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RIVERINE LANDSCAPES: BIODIVERSITY PATTERNS, DISTURBANCE REGIMES, AND AQUATIC CONSERVATION

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Abstract

The term riverine landscape implies a holistic geomorphic perspective of the extensive interconnected series of biotopes and environmental gradients that, with their biotic communities, constitute fluvial systems. Natural disturbance regimes maintain multiple interactive pathways (connectivity) across the riverine landscape. Disturbance and environmental gradients, acting in concert, result in a positive feedback between connectivity and spatio-temporal heterogeneity that leads to the broad-scale patterns and processes responsible for high levels of biodiversity. Anthropogenic impacts such as flow regulation, channelization, and bank stabilization, by (1) disrupting natural disturbance regimes, (2) truncating environmental gradients, and (3) severing interactive pathways, eliminate upstream–downstream linkages and isolate river channels from riparian/floodplain systems and contiguous groundwater aquifers. These alterations interfere with successional trajectories, habitat diversification, migratory pathways and other processes, thereby reducing biodiversity. Ecosystem management is necessary to maintain or restore biodiversity at a landscape scale. To be effective, conservation efforts should be based on a solid conceptual foundation and a holistic understanding of natural river ecosystems. Such background knowledge is necessary to re-establish environmental gradients, to reconnect interactive pathways, and to reconstitute some semblance of the natural dynamics responsible for high levels of biodiversity. The challenge for the future lies in protecting the ecological integrity and biodiversity of aquatic systems in the face of increasing pressures on our freshwater resources. This will require integrating sound scientific principles with management perspectives that recognize floodplains and groundwaters as integral components of rivers and that are based on sustaining, rather than suppressing, environmental heterogeneity. *© 1998 Published by Elsevier Science Ltd. All rights reserved*

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INTRODUCTION

River channels are only part of an extensive interconnected series of biotopes and environmental gradients that, with their respective biotic communities, constitute lotic ecosystems. In the unaltered state, river systems are characterized by multiple interactive pathways operating across a range of spatio-temporal scales (Frissell *et al.*, 1986; Amoros and Roux, 1988; Minshall, 1988; Ward, 1989*a*,*b*). The mosaic structure and dynamic nature of river systems maintain their functional integrity (Ward and Stanford, 1995*b*). Effective ecosystem management of running waters necessitates a strong conceptual foundation that is based on understanding structural and functional attributes, including longitudinal resource gradients, floodplain dynamics, interactions with ground waters, and the role of disturbance regimes (Stanford and Ward, 1992).

The term riverine landscape or riverscape is used herein to indicate a holistic perspective of the broad-scale patterns and processes associated with fluvial systems. This paper treats aspects of biodiversity and disturbance from a riverscape perspective. The focus is on interactions between geomorphic features and fluvial dynamics as major determinants of biodiversity patterns in riverine ecosystems, with emphasis on aquatic invertebrates. Human-induced alterations to rivers are considered from the same perspective. Anthropogenic impacts such as acid precipitation, sewage pollution and logging are not dealt with here. For a recent ecological treatment of such topics see Harper and Ferguson, (1994). The ensuing material begins with a general description of the geomorphic features of riverine landscapes. This is followed by a multidimensional examination of biodiversity patterns, with examples of anthropogenic influences on such patterns. The role of natural disturbance as an important structuring agent is emphasized throughout the paper. Lastly, river protection and restoration are discussed in the context of ecosystem management.

GEOMORPHIC FEATURES

Biodiversity patterns are directly and indirectly influenced by the geomorphology of riverine landscapes, which may be perceived as a nested hierarchy (Fig. 1; see also Frissell *et al.*, 1986). There is a general

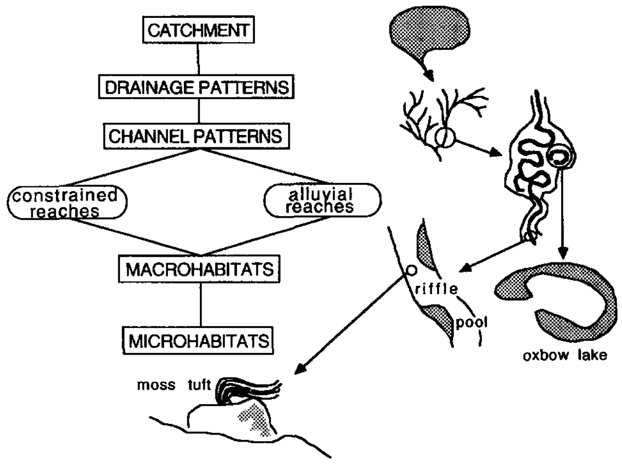

Fig. 1. A geomorphic hierarchy of riverine landscapes.

correspondence between the size of geomorphic features and their temporal persistence (Schumm and Lichty, 1965; Frissell *et al.*, 1986). For example, the catchment of a small mountain stream may have a linear extent of a kilometre and will persist as a coherent entity for many millennia, whereas its riffle/pool units occur on a spatial scale of metres with an average temporal persistence of years/decades.

