plays in structuring successional patterns.

Ecological succession

Successional processes are responsible for much of the spatio-temporal heterogeneity of riverine floodplains (Salo *et al.*, 1986; Amoros *et al.*, 1987; Terborgh and Petren, 1991; Ward and Stanford, 1995; Décamps, 1996). Flooding and channel migration maintain a diversity of lotic, semi-lotic and lentic water bodies on the floodplain and create a diverse mosaic of riparian vegetation across the riverine landscape.

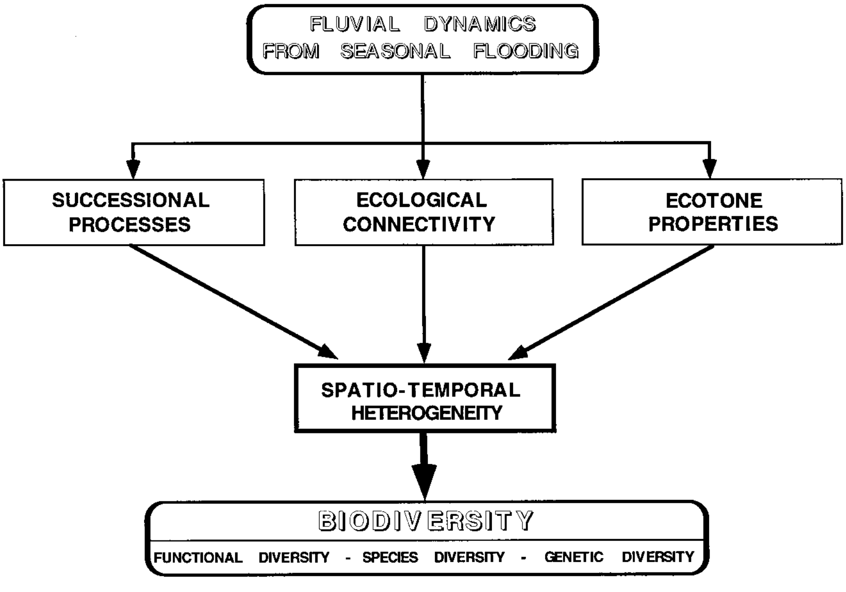

Figure 2. Simplified flow diagram to illustrate the important role of fluvial dynamics in sustaining ecotones, connectivity and succession as major determinants of habitat heterogeneity in riverine floodplains

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Floodplain water bodies include the main channel and side arms (eupotamal), dead arms connected to the main channel at their downstream ends (parapotamal), abandoned braids (plesiopotamal), abandoned meander bends (palaeopotamal), alluvial spring brooks, entering tributaries, swamps and marshes. These water bodies may be arrayed along a gradient of connectivity with the main channel from eupotamal side arms permanently connected with the main channel to plesiopotamal habitats reconnected to the channel during the annual flood, to isolated palaeopotamal lakes that are rarely inundated by flood waters (Ward and Stanford, 1995). Therefore, each type of water body exhibits a different pattern of hydrarch succession and each is characterized by a distinctive biotic community in both surface waters (Castella *et al.*, 1984; Copp, 1989) and ground waters (Marmonier *et al.*, 1992).

Fluvial dynamics and channel migration also maintain a diversity of successional stages among the riparian vegetation. Salo *et al.* (1986) and Terborgh and Petren (1991) provide vivid descriptions of the role of natural disturbance by fluvial action in creating a mosaic of alluvial forest stands in different successional stages. Forests on the concave bends of laterally migrating rivers are undercut by erosion and primary succession is initiated on point bars of alluvium deposited as annual increments on convex bends. The mature forest stage on the floodplain of the Manu River in Upper Amazonia has high structural diversity (five vertical strata) and > 200 species of trees per hectare (Terborgh and Petren, 1991).

