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Landscape ecology: a framework for integrating pattern and process in river corridors

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Abstract

Investigations of European floodplain rivers demonstrate how landscape ecology can provide an effective framework to integrate pattern and process in river corridors, to examine environmental dynamics and interactive pathways between landscape elements, and to develop viable strategies for river conservation. The highly complex and dynamic nature of intact river corridors is particularly amenable to a landscape ecology perspective. Analysis of spatial patterns has provided considerable insight into environmental heterogeneity across river corridors and is an essential prelude to examining dynamic interactions. For example, data from aerial photographs, digitized maps and year-round field measurements in a glacial flood plain, enabled us to distinguish six channel types, based on the correspondence between connectivity and physicochemical attributes. Spatial data were also used to analyze longitudinal changes in landscape elements along the course of a morphologically-intact riverine corridor, providing insight into the structural complexity that must have characterized many Alpine rivers in the pristine state. Landscape indices were employed to investigate seasonal dynamics in a glacial flood plain of the Swiss Alps which exhibits a predictable expansion/contraction cycle, with corresponding shifts in flow paths (surface and subsurface) and water sources (snowmelt, englacial, subglacial, alluvial aquifer, hillslope aquifer). Surface connectivity exhibited an unexpected biphasic relationship with total channel length, whereas riverscape diversity progressively increased along the entire range of channel length. Reconstituting the functional integrity that characterizes intact river corridors should perhaps be the major goal of river conservation initiatives. Although understanding functional processes at the landscape scale is essential in this regard, few data are available. In the Alluvial Zone National Park on the Austrian Danube, three phases of hydrological connectivity were identified (disconnection, seepage connection and surface connection) that corresponded to the predominance of three functional processes (biotic interactions, primary production and particulate transport) within the river corridor.

Introduction

Landscape ecology holds the potential for developing a truly holistic perspective of river corridors, one that rigorously integrates structure, dynamics, and function. Forman and Gordon (1981) identified the river corridor as a major component of the landscape. Décamps (1984) applied this viewpoint to highly managed rivers, and Ward (1998) emphasized the importance of viewing all river systems in a landscape context. Here we expand upon this general theme, using examples from our recent research on European rivers. We attempt to demonstrate that landscape ecology offers an effective framework to integrate pattern and process in river corridors, to examine environmental dynamics and interactive pathways between landscape elements, to link research with management, and to develop viable strategies for river conservation.

Because nearly all European river corridors were already substantially modified by humans before the science of river ecology developed (Petts et al. 1989), established research and management concepts often fail to fully recognize the crucial roles played by habitat heterogeneity and fluvial dynamics. We believe that this incomplete understanding constrains scientific advances in river ecology and renders management and restoration initiatives less effective. Although it is neither possible nor necessarily desirable to restore anthropogenetically-modified rivers to their pristine condition, a valid understanding of natural patterns and processes is an essential prerequisite for viable ecosystem management (Stanford et al. 1996). For this reason, we have focused research efforts on investigating patterns and processes in riverine landscapes that are in a near-natural condition.

The term landscape is used in its simplest sense, i.e., a spatially heterogeneous area (Turner and Gardner 1991; Wiens 1995). The riverine landscape or river corridor corresponds to the surface area composed of interacting terrestrial and aquatic units that are directly influenced by the river (i.e., aquatic habitats, floodplain surface, and riparian zone). Riverscape refers only to the aquatic components of the riverine landscape. Ward (1997) introduced the term fluvial stygoscape as a subterranean equivalent of landscape to designate aquifers beneath alluvial flood plains.

The overall goal of this paper is to demonstrate how a landscape ecology approach resulted in a broader and more integrative understanding of natural processes in European river corridors by elucidating the strong links between spatiotemporal heterogeneity and hydrodynamic processes, including interactions between surface waters and ground waters. The ensuing material begins by demonstrating how (1) static spatial patterns, (2) dynamic interactions, and (3) functional processes in river corridors can be examined from a landscape perspective. Examples are used to illustrate the remarkable level of spatiotemporal heterogeneity that may be attained in rivers where natural processes still operate on a large scale. Then a landscape approach to hierarchical studies of biodiversity in river corridors is described. Finally, we present a landscape approach to river conservation and restoration.