The catchment, the highest level of the hierarchy, encompasses all other geomorphic units. The watershed is the boundary or divide between adjacent catchments. Catchments themselves occur in hierarchical series. For example, the Rhone catchment is the entire area drained by that river, which consists of the subcatchments of its major tributaries, each of which consists of smaller subcatchments. Stream order analysis (*sensu* Strahler, 1957) offers a convenient, though imperfect, means of designating the hierarchical level for a given stream and its catchment. First-order streams are headwater segments without tributaries that drain first-order catchments. The confluence of two first-order streams forms a second-order stream, two second-order streams join to form a third-order stream, and so on. The world's largest rivers are twelfth-order or greater.

Drainage patterns formed by the stream network reflect surficial geology of the catchment. In areas where the bedrock is uniformly resistant, the common dendritic pattern shown in Fig. 1 prevails. Stream channels follow weaker strata, thereby forming parallel, trellis, rectangular or other drainage patterns in catchments where resistance to erosion is not uniform. In karstic terrain much of the drainage follows subterranean pathways. Because drainage patterns reflect bedrock resistance to erosion, remote sensing can yield important data on the surficial geology within a catchment.

Channel patterns are of two main types, constrained and alluvial (Fig. 1). In constrained reaches geological controls severely limit channel migration. Such streams traverse generally straight courses through steep canyons, have substrata consisting of shallow deposits of coarse-grained sediment overlying bedrock, lack flood plains, and wetland vegetation is limited to a narrow riparian corridor.

Alluvial reaches flow through unconsolidated sediments (alluvium) transported and deposited by running water. Floodplains are broad valleys of alluvium formed by erosional/depositional processes of the present-day river as it migrates laterally (Kellerhals and Church, 1989). Terraces, remnants of abandoned floodplains formed when the river flowed at a higher level, may occur between the floodplain and the uplands. Alluvial rivers are highly dynamic and assume a complex array of channel morphologies of which braided and meandering are the most common types (Leopold and Wolman, 1957; Allen, 1965; Schumm, 1985; Church, 1992; Nanson and Croke, 1992). Meandering rivers are sinuous single-thread channels that migrate across the floodplain by erosion of concave banks and deposition on convex banks. Some meander segments are separated from the active channel as the river migrates across the floodplain, thereby contributing to overall habitat diversity. Braided rivers are characterized by multiple channels flowing around alluvial islands. Typically such rivers are highly unstable, with islands consisting of transient sand and gravel bars, although vegetation cover increases island stability under certain conditions (Schumm, 1985). Alluvial floodplains contain a diverse array of habitat types and successional stages, as discussed in subsequent sections of this paper.

Much of the biodiversity associated with riverine landscapes is attributable to heterogeneity at the habitat scale. From a holistic landscape perspective, riverine habitats comprise running and standing waters (abandoned channels), permanent and temporary waters, wetlands and groundwaters. In the following section, biodiversity patterns (across habitats and environmental gradients) are examined along three spatial dimensions: longitudinal, lateral and vertical. The fourth dimension, time, is also included because of the importance of temporal phenomena in habitat diversification.

BIODIVERSITY

Running waters harbour diverse biotic communities, although few comprehensive data exist. The Breitenbach, a tiny brook in northern Germany, is a notable exception (Zwick, 1992). Intensive collecting and a complete taxonomic inventory of all groups along 2 km of this first-order stream revealed 1085 species of metazoans (Fig. 2). One can only ponder the total number of species that must occur in a major river system.

The concept of species diversity, a central issue of community ecology (MacArthur, 1957; Margalef, 1957; Hutchinson, 1959), has assumed a new vitality and an expanded perspective, perhaps reflecting heightened concern for and awareness of threats to biodiversity on

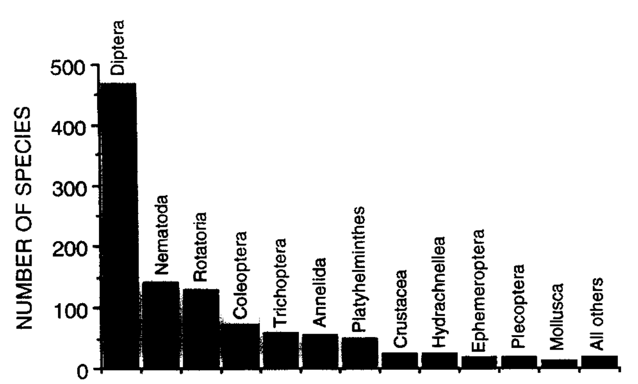

Fig. 2. Biodiversity of metazoans in the Breitenbach, a small brook in northern Germany (plotted from data in Zwick, 1992).

a global scale (Wilson, 1992; Ricklefs and Schluter, 1993; Huston, 1994; Schulze and Mooney, 1994; Rosenzweig, 1995). In this paper I treat biodiversity (i.e. species richness) patterns from a spatio-temporal perspective that focuses on habitat/landscape spatial scales and ecological time scales.

Longitudinal patterns

Downstream changes in assemblage structure along river courses has been a dominant theme in running water ecology (Hawkes, 1975). Most European research on this topic has taken a zonal perspective in attempts to delineate more-or-less discrete communities separated by transitional boundaries (e.g. Thienemann, 1912; Huet, 1954; Illies and Botosaneanu, 1963; Kawecka, 1971). The River Continuum Concept (Vannote *et al.*, 1980), developed in North America, perceives river systems as resource gradients along which the biota are predictably structured, thereby approaching longitudinal changes from a clinal rather than a zonal perspective. European work has focused on biocoenoses rather than biodiversity; both zonal and clinal approaches, however, implicate temperature as a major variable responsible for biotic patterns (but see Statzner and Higler, 1986).