Suppression of natural disturbance

Various forms of river regulation, including modification of natural flow dynamics, dredging, channel straightening, bank stabilization and construction of artificial levees, have altered successional trajectories and disrupted connectivity between ecological units of the floodplain/aquifer complex in many of the world's rivers. Regulation has fragmented river systems (Dynesius and Nilsson, 1994). River regulation disrupts the natural disturbance regimes that maintain a diversity of successional stages and high levels of connectivity across the riverine landscape, resulting in a loss of habitat heterogeneity and biodiversity.

BIODIVERSITY IN NATURAL AND REGULATED FLOODPLAINS

In this section, a hierarchical approach for examining biodiversity in floodplain rivers is proposed. In addition, comparisons are made between the biodiversity of selected groups of organisms in connected and disconnected floodplains, relying primarily on data from the Danube catchment.

Hierarchical patterns

The hierarchical approach is presented in Figure 3. Note that the alpha diversity of one hierarchical level becomes the gamma diversity for the next (lower) level. At the highest level, gamma diversity encompasses a major physiographic region, the Alps in this example. The Alps are drained by numerous river catchments, including the Danube. The Danube catchment containes numerous floodplains in a semi-natural state, including a floodplain complex downstream from Vienna recently designated as the Alluvial National Park (Tockner *et al.*, 1998). The functional types of floodplain water bodies, representing different successional stages and degrees of connectivity with the main channel (eupotamal), form the next hierarchical level. Finally, the alpha diversity of the individual patches within one type of water body (parapotamal in Figure 3) collectively constitute the gamma diversity for that water body.

Hierarchical arrangements of species richness numbers for gastropods, fish and amphibians are presented in Figures 4–6. In all cases, species richness values for the 'Alps' refers only to the three Alpine rivers indicated (Rhone, Rhine and Austrian Danube). All of these rivers are highly regulated, with only fragmented segments sustaining near-natural conditions. The next-lowest hierarchical level includes three floodplain complexes. Below this are three floodplain segments within the Alluvial Zone National Park (AZNP). Three types of water bodies within the Regelsbrunn floodplain constitute the next level. The lower, middle and upper portions of a parapotamal habitat form the lowest level of the hierarchy.