Methods and study areas

This paper is based on studies of three riverine landscapes, the Val Roseg, a glacial flood plain in the Swiss Alps; the Fiume Tagliamento, an island-braided Italian river; and the Alluvial Zone National Park, a lowland floodplain complex on the Austrian Danube. These three systems represent a range of formerly widespread temperate riverine landscapes. Information derived from historical records, digitized maps, and aerial photographs, were combined with data from ground surveys and extensive field sampling. Brief descriptions of the three study areas and the field methods follow (see the references cited for additional details). Studies continue at all three locations.

The Roseg River, a tributary of the River Inn, is located in the Bernina Massif of the Swiss Alps. Its primary water source originates from two valley glaciers. Research focused on the glacial flood plain of Val Roseg, which is 2.6 km long and up to 510 m wide, situated at ca. 2,100 m a.s.l. (Tockner et al. 1997; Malard et al. 1999; Ward et al. 1999a). Channel patterns were digitized from aerial photographs (color and IR images, resolution 0.1 m) and data from ground surveys along 17 transects. The channel network was mapped, and turbidity and specific conductance were measured monthly, at each channel along the 17 transects from July 1996 to January 1998. A suite of other chemical variables was measured at selected locations.

The Fiume Tagliamento, the last morphologically intact river corridor in the Alps, arises in the limestone Alps of northern Italy and flows 172 km to the Adriatic Sea (Ward et al. 1999b; Tockner et al. in press). The active flood plain is up to 2 km wide and contains numerous vegetated islands. Maps (1:10,000) and B/W air photographs (scales: 1:19,000–1: 30,000) taken along the whole river corridor were digitized using MapInfo Professional 4.1. Slope (%), shoreline length (at ca. mean water level), the areas of bare gravel and wetted channels, and the number, size and perimeter of individual islands have been estimated for each river km along the entire length of the river.

The Alluvial Zone National Park (AZNP), situated in the free-flowing section of the Danube downstream from Vienna, consists of a floodplain complex that was partially disconnected from the river in 1850 (Tockner et al. 1998). The relatively diverse riverine landscape of the AZNP was formed prior to human intervention. Since that time, a slow unidirectional succession has virtually eliminated areas of bare gravel and increased the extent of forest cover. However, in autumn 1996 artificial levees were breached in prescribed locations as a means to restore the fluvial dynamics. In a 5.2 km^2 large floodplain, 49 sites were sampled for physicochemical variables at different water levels over an annual cycle. In, addition, the Danube channel and the downstream end of the floodplain were sampled 50 times over a 15-month period (Tockner et al. 1999). These data were used for mass-balance calculations of organic matter and nutrients.

Structure, dynamics and function

Static spatial patterns

Analysis of spatial patterns has provided considerable insight into environmental heterogeneity across river corridors (e.g., Amoros and Petts 1993; Tockner et al. 1997). In highly regulated river segments, landscape patterns may be 'frozen in time' by dams and artificial levees. For example, although floodplain segments of the French Rhone may contain highly diverse aquatic and riparian habitats, in many cases these are relicts of the formerly dynamic river system.

Channel types in a glacial flood plain.
Even in highly dynamic natural river corridors, analyzing static landscape patterns is a necessary first step. For example, combining data from aerial photographs, digitized maps, and detailed field measurements revealed a remarkable spatial heterogeneity in the glacial flood plain of Val Roseg. The channel network within the glacial flood plain by no means consists of uniformly cold, highly turbid waters. A landscape approach enabled us to identify 6 distinctive channel types, based on the correspondence between connectivity and physicochemical attributes (Tockner et al. 1997). Channel types in the Val Roseg include (1) the main thalweg channel, (2) side channels, (3) intermittently-connected channels, (4) groundwater channels (alluvial and hillslope-fed), (5) mixed channels carrying water from different sources, and (6) tributaries. Channel types were separated based on the origin of their water, the degree of hydrological connectivity, and corresponding physicochemical attributes. This detailed knowledge of the spatial pattern was necessary to fully understand the dynamics described in the next section of this paper.