Based on the deciduous forest river system used to derive the River Continuum Concept, biodiversity should exhibit a unimodal pattern (Fig. 3, top) with maximum values in the middle reaches (stream order 4 or 5). According to the continuum model, biodiversity in the headwaters is limited by low thermal heterogeneity, low light (heavily canopied), and low nutrients. Low biodiversity of the lower reaches is attributed to limitations induced by shifting and homogeneous substratum, high turbidity, and oxygen deficits. In the middle reaches, by contrast, light and nutrient levels are adequate, water clarity is high, and the substratum consists of a mosaic of habitat patches. Thermal heterogeneity is highest in the middle reaches, which are no longer dominated by ground water (headwater sources) nor buffered from change by a sheer volume of water (lower reaches).

The longitudinal biodiversity pattern of total zoobenthos of the St Vrain River (stream orders 1–5) corresponds to the prediction of the River Continuum Concept (compare curve segment A–B of Fig. 3, top, with total zoobenthos curve (T) of Fig. 4). This Rocky Mountain snowmelt stream exhibits both clinal and zonal features as it flows from alpine tundra (3414 m asl) to the high plains (1544 m asl). The entire mountain river segment, from tundra to lower foothills, is clinal in nature, with no evidence of zonation. There is, however, an abrupt faunal discontinuity from the lower foothills to the plains. Many members of the mountain stream fauna do not extend into the plains river and many other species and higher taxonomic categories were collected only from the plains location. The faunal discontinuity corresponds to the transition from rhithral to potamal conditions, which occurs where summer temperatures exceed 20°C (Illies and Botosaneanu, 1963). Maximum temperatures recorded at the lower foothills site did not exceed 16°C, whereas summer water temperatures above 20°C were common at the plains site (Ward, 1986).

Individual faunal groups show widely divergent spatial patterns of biodiversity, three of which are illustrated in Fig. 4 for a Rocky Mountain stream. Mayflies, Ephemeroptera (curve A) exhibited a more-or-less continuous increase in species richness along the stream

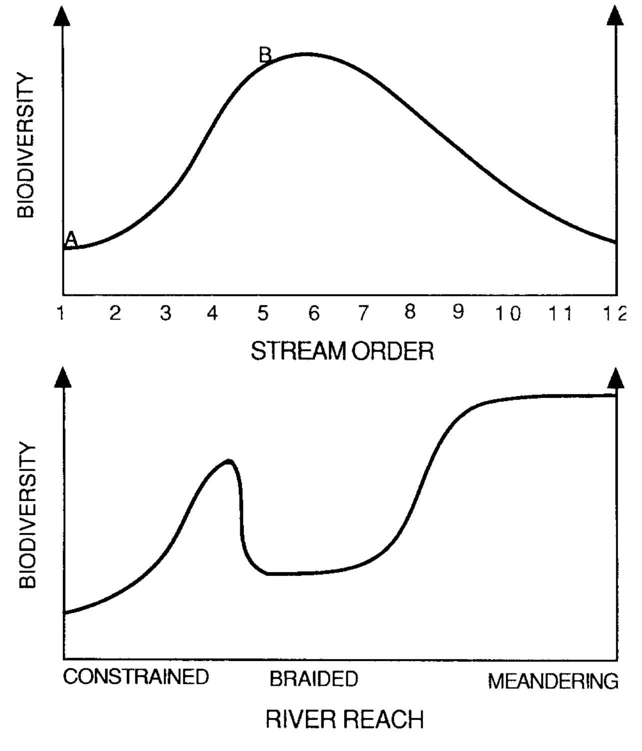

Fig. 3. Two idealized perspectives of biodiversity (species richness of stream macroinvertebrates) along river courses. Top: river continuum model of Vannote *et al.* (1980). The curve segment A–B corresponds to the St Vrain River, Colorado, (Ward, 1986), in which the number of taxa ranged from 34(A) to 106(B). Bottom: the three-reach model of Ward and Stanford, 1995*a*.

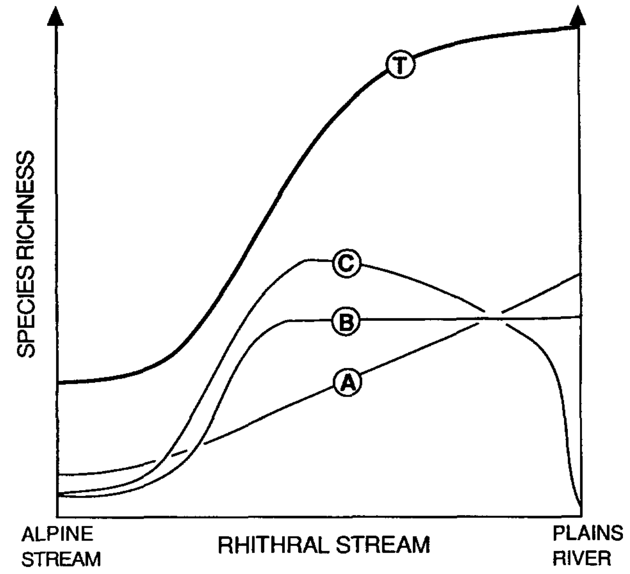

Fig. 4. Idealized biodiversity patterns exhibited by mayflies (A, total no. of species at different sites ranged from 4 to 19); caddisflies (B, total ranged from 3 to 14); stoneflies (C, total ranged from 3 to 20); and total zoobenthos (T, 34–106) along the longitudinal gradient (3414–1544 m asl) of a Rocky Mountain stream (Ward, 1986).