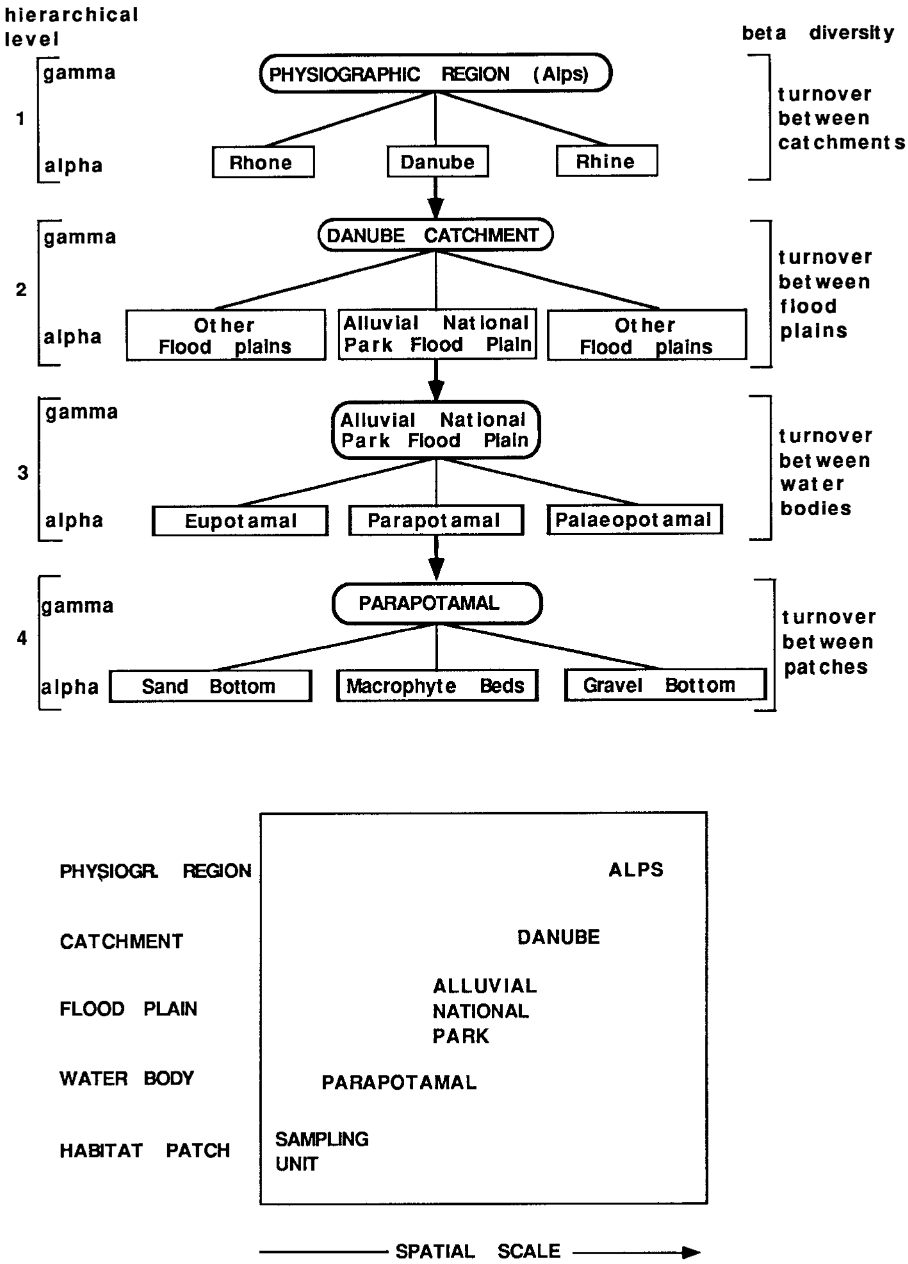

Figure 3. Hierarchical approach to diversity in river–floodplain ecosystems

The species richness of gastropods is similar in the three rivers (Figure 4). At the next level, there is little difference in species richness between the AZNP (free-flowing sector) and Greifenstein (impounded sector), whereas Altenwoerth (also impounded) exhibits a lower diversity of gastropods. The AZNP contains 93% of all the aquatic gastropod species in the Austrian Danube. The three floodplain segments of the AZNP exhibit similar species richness values. The parapotamal at Regelsbrunn has a slightly higher diversity than the other water bodies and the upper portion of the parapotamal has twice the diversity of the other portions. Based on these data, it appears that gastropod biodiversity is less severely impacted upon by regulation than are some other taxa.

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The high diversity of the Danubian ichthyofauna (Figure 5), with over twice as many species as the Rhone, is attributable to the E–W orientation of the river and the addition of Pontoaralcaspian elements, plus a few endemic species (Schiemer *et al.*, 1994). The AZNP contains 90% of all the fish in the Austrian Danube and appreciably more species than other sectors of the river. At the next hierarchical level, Regelsbrunn contains a similar number of species as Stopfenreuth, another floodplain in a free-flowing reach, whereas Lobau, a disconnected floodplain, has fewer species of fish. The parapotamal contains a richer fish fauna than other water bodies, with more species (particularly rheophilous species) in middle and lower portions nearer to the river channel.

Amphibians exhibit quite a different pattern, with approximately the same number of species within and across several hierarchical levels (Figure 6). Amphibians attain maximum diversity in more isolated water bodies that exhibit low connectivity with the river (Tockner *et al.*, 1998). They also favor temporary floodplain water bodies, undoubtedly as a means to reduce fish predation.