Landscape elements along a river corridor.
Analysis of spatial landscape patterns along the length of the Fiume Tagliamento provided a rare glimpse into the structural complexity that must have characterized many Alpine rivers in the pristine state (Ward et al. 1999b). The active flood plain is up to 2 km wide and contains a riparian vegetation mosaic encompassing a range of successional stages. The ca. 150 km^2 river corridor (excluding tributary corridors) connecting the Mediterranean with the Alps consists of four major landscape elements (Figure 1; Tockner et al. in press). The Tagliamento has up to 11 channels per cross section and more than 650 vegetated islands. The total ecotone length (riparian forest boundary zone) of 668 km along this 172-km long river is largely attributable to islands (Figure 2), which cover 17% of the active corridor. Islands occur along virtually the entire length of the river, being absent only from the uppermost canyon-constrained headwaters and the lower meandering reach near the sea. Riverine islands, proposed as an ecosystem-level indicator of the condition of a river corridor (Ward et al. 2000), are an endangered landform in Europe. For example, only 6 islands remain of the ca. 2,000 islands historically present in the Austrian Danube. Figure 3 illustrates the complex spatial array of vegetated islands in three short segments of the active Tagliamento river corridor. Even at this coarse level of resolution, the high spatial diversity of islands possible within a river corridor is apparent. Additionally, these graphs also demonstrate the different geomorphic processes that may be involved in forming islands (erosion, sedimentation, dissection, etc., Osterkamp 1998; Gurnell et al. 2001). Ongoing research investigates the role of islands in structuring the riverine landscape, with major implications for the diversity of aquatic and riparian biota.

Dynamic interactions

A shifting habitat mosaic.
Landscape indices (Gustafson 1998) were used to investigate seasonal dynamics in the spatial configuration of the channel network and corresponding shifts in water sources at Val Roseg, the glacial flood plain in the Swiss Alps (Malard et al. 1999). Monthly measurements documented the annual expansion/contraction cycle of the channel network (Figure 4). Connectivity was expressed as the relative proportion (%) of the channel network length having an upstream surface connection with the main river channel. However, when surface connectivity is plotted against total channel length, two distinct phases are apparent (Figure 5). During the first expansion phase (A$\rightarrow$B) channel length more than doubled without a substantial increase in surface connectivity. During this period snow melt recharged hillslope and floodplain aquifers via subsurface pathways; increased surface flow was largely restricted to groundwater-fed tributaries and alluvial channels. Nor did surface

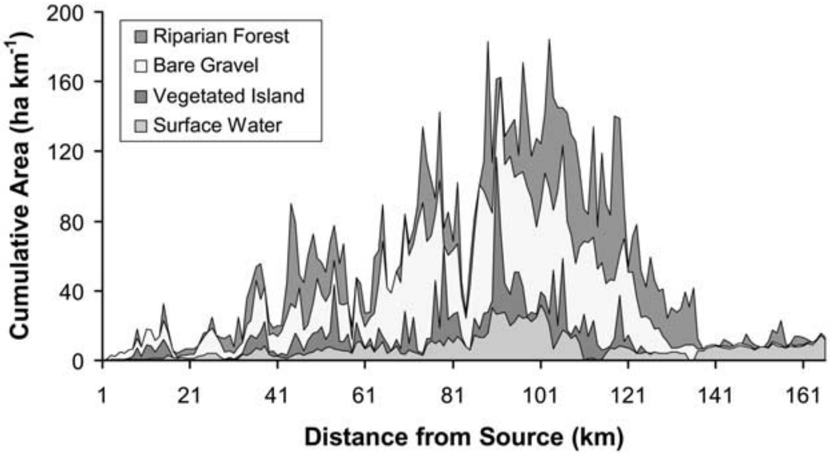

Figure 1. Areal representation of four major landscape elements along the riparian corridor of the Fiume Tagliamento, Italy (after Tockner et al. in press).