profile, with a general pattern of species addition downstream (without loss of those present at higher elevations). In contrast, species richness of caddisflies, Trichoptera (curve B) remained low in the headwaters, exhibited a precipitous increase in the upper montane zone, then remained at a similar level over the remaining stream profile. The caddisfly fauna consisted of distinct headwater and plains elements, species restricted to the middle reaches, to montane sites, and to the foothills. The stoneflies, Plecoptera (curve C) exhibited a distinctive biodiversity pattern with maximum values in the middle reaches (see also Ward, 1984). Stoneflies are the most stenothermal order of aquatic insects (Ward, 1992), but few species tolerate the extended period of ice and snow cover (7+ months/year), low summer temperatures (≤6°C), and low number of annual degree days (< 500) of the headwaters. The species occurring at the upper stations were mainly eurythermal species that occupied a wide range of elevation. The lower foothills mark the downstream distributional limits of many stoneflies. Although a diverse insect fauna occurs at the plains river, most species of stoneflies are unable to tolerate the summer temperatures at that location. In the middle reaches of the St Vrain River where stonefly biodiversity attains maximum values, thermal heterogeneity is high, yet maximum temperatures do not exceed 16°C. The broad annual temperature range of the middle reaches, where maxima were well below 20°C, may have facilitated temporal niche segregation mechanisms and enhanced species diversity.

Stream regulation by dams induces major discontinuities to resource gradients and zonation patterns along the longitudinal dimension (Ward and Stanford, 1995*a*). Biodiversity patterns along regulated rivers are characterized by major declines at riverine sites immediately downstream from dams, followed by relatively rapid increases concomitant with the recovery of environmental conditions (Fig. 5). Stream regulation alters virtually all environmental variables downstream; the sublethal effects (direct and indirect) of modified flow and temperature regimes are paramount in structuring biotic communities below many dams throughout the world (Ward, 1982; Petts, 1984; Walker, 1985; Dudgeon, 1992).

The summer-cool water released from the bottom of the high dams on the Gunnison River, a major tributary of the Colorado River, has shifted the rhithral–potamal boundary downstream 60–70 km, a vertical drop of around 500 m elevation (Ward and Stanford, 1991). As a result, salmonids have extended their ranges downstream and a trout fishery now occurs in an area previously inhabited by the endemic warm-water fishes of the Colorado River basin (Stanford and Ward, 1986). Note the relatively high biodiversity at Site 7 (Fig. 5), located downstream from a re-regulation reservoir. The function of the re-regulation operation is to dampen the severe flow fluctuations from the two hydropower dams immediately upstream. Flow regulation also disrupts interactions along other spatiotemporal dimensions, as will be demonstrated subsequently.

Lateral patterns

Interactive pathways along the lateral dimension are especially pronounced in riverine reaches with fringing floodplains (Antipa, 1928; Botnariuc, 1967; Welcomme, 1979; Junk *et al.*, 1989; Ward, 1989*a*). As the river channel migrates laterally across the floodplain, a

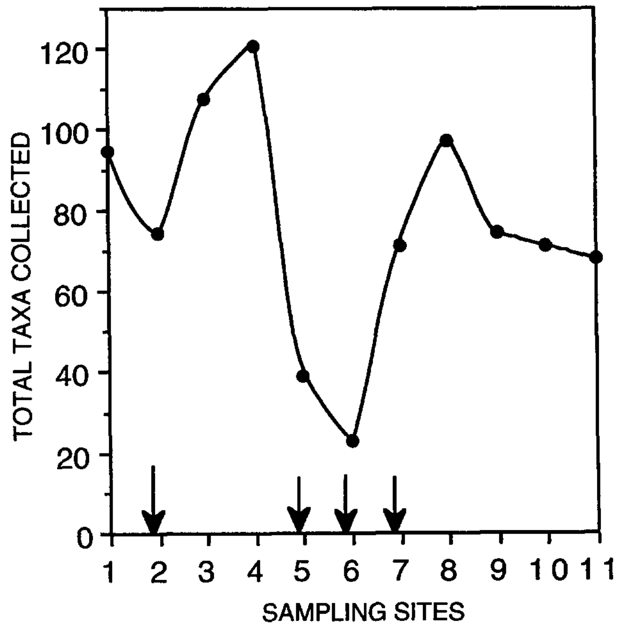

Fig. 5. Biodiversity pattern of total zoobenthos along the longitudinal gradient of the Gunnison River, a seventh-order tributary of the Colorado River. Arrows indicate locations of high dams (Ward and Stanford, 1991).