Alpha, beta and gamma diversity values were calculated for different groups at different levels (Table II). Care must be excercised in interpreting the data in the table; A, B, C and D cannot be directly compared with each other because of differences in methods and sampling strategies. There is, however, some consistency within each of these categories; for example, within the Regelsbrunn floodplain (B), amphibians, macrophytes and odonates were sampled within comparable segments, although only amphibians were collected from temporary waters. Therefore, only relative comparisons are possible.

The turnover of amphibian species (beta diversity) is low between floodplains (Table II). This means that essentially the same total pool of amphibian species is present in each of the floodplains along the Danube, as illustrated in Figure 6. Amphibians also show low beta diversity within a single floodplain (B). In contrast, molluscs exhibit the highest turnover rates. This group appears to be most affected by fragmentation processes, both between and within floodplains (Tockner *et al.*, 1999), which is not too surprising given their low vagility. The beta diversity of molluscs is two to three times higher in palaeopotamal and plesiopotamal water bodies than in the parapotamal channel (D). For molluscs, fragmentation processes clearly favor beta diversity. This has important implications for the development

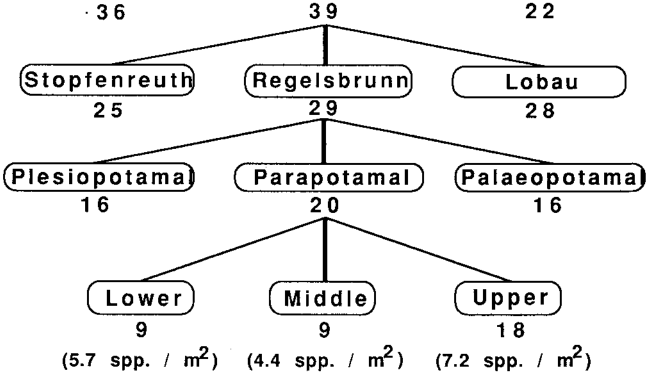

Figure 4. Species richness for aquatic gastropods at different hierarchical levels. The Rhone includes the segment from Lyon to Geneva, the Rhine includes the Oberrhein and Hochrhein, and the Alps includes only the three rivers indicated. The number for the Rhone is an estimate. The data are from Frank (1981, 1982), Koehler-Haberlehner (1990), Moog *et al.* (1995), Obrdlik *et al.* (1995), Tockner *et al.* (1999) and E. Weigand (personal communication)

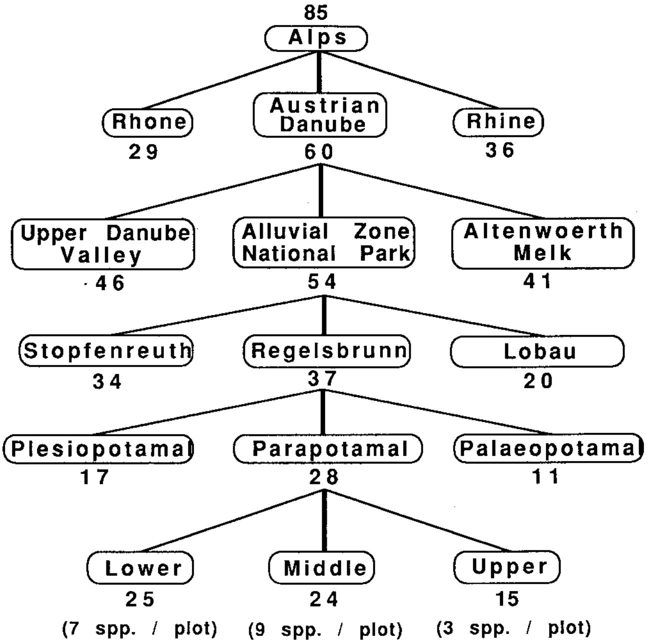

Figure 5. Species richness for fish at different hierarchical levels. The Rhone includes the Upper Rhone River, the Rhine includes the Oberrhein and Hochrhein, and the Alps includes only the three rivers indicated. The bottom line indicates the mean number of species collected from 200-m sample plots in the lower ($n = 16$), middle ($n = 13$) and upper ($n = 10$) regions of a parapotamal arm at Regelsbrunn. The data are from Hary and Nachtnebel (1989), Waidbacher *et al.* (1991), Persat *et al.* (1994), Schiemer *et al.* (1994), Tittizer and Krebs (1996), Spindler (1997) and Tockner *et al.* (1998, 1999)