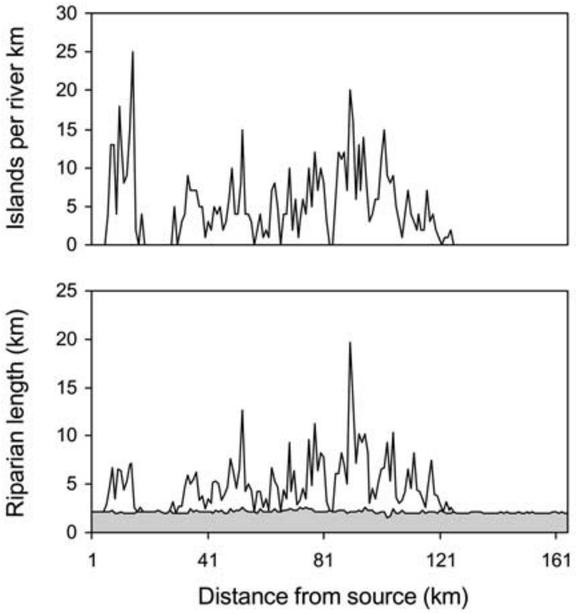

Figure 2. Number of vegetated islands along the course of the Fiume Tagliamento and the contribution of islands to riparian ecotone length. The lateral floodplain forest along the edge of the river corridor accounts for the shaded area on the bottom graph; everything above this is attributable to islands (modified after Ward et al. 2000).

connectivity decrease during the contraction phase B→A, which mainly reflected a progressive decline in the water table of the floodplain aquifer. Only when total channel length exceeded 15 km, there was a corresponding increase in surface connectivity (B→C). In contrast, riverscape diversity, calculated using the Shannon Index with 8 turbidity classes representing 'species' and the proportion of channel length in each class representing 'abundance', progressively increased across the entire range of channel length (Figure 6). Turbidity is an indicator of surface connectivity. Water samples were taken at monthly intervals from July 1996 to January 1998 along 17 study transects crossing the river corridor. The number of sampling points ranged from 27–130, depending on the number of channels carrying water. Turbidity values were separated into a geometric series of eight classes (Malard et al. 2000).

Hydrochemical tracers and groundwater dating showed how water sources (subglacial water, englacial water, snowpack, alluvial aquifer, hillslope aquifer) and flow paths (surface, shallow ground water, deep ground water) shifted throughout the year concomitant with the expansion/contraction cycle. A diverse array of aquatic habitats was sustained even during the maximum expansion phase in summer, when glacial melt is the major water source. Different water sources and flow pathways, in concert with the dramatic expansion/contraction cycle, create the shifting mosaic of channel types and the remarkable diversity of habitat conditions. Preliminary results from zoobenthic studies suggest that a highly diverse aquatic fauna inhabits the glacial flood plain. For example, 21 species of water mites (Hydracarina) have been identified from the springbrook habitat (Klein and Tockner 2000), comparable to species richness values reported from lowland springbrooks. We believe that the patchiness engendered by a wide range of connectivity levels is responsible for the unexpectedly diverse fauna. High patch diversity apparently enables a greater proportion of the regional species pool to colonize and maintain viable

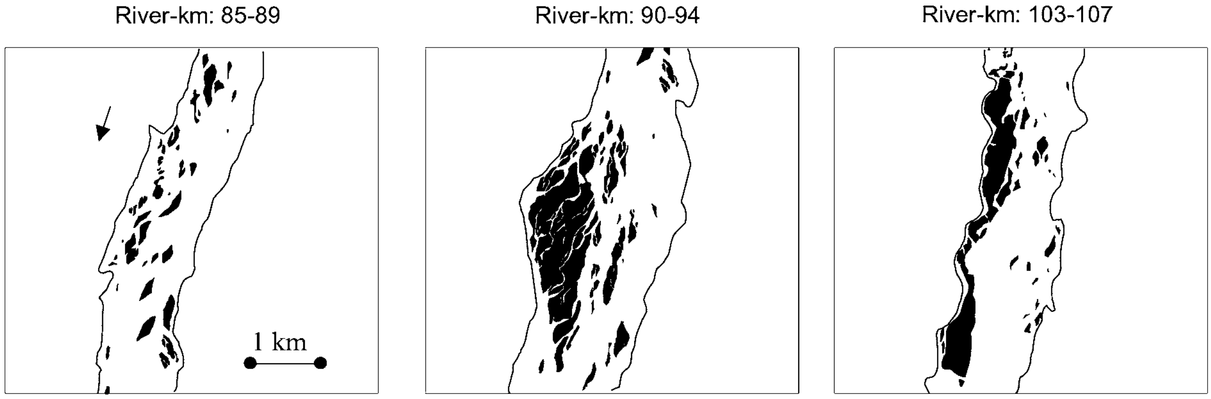

Figure 3. Distribution of islands in three river sections within the active corridor of the Fiume Tagliamento.