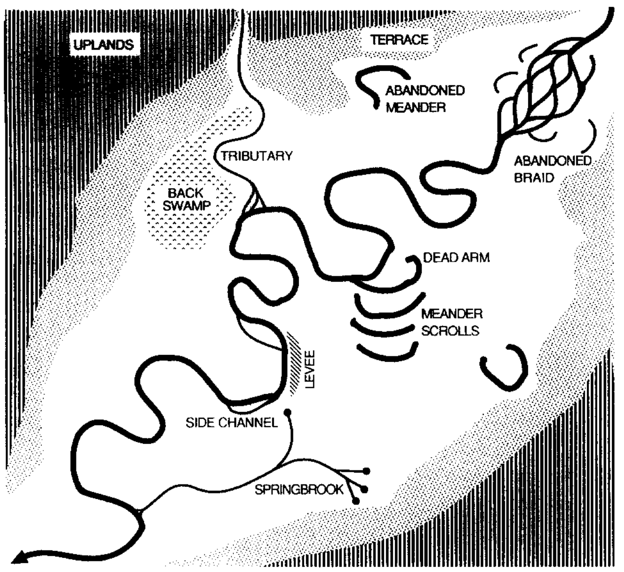

Fig. 6. Some major geomorphic features of river-floodplain systems.

diverse array of lotic, semi-lotic, and lentic environments are formed by fluvial action (Fig. 6). These environments include side channels, dead arms connected with the main channel at one end, abandoned meander loops, abandoned braids, backswamps, and marshes, in addition to tributary streams, and alluvial springbrooks (see Amoros *et al.*, 1982, for a functional classification of floodplain water bodies). This results in a mosaic of habitat patches, ecotones, and successional stages (Amoros *et al.*, 1982; Terborgh and Petren, 1991; Décamps, 1996; Ward and Wiens, in press), characterized by different biotic communities (Castella *et al.*, 1984; Copp, 1989; Mitsch and Gosselink, 1993). Natural disturbance (fluvial action) induced by flooding, therefore, enhances ecological connectivity and biodiversity (Salo *et al.*, 1986; Amoros and Roux, 1988; Ward and Stanford, 1995*b*).

The River Continuum Concept, as initially formulated (Vannote *et al.*, 1980), did not consider interactions between the river channel and its floodplain. Ward and Stanford, (1995*a*) revised their original perspective of longitudinal biodiversity patterns of zoobenthos to accommodate the lateral dimension. The three-reach model includes not only the channel, but also the diverse water bodies of the floodplain as integral components of the river ecosystem, resulting in the theoretical biodiversity pattern shown in Fig. 3 (bottom). The canyon-constrained headwater reach is not influenced by floodplains and the idealized biodiversity pattern of the upper segment is not altered from the original model. Low values of biodiversity are postulated for the braided reach because of channel instability and shifting substratum, at least in the most extreme form (bar braided, sensu Schumm, 1985). It is within the meandering reach that biodiversity should attain the highest values. Different types of floodplain water bodies, indeed different successional stages within them, contribute to biodiversity as the biota exploit the predictable spatiotemporal heterogeneity.

Riparian vegetation exhibits distinct zonation patterns from the channel to the uplands, resulting in broad-scale spatial segregation of species along the floodplain's elevation gradient. At a finer scale, species segregate according to microsite. Gregory *et al.* (1991) attribute the high biodiversity of riparian plant communities (twice that of the adjoining hillslope for the McKenzie River, OR) to habitat diversity and disturbance regimes.

The species richness of wetland vegetation generally increases with increasing water flow (Mitsch and Gosselink, 1993). Flooding renews nutrients, reduces anaerobic conditions, increases sediment diversity, and opens new patches for colonization. Based on an extensive literature review, Brown and Lugo, (1982) calculated the number of tree species for freshwater wetlands, which averaged 11·0 for riverine wetlands (flowing water), 4·4 for basin wetlands (still water), and 2·4 for scrub wetlands (nutrient-limited, still water).

In one section of the Amazon floodplain, Junk and Piedade, (1994) identified 387 species of herbaceous plants from 182 genera and 64 families. They attribute the high biodiversity to several factors, including habitat diversification from fluvial action, the predictability of the floodpulse that allows different species to colonize different portions of the elevation gradient and to develop adaptations to both flood (wet-phase) and drought (dry-phase) conditions, and reduction of interspecific competition by alternating aquatic and terrestrial phases. They conclude that their "results are in full accordance with the Intermediate Disturbance Hypothesis and the Floodpulse Concept" (Junk and Piedade, 1994).

Only a few species of riverine fishes remain in the main channel during all life stages. Other species reside in floodplain water bodies during the dry phase, moving to the inundated floodplain surface to exploit the rich food resources that develop during the wet phase. The 'moving littoral' that traverses the elevation gradient from the river channel to the uplands as floodwaters rise produces a dynamic edge effect (Junk *et al.*, 1989). Many species of riverine fishes are 'flood dependent' in the sense of requiring lateral migrations between the river channel and the floodplain as part of the life cycle (Welcomme, 1979). Lateral migrators use the inundated floodplain as feeding, spawning, and nursery areas.