of conservation strategies (Tockner *et al.*, 1998). A high proportion of the mollusc species occurring in the floodplains of the Danube are endangered and are becoming more and more isolated from each other as a consequence of river regulation. Their low vagility also decreases the rate of recovery following conservation efforts to restore connectivity. For fish, alpha diversity declines with increasing isolation of

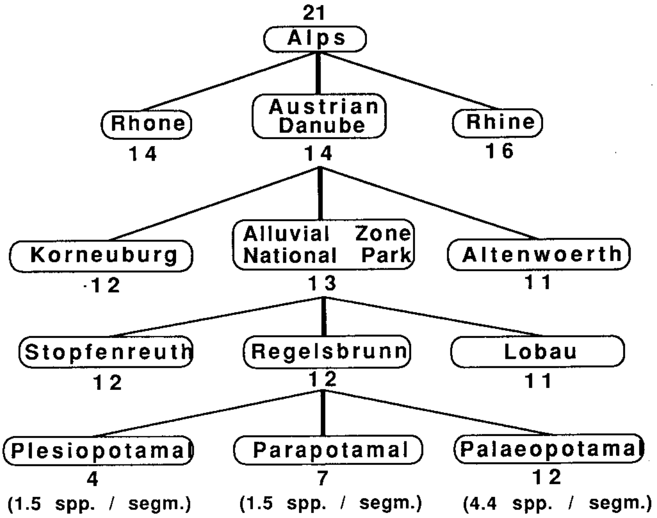

Figure 6. Species richness for amphibians at different hierarchical levels. The Rhone includes the segment from Lyon to Geneva, the Rhine includes the Oberrhein and Hochrhein, and the Alps includes only the three rivers indicated. The data are from Castanet and Guyetant (1989), Pintar and Straka (1990), Waringer-Loeschenkohl and Waringer (1990), Waringer-Loeschenkohl and Wanzenboeck-Endel (1992), Tittizer and Krebs (1996) and C. Baumgartner (personal communication)

Table II. Alpha-, beta- and gamma diversity for different groups at four different levels

	Gamma diversity	Alpha diversity	Beta diversity	Habitat diversity
A) Between floodplains				
Amphibia	10	7.8	0.10	13
Fish	60	41	0.24	6
Mollusca	65	32.2	0.34	6
B) Within floodplain				
Amphibia	10	2.2	0.06	71
Macrophyta	24	4.8	0.09	53
Odonata	28	7.0	0.11	35
C) Within channel types between floodplains				
Parapotamal	35	23.3	0.38	4
Plesiopotamal	23	13.5	0.43	4
Palaeopotamal	16	7.7	0.52	4
D) Within channel types within floodplain				
Parapotamal	36	12.7	0.13	22
Plesiopotamal	23	6.4	0.36	10
Palaeopotamal	24	8.5	0.26	11

Habitat diversity corresponds to the number of sites investigated.
A, between floodplains (along the River Danube, Austria); B, within floodplain (Regelsbrunn); C, fish: within different channel types between four floodplains; and D, mollusca: within channel types and within floodplain (Regelsbrunn).

floodplain water bodies (parapotamal > plesiopotamal > palaeopotamal), but beta diversity exhibits the opposite pattern (C). In palaeopotamal water bodies, there is a similar number of fish species in different floodplains, but the species composition is very different. In parapotamal channels (connected to the river downstream), the number of species differs between individual floodplains, but the species composition is generally similar, consisting mainly of rheophilous species.