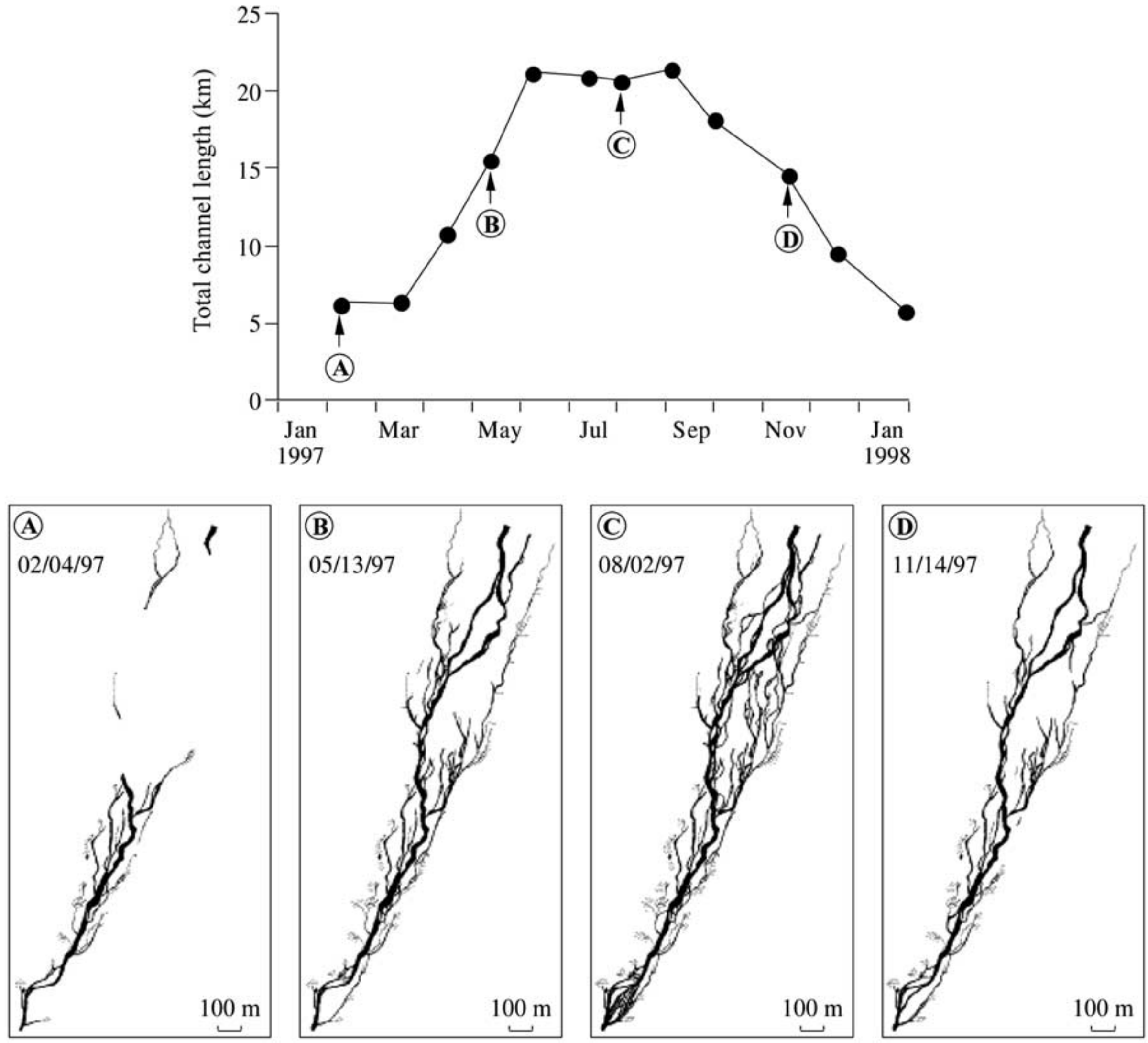

Figure 4. Seasonal changes in total channel length and spatial configuration of the channel network in the Val Roseg flood plain, Switzerland.