Many human-induced alterations to rivers have, intentionally or not, profoundly disrupted interactions along the lateral dimension. In Europe, for example, massive river training works were completed prior to the 20th century (e.g. Vischer, 1989). Coupled with flow regulation, wetland drainage, floodplain reclamation, and other practices, many segments of formerly dynamic anastomosed floodplain rivers became highly managed single-thread channels isolated from their floodplains (Petts *et al.*, 1989; Ward and Stanford, 1995*b*). This disruption of lateral connectivity is so pervasive, especially in Europe and North America, that many lotic ecologists failed to appreciate until quite recently the extent to which the lower reaches of managed river systems have been modified from the natural state.

The hydrologic changes resulting from flow regulation provide a clear example of anthropogenic effects on downstream river-floodplain systems (Fig. 7). Most of these effects, and their interactions, reduce connectivity and all decrease spatiotemporal heterogeneity, which ultimately reduces biodiversity. Many of the disruptions leading to reduced habitat heterogeneity in Fig. 7 involve alterations in successional trajectories, a topic addressed subsequently in the section on temporal patterns.

Vertical patterns

The vertical dimension considered herein consists of the alluvial aquifers beneath rivers and floodplains. Whereas alluvial aquifers are hydraulically active with surface waters, on ecological time scales there is little exchange between alluvial and contiguous bedrock aquifers.

The general vertical structure of an alluvial aquifer is illustrated in Fig. 8. The hyporheic zone is an ecotone between surface waters and true phreatic groundwaters. The term hyporheic zone, as coined by Orghidan (1959), referred to the alluvium beneath the river channel. However, in alluvial rivers with high porosity, considerable lateral exchange may occur between the surface waters of the channel and interstitial waters beneath the floodplain (Stanford and Ward, 1988; Marmonier *et al.*, 1992; Gibert *et al.*, 1994; Ward and Palmer, 1994). The hyporheic zone may be defined in physical terms as the area of the aquifer penetrated by surface water or in biological terms by the penetration of riverine fauna (Gibert *et al.*, 1994). By either definition, the extent of the hyporheic zone may under some conditions be metres thick and extend laterally away from the channel for kilometres (Stanford and Ward, 1988). More commonly, the hyporheic zone is centimetres thick and extends only metres away from the channel.

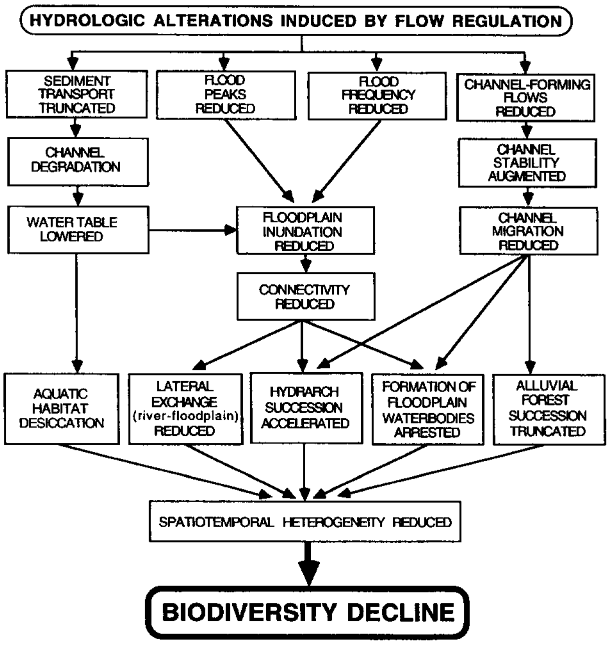

Fig. 7. Some major interactions resulting from hydrologic changes induced by flow regulation that lead to declines in biodiversity (modified from Ward and Stanford, 1995*b*).

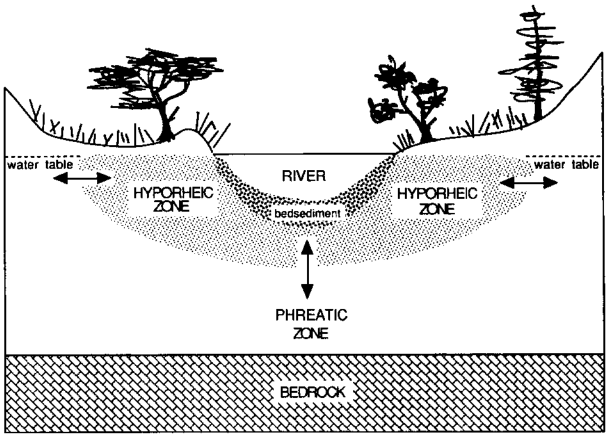

Fig. 8. Diagrammatic vertical structure of a river-aquifer system, showing the hyporheic and phreatic zones.

Only recently has it been recognized that the subterranean landscape is by no means homogeneous and that groundwater organisms are not a homogeneous group (Marmonier *et al.*, 1993; Gibert *et al.*, 1994). The diversity of groundwater biota has been little studied and has been largely or totally ignored in estimates of global biodiversity. Because subterranean waters represent 97% of global freshwaters (Marmonier *et al.*, 1993), and those that have been studied exhibit high levels of endemism, it is reasonable to presume that groundwater biotopes contain a large reservoir of biodiversity. In reference to epigean species, Pimm *et al.*, (1995) state that areas high in endemics "dominate the global patterns of extinction". This would suggest that the subterranean fauna, given high levels of endemism, is especially vulnerable.