Much of the attention given to biodiversity has dealt solely with alpha diversity, which the authors believe has constrained the comprehensive understanding of natural patterns and processes and hindered the development of effective conservation strategies. The value of measuring beta diversity, as an integrator of habitat heterogeneity across scales, deserves more attention from ecologists and managers.

Connected and disconnected environments

Species richness data for three benthic invertebrate groups allow comparisons between impounded and free-flowing channel sections and between connected and disconnected floodplains for a reach of the Austrian Danube (Figure 7). At least for these zoobenthic groups, diversity is similar in the impounded river channel (242 species), compared with the remaining free-flowing channel section (241 species). However, this has been accomplished by species replacement, resulting in a markedly different benthic assemblage in the impounded section (Moog *et al*., 1995). The fauna is much more diverse in the connected floodplain (494 species), whereas the disconnected floodplain has a depauperate fauna (149 species) even less diverse than that in the channel, consisting of a greatly attenuated version of the species assemblage in the intact floodplain.

Figure 8 compares the species richness of fish assemblages along a gradient of connectivity (distance from the main channel) in four floodplains along the Danube (A–D). The total number of species collected from these four floodplains combined was 48 out of 60 species of fish known from the Austrian Danube (Schiemer *et al*., 1994; Spindler, 1997). In addition to declining species richness from free-flowing (A and B) to regulated (C and D) reaches, three trends are apparent: (1) the number of fish species decreases from partially connected side channels (parapotamal) to isolated water bodies (palaeopotamal), irrespective of overall connectivity; (2) differences in species richness between floodplains are attributable primarily to lower diversity in parapotamal habitats of the regulated floodplains; and (3) the proportion of endangered species declines with decreasing connectivity. This is because most of the endangered fishes are rheophilic species that occur in the channel and parapotamal habitats (if connected), whereas the disconnected floodplains are inhabited mainly by eurytopic fishes with a low proportion of endangered species (Schiemer *et al.*, 1994).

Some disconnected floodplains retain partial connectivity via groundwater pathways. In contrast to dynamic floodplains, however, in which ephemeral water bodies fill during the early spring flood, the ephemeral water bodies of disconnected floodplains are filled much later by emerging ground water. Therefore, *Rana dalmatina*, an early spring spawner and the most common amphibian of the Danubian floodplains, is forced to spawn in permanent water bodies in disconnected floodplains, where it is exposed to higher levels of fish predation (Baumgartner *et al.*, 1997). This is clearly illustrated in Figure 9, which shows the dramatic differences in spawning habitat used by *R. dalmatina* in connected versus disconnected floodplains, even though the proportion of permanent and temporary water bodies is similar in the two floodplains.

BIODIVERSITY AS A MANAGEMENT OBJECTIVE

Although 'biodiversity' is viewed as the ultimate measure of effective management of riverine floodplains, it remains a long-term objective (e.g. alluvial forest succession operates on a time scale of centuries). The immediate goals of holistic ecosystem management are to restore the functional integrity of the river–floodplain complex; biodiversity should follow, although it must not be forgotten that biodiversity,