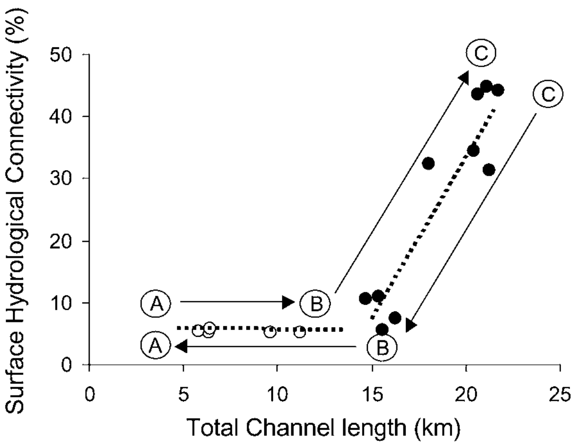

Figure 5. Relation between surface hydrological connectivity (SC) and channel expansion in the Val Roseg flood plain. SC = length of channels having an upstream connection with the main channel/total channel length. Letters (A–D) refer to the four phases in Figure 4.

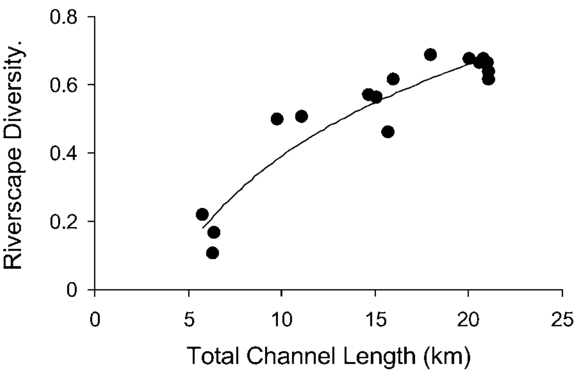

Figure 6. Riverscape diversity as a function of channel length in the Val Roseg flood plain (r^2 = 0.90; see text).

populations within the glacial flood plain. Elucidating the dynamics of these complex connectivity patterns is essential for investigating the adaptive strategies of the aquatic fauna in this harsh environment (Ward et al. 1999a).

Island dynamics.
Field studies on the Fiume Tagliamento, coupled with analyses of digitized maps and aerial photographs, show that islands are simultaneously forming, building, and eroding by complex processes that differ somewhat between river reaches and that operate over different time scales (Gurnell et al. 2001). Vegetated islands are 'high energy landforms' (Osterkamp 1998), since they form through erosional and depositional processes, generally during flood and/or episodes of accelerated sediment flux. 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 (Ward et al. 2000), a combination of conditions not present in highly managed river systems. Flow regulation by dams, for example, truncates the downstream transport of sediment and large woody debris and reduces the frequency and severity of flood events (Stanford et al. 1996). However, regulation of braided rivers may result in woodland expansion and a loss of channel area, as the wide multiple channel system largely devoid of woody vegetation is transformed into a single thread channel with a dense alluvial forest corridor (Schumm 1985; Johnson 1994). Preliminary results from research on the Tagliamento suggest that island dynamics contribute to biodiversity by increasing aquatic habitat heterogeneity (Arscott et al. 2000) and by providing habitats for both diverse aquatic and terrestrial communities (e.g., carabid beetles; Tockner, unpublished data).

The individual landscape elements (e.g., islands, gravel bars, water bodies) exhibit high turnover in the Tagliamento (ca. 30% in 3–5 years), yet the relative composition of landscape elements remains relatively constant (Edwards et al. 1999; Kollmann et al. 1999; Tockner et al. in press). This contrasts with highly managed European rivers such as the Rhone or Danube, in which relatively high landscape diversity in certain floodplain segments occurs without rejuvenation (Tockner et al. 2000). Nonetheless, because such river segments still retain high structural diversity, they are prime locations for restoration measures based on reconstituting fluvial dynamics (see below).

Functional processes

Most applications of landscape ecology to river systems have dealt with spatial patterns; very few studies have examined dynamic interactions; and there has been almost no work on functional processes in river corridors from a landscape perspective. We predict that this will change as river ecologists recognize the insight to be gained by employing a landscape approach in process-oriented studies.