Subterranean animals inhabiting alluvial aquifers reside in the interstitial spaces between mineral particles. Their distribution patterns are influenced by vertical and horizontal gradients in substratum characteristics (particle size, porosity), oxygen concentrations, food resources, and water exchange. The same processes that create habitat heterogeneity in the surface waters of alluvial rivers (e.g. lateral migrations of river channels across floodplains) also result in habitat diversity within contiguous aquifers. The remainder of this section examines biodiversity patterns of interstitial faunal assemblages using examples from studies conducted at different scales.

Interstitial fauna was examined at two spatial scales along the course (475 km) of a Rocky Mountain river (nine sampling sites, three habitats per site) (Ward and Voelz, 1994). At the habitat scale (combining data from all sites) aquatic insect diversity declined from surficial gravel (102 taxa) to hyporheic habitats (69 taxa) to phreatic habitats (34 taxa). Crustacean biodiversity, however, did not differ greatly between habitat types. Biodiversity of the interstitial fauna did not exhibit a distinct pattern along the altitudinal profile, despite a drop in elevation from 3194 to 1199 m asl, in stark contrast to the dramatic increase in diversity of surface-dwelling stream invertebrates along a similar elevation transect in another Rocky Mountain river (Ward, 1986). Results from a variety of gradient analysis techniques suggest that the distribution patterns of groundwater animals are not directly related to variables associated with elevation, such as temperature, and that site-specific geomorphic and hydrologic features are major structuring agents.

The intermediate diversity level that typifies hyporheic habitats does not conform to the concept of the 'edge effect', which predicts the highest number of species in ecotones (Gibert *et al.*, 1990). Declining levels of oxygen, light, and organic matter with increasing depth likely account for a corresponding decline in the biodiversity of interstitial animals.

In the natural state, alluvial aquifers are highly interactive with contiguous surface waters (Stanford and Ward, 1988; Gibert *et al.*, 1990; Vervier *et al.*, 1992). This means that polluted river water can enter groundwater aquifers (Gibert, 1990). However, the soil vegetation complex of an intact floodplain is an effective self-purification agent that may maintain high groundwater quality even in polluted rivers (Roeck *et al.*, 1993). River regulation not only lowers the water table downstream (Fig. 7), but also reduces hydraulic conductivity leading to clogging of interstitial spaces (Schälchli, 1992). In addition to reducing living space for groundwater animals, low exchange rates lead to poorly oxygenated interstitial waters. In a segment of the Rhine regulated by a hydroelectric dam, microcrustaceans dominated interstitial assemblages; aquatic insects were rare and true groundwater forms were absent (Creuzé des Châtelliers *et al.*, 1992).

Temporal patterns

Spatial patterns of biodiversity partly reflect the superimposition of temporal dynamics on environmental gradients. Nonequilibrium theories of community structure invoke disturbance as a major contributor to the maintenance of biodiversity on ecological time scales (e.g. Connell, 1978; Ward and Stanford, 1983; Resh *et al.*, 1988; Huston, 1994; Reice, 1994). Ecological succession provides clear examples of the role of disturbance in engendering habitat heterogeneity and high levels of biodiversity. Alluvial forest succession and hydrarch succession are major determinants of biodiversity patterns across riverine floodplains. Each of these phenomena is treated briefly in the following paragraphs.

Lateral channel migration undercuts forests growing along concave banks and initiates primary succession on alluvium deposited on convex banks, resulting in a mosaic of habitat patches and successional stages (Salo *et al.*, 1986; Terborgh and Petren, 1991). It appears that intermediate levels of disturbance induced by the flooding regime may thwart the realization of competitive exclusion, leading to high levels of alpha diversity. Fluvial dynamics create a variety of edaphic conditions and a diversity of ages of habitat patches. Because forests of many different ages (successional stages) occur in close proximity, beta diversity is also high. More than 200 tree species per ha have been recorded in floodplain forests of Amazonia (Terborgh and Petren, 1991). Anthropogenic regulation of river flow reduces or eliminates the natural disturbance regime, leading to a simplification of the floodplain vegetation as pioneer stages are eliminated and successional processes are truncated (Fig. 7; Décamps and Tabacchi, 1994).

Fluvial dynamics also maintain a diversity of floodplain water bodies collectively encompassing the entire range of hydrarch succession. Different types of floodplain water bodies undergo different successional trajectories. Each type of water body, indeed each seral stage, may be characterized by a distinct assemblage of organisms (Castella *et al.*, 1984; Copp, 1989; Schiemer and Waidbacher, 1992). The trend toward terrestrialization is interrupted to varying degrees by fluvial action. Floods form new water bodies and rejuvenate those formed by past floods. The result of these dynamic interactions is the high levels of habitat heterogeneity and biodiversity at the floodplain scale.

Anthropogenic activities such as flow regulation tend to isolate the river from its flood plain, partly by suppressing the temporal dynamics of flooding that are necessary to maintain a diversity of water bodies, each encompassing a range of successional stages. This lost connectivity arrests the formation of new floodplain water bodies and accelerates terrestrialization of extant water bodies (Fig. 7). The implications for biodiversity are exemplified by the following comparison of two Danube floodplains (Löffler, 1990), one isolated from the river channel, the other with connectivity largely intact: 20 species vs 60 species of macrophytes, respectively, in disconnected and connected floodplains; 16 species vs 35 species of molluscs; and 4 species vs 30 species of fishes.