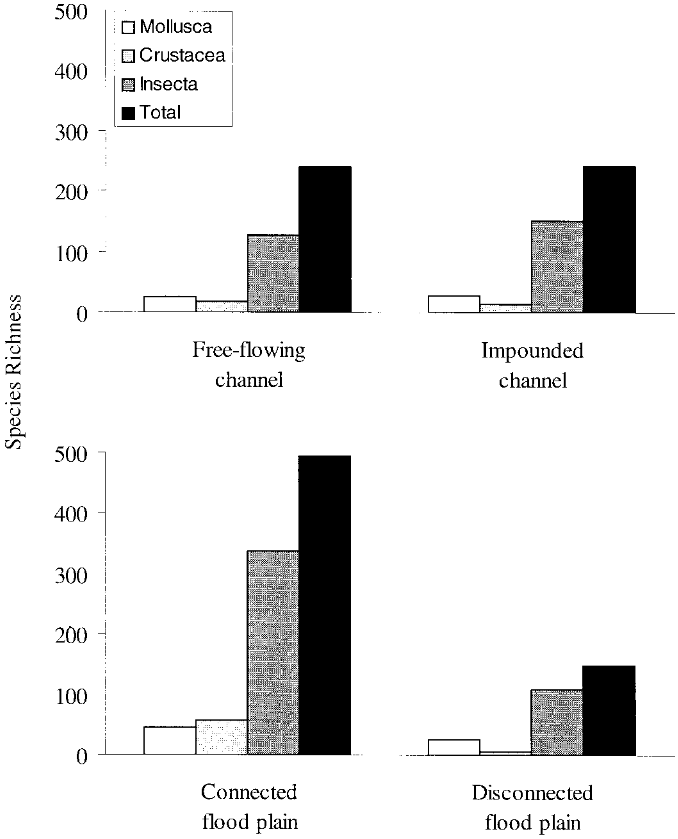

Figure 7. Number of benthic species in channel segments and floodplains of the Austrian Danube (modified from data in Moog *et al.*, 1995)

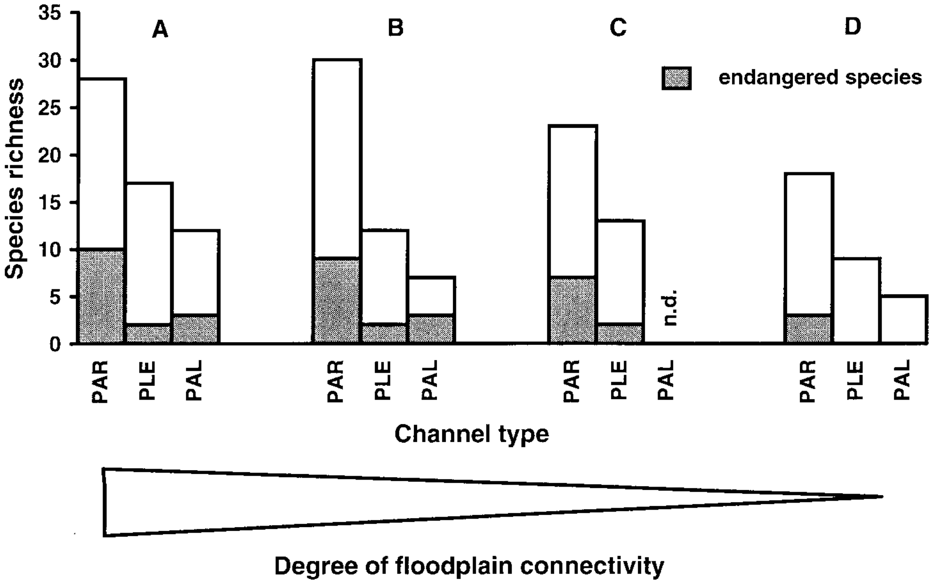

Figure 8. Species richness of fish assemblages in different floodplain water bodies along a gradient of connectivity in the Austrian Danube. A (Regelsbrunn) and B (Stopfenreuth) are floodplains in free-flowing reaches; C (Altenwoerth) is a floodplain in an impounded reach; and D (Lobau) is a disconnected floodplain near Vienna. PAR, parapotamal; PLE, plesiopotamal; PAL, palaeopotamal; n.d., no data

in its various forms, is a critical part of that functionality (Ward, 1998b). Functional floodplains with high species diversity and habitat heterogeneity also provide economic benefits in the form of natural flood control and natural water purification (Tremolieres *et al.*, 1997).