Our example of this approach comes from recent research conducted on the Austrian Danube within the Alluvial Zone National Park (Tockner et al. 1998, 1999). A high species diversity has been recorded in the river corridor and many endangered species are present. However, this river segment downstream from Vienna has embankments that stabilize the main chan-

Table 1. Functional processes in the 'Regelsbrunn Flood Plain', Alluvial Zone National Park, Austria, during a 15-month sampling period in 1995/96 prior to restoration measures (modified from Tockner et al. 1999).

Process/Property	Disconnected Phase	Seepage Phase	Connected Phase
Phase duration (%)	67.5	29.3	3.2
Retention time (d)	>13	2-13	<2
Water surface area(ha)	85	120	520
Nutrient dynamics	closed system cycling	open system cycling	open system spiraling
Nutrient uptake	autogenic	autogenic	allogenic
Primary productivity	Medium	High	Low
P/R	Balanced	Autotrophic	Heterotrophic
Sink or source	Sink (autochthonous)	Source (DOC,Chl a)	Sink (particulates)
DOC:POC ratio	1.27	0.22	0.07
Ecological state	Biotic Interactions	Primary Productivity	Transport

nel and reduces surface connectivity with the extensive floodplain system (Table 1). Three phases of hydrological connectivity between the Danube channel and its flood plain may be distinguished: (1) a disconnection phase, (2) a seepage connection phase and (3) a surface connection phase. During the disconnection phase distinctive water bodies characterize the riverine landscape with internal (autogenic) processes dominating. This is also designated the 'biotic interaction phase', during which internal processes dominate (e.g., nutrient uptake, grazing). During the seepage connection phase the river and flood plain are connected via subsurface pathways. Large amounts of nutrient-rich ground water enter the flood plain, yet retention is relatively high. This is the 'primary production phase', during which periodic nutrient pulses (via seepage flow) stimulate algal production. When the river and its flood plain are interconnected by surface water, hydrological exchange processes dominate; because the majority of particulate matter is transported during this high-water period, this is referred to as the 'transport phase'. Therefore, there are spatial and temporal shifts in functional processes across the riverine landscape. For example, during surface connection (transport phase), when the water level in the channel exceeds bankfull level, dissolved nutrients are at intermediate levels, with more or less similar concentrations at all location across the inundated river landscape (Figure 7A). Suspended solid concentrations, however, exhibit a wide range, reflecting the heterogeneous pattern of current velocities. These processes are rapidly altered as the water level recedes and surface connections are severed. Only one week after a major flood (beginning of primary production phase) suspended solid concentrations approach uniformity, whereas nitrate concentrations exhibit a heterogeneous pattern, apparently reflecting the balance between river input and biological uptake (Figure 7B). After extended periods of low water conditions both nutrient and suspended sediment concentrations are very low (Figure 7C; see also Table 1).

Reconstituting functional processes.

To be viable, river restoration strategies must be based on reconstituting functional processes to the extent that a semblance of natural dynamic interactions is possible. River rehabilitation strategies should not, for example, involve the construction of islands, but should create conditions whereby rivers have the capacity to construct their own islands. The concept is to 'let the river do the work' (Stanford et al. 1996). This is the approach employed in the restoration scheme for the Alluvial Zone National Park (Schiemer et al. 1999). During an average year prior to restoration, surface connectivity between the Danube main channel and the flood plain occurred <8 days per year (ca. 12 days during the 15-month study period used in Table 1). Beginning in autumn 1996 hydrological connectivity was restored in two stages, first by lowering short sections of the embankments and then by creating artificial openings to increase the period of surface connectivity to more than half of an average year. Pre-restoration sampling was initiated in 1990 and intensified in 1995. It is intended that post-restoration sampling will continue in a consistent manner for up to ten years, including abiotic parameters, biota and limnological processes within floodplain water bodies.