The approach taken throughout this paper has been to emphasize general patterns and processes. This should not convey the impression that all river systems function in the same way or that their responses to anthropogenic impacts are necessarily similar. Indeed, at a fine scale of resolution each river system is unique, as are all segments within it. Nevertheless, rivers and river reaches may be grouped into common types (e.g. alluvial, constrained, braided, meandering) that function in a similar fashion across a range of scales. A meandering reach will exhibit different responses from a braided reach to a given impact, such as damming or diversion, and position along the longitudinal profile may greatly influence response variables (Ward and Stanford, 1995*a*).

ECOSYSTEM MANAGEMENT

Ecosystem management, defined here simply as a holistic catchment approach that recognizes the importance of processes that operate across a wide range of spatial and temporal scales, is necessary to protect and restore aquatic biodiversity. Aquatic conservation, to be effective, must be based on a solid conceptual foundation and a fundamental understanding of the structure and function of natural river ecosystems (Stanford and Ward, 1992). In the past, management efforts have too often been conducted without consideration of natural dynamics or even as attempts to suppress spatio-temporal heterogeneity. As stated by Reice, (1994), 'Human efforts to stabilize ecosystems have resulted in the loss of biodiversity, when the opposite result was the goal'. It must be remembered that rivers are 'flood-dependent' ecosystems and that the flood plains are an integral part of the river. The biota, aquatic and terrestrial, that inhabit flood plains employ an amazing array of adaptive strategies to exploit the spatio-temporal dynamics. In a floodplain river, the absence of floods constitutes a disturbance (Sparks, 1995).

Within the last decade or so, lotic ecologists have developed sufficient knowledge to . propose mechanisms that structure biodiversity patterns at the riverscape scale. Figure 9 represents such a conceptual model. In pristine rivers natural disturbance regimes include the actions/reactions of fluvial energy (erosional and depositional processes) and thermal heterogeneity. Environmental gradients, occurring along longitudinal and lateral dimensions, across ground water–surface water ecotones, and along time scales, lead to high levels of spatio-temporal heterogeneity (Ward and Wiens, in press). Natural disturbance regimes also contribute to spatio-temporal heterogeneity and facilitate exchanges of matter and energy (CONNECTIVITY) between landscape elements. A positive feedback loop is shown in Fig. 9 to emphasize that spatio-temporal heterogeneity is both a contributor to and a result of connectivity. Except for migration pathways, the components at the third level in Fig. 9 have been dealt with in previous sections of this paper. Movements and migration also contribute to high biodiversity levels over an annual cycle. Flood-dependent fishes exhibit regular patterns of migration between the river channel and the inundated floodplain for purposes of spawning and feeding (Welcomme, 1979; Ward, 1989*a*). Some invertebrates also exhibit movements between the channel and floodplain waterbodies as part of their life cycles (Soderstrom, 1987). In addition, terrestrial species of plants and animals colonize the floodplain surface during the dry phase, but are replaced by aquatic species during the period of inundation (Junk *et al.*, 1989).

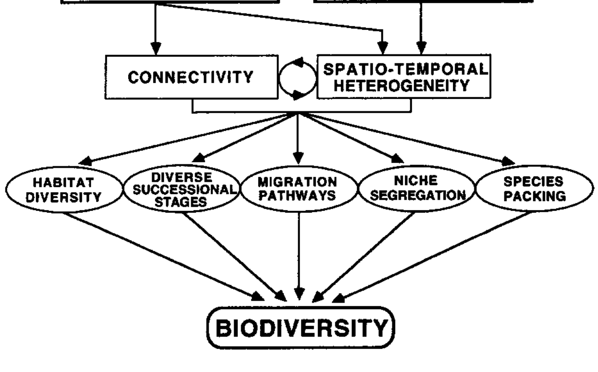

Fig. 9. Proposed interactions that structure biodiversity patterns in riverine landscapes.

Anthropogenic impacts on riverine landscapes, such as damming, dredging, and channelization, disrupt natural disturbance regimes, truncate environmental gradients, and sever interactive pathways (Ward and Stanford, 19891). Ecosystem management, therefore, becomes a matter of (1) re-establishing environmental gradients along longitudinal, lateral, and vertical dimensions across a range of scales, (2) re-establishing ecological connectivity between landscape elements, and (3) reconstituting some semblance of the natural dynamics.

Attempts to re-establish ecological connectivity have been initiated on a few river systems (e.g. Bravard *et al.*, 1992; Jungwirth *et al.*, 1993). Such projects require compromises because of the historical use of floodplains by humans. One compromise proposed for rehabilitation of the Rhine is to remove the inner (summer) dykes, but retain the outer (winter) dykes, thereby restoring connectivity to part of the original floodplain (Van Dijk *et al.*, 1995). Purchasing private holdings along flood plains, to allow managed river segments to revert to riverine–floodplain ecosystems, has been proposed as an ecologically sound and economically viable approach to natural flood control (Mitsch and Gosselink, 1993). Dynesius and Nilsson (1994) call for "immediate action . . . to create an international preservation network of free-flowing river systems ...." to counter the fragmentation of river habitats by flow regulation. The success of such initiatives can be evaluated by the extent to which the conservation of biodiversity is achieved.

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