In order to be sustainable, management and restoration of regulated rivers must be based on principles of contemporary river ecology (Henry and Amoros, 1995; Stanford *et al.*, 1996). This means understanding the multidimensionality of lotic ecosystems (Ward, 1989). It means understanding that floodplain rivers are non-equilibrium systems, whose ecological integrity depends upon a certain level of disturbance. Ecological integrity also depends on maintaining interactive pathways between river channels and their

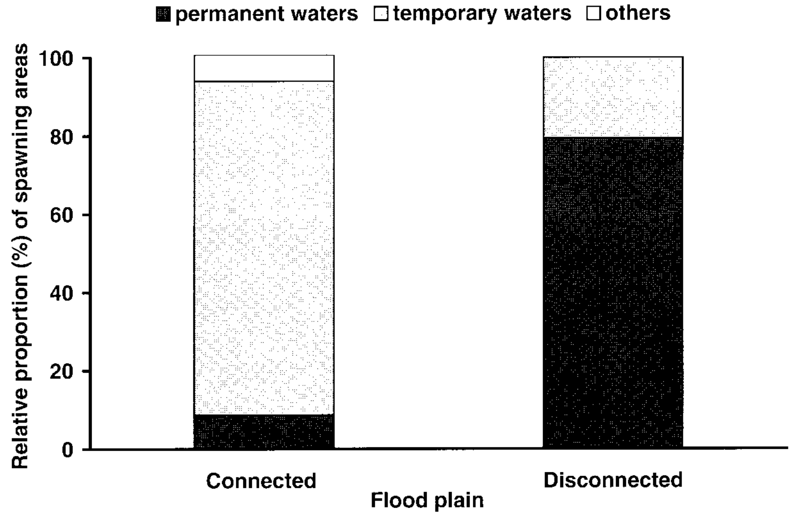

Figure 9. Spawning habitat used by *Rana dalmatina* in connected and disconnected floodplains of the Austrian Danube (from Baumgartner *et al.*, 1997)

floodplains and contiguous aquifers, as well as sustaining a diversity of successional stages. Much of this will be accomplished by the river itself if some semblance of fluvial dynamics is reconstituted and if the river is allowed some freedom of lateral migration.

Although intermediate disturbance may indeed contribute to high diversity, we believe that maintaining a *diversity of disturbance regimes* is also of major importance in maximizing the total biodiversity across a floodplain. Disturbance from fluvial dynamics generally exhibits a progressive decline from the channel to the uplands corresponding to declining connectivity. Floodplain water bodies and riparian assemblages far from the channel are less frequently disturbed by flooding than those situated in close proximity to the active channel. This disturbance/connectivity gradient further enhances the diversity of successional stages. In addition, because different species are favored by different levels of disturbance, a diversity of disturbance regimes provides suitable conditions for a greater variety of organisms. This was clearly demonstrated by the diversity of aquatic species in several major taxa at six sampling stations across a lateral transect of a Danube floodplain (Tockner *et al.*, 1998). The species richness of fish exhibited a progressive decline with distance from the channel. Amphibians, in contrast, attained their greatest diversity in aquatic habitats far from the active channel, no doubt partly in response to lower fish predation. Diversity maxima for other groups (molluscs, odonates, other macrozoobenthos and macrophytes) were arrayed along intermediate levels of the disturbance/connectivity gradient. The interstitial faunas exhibit a similar pattern (Dole, 1983; Dole-Olivier *et al.*, 1993; Marmonier *et al.*, 1997), with strictly epigean species attaining their highest diversity under conditions of high disturbance/connectivity, whereas strictly hypogean forms are most diverse under more stable conditions away from the active channel. A wide range of disturbance/connectivity, therefore, allows optimal conditions for a wider range of species.

In much of the world, however, river regulation has been so extensive that species-rich river–floodplain environments exist only as isolated fragments. These islands of biodiversity are endangered ecosystems. Without ecologically sound restoration of disturbance regimes and connectivity, these remnants of biodiversity will proceed on unidirectional trajectories toward senescence, without rejuvenation.

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