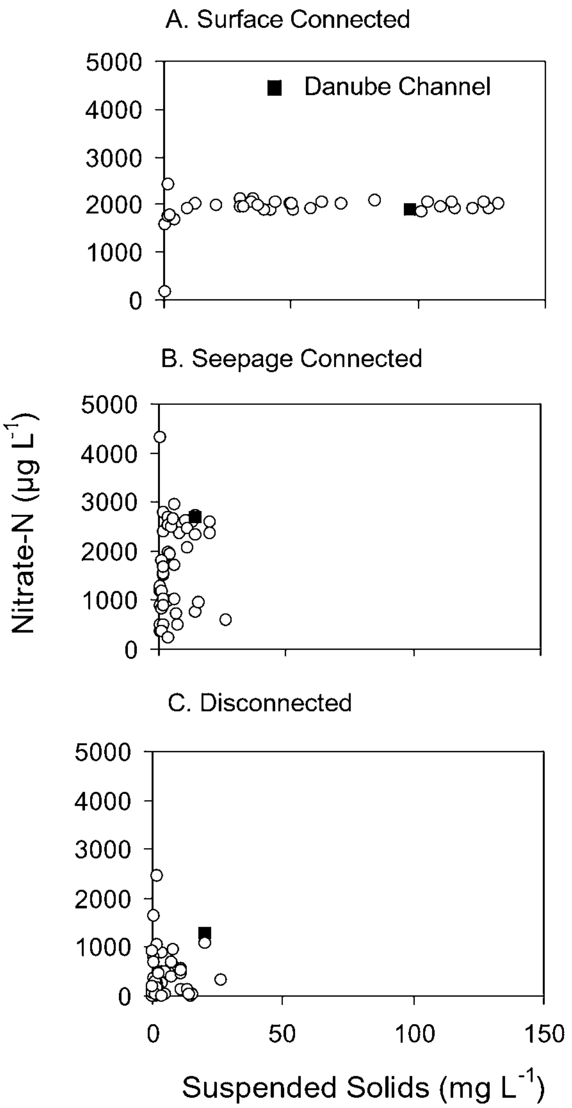

Figure 7. Temporal changes in the relationship between nitrate concentrations and suspended solids during connected (44 sites) and disconnected (48 sites) phases across the Alluvial Zone National Park, Austrian Danube (K. Tockner & C. Baumgartner, unpubl. data).

This is important; not only to document recovery trajectories, but also to gain insight into the role played by hydrodynamic processes in the river corridor.

A hierarchical biodiversity model for river corridors

Diverse biotic communities arrayed along multidimensional environmental gradients characterize river corridors. Biodiversity, a scalar phenomenon inextricably linked with succession, ecotones and connectivity, may provide a sound basis for examining patterns and processes across the riverine landscape and for assessing the effectiveness of river rehabilitation measures. Ward et al. (1999c) proposed a hierarchical framework to investigate biodiversity in floodplain rivers (Figure 8) and provided examples of species richness values (fishes, amphibians, gastropods) across hierarchical levels for connected and disconnected landscape units. Gamma diversity is the total number of species occupying a given region; alpha diversity refers to the number of species in a defined unit within that region; and beta diversity (a measure of species overlap) is the turnover of species between different units. The hierarchical structure of Figure 8 emphasizes that what constitutes a region (gamma diversity) depends on the spatial scale of the investigation, which is a function of the questions being addressed. In the model the alpha diversity of one hierarchical level becomes the gamma diversity for the next level and beta diversity (species turnover) is also hierarchically arrayed. Using this hierarchical framework enabled us to discern differential responses of taxa to habitat fragmentation, with important implications for conservation strategies.

Landscape ecology and river conservation

Rivers in much of the world have been highly modified for centuries, with few remnants of their original complexity and dynamics. Therefore, the limited success of many river conservation efforts may be attributable to a lack of appreciation of the critical roles of disturbance, successional processes and interactive pathways between landscape elements in sustaining the ecological integrity of natural river ecosystems. Ideally, river conservation should protect/rehabilitate entire river corridors, including flood plains and contiguous groundwater aquifers. Realistically, it is neither possible nor necessarily desirable to restore highly managed rivers to their pristine state (Stanford et al. 1996). However, reconstituting part of the river's natural fluvial dynamics is possible, which may prove to be the most effective way to form and sustain a diversity of interactive aquatic/riparian landscape elements within the river corridor. In other words, create a situation where the river itself structures the fluvial landscape and maintains interactions between land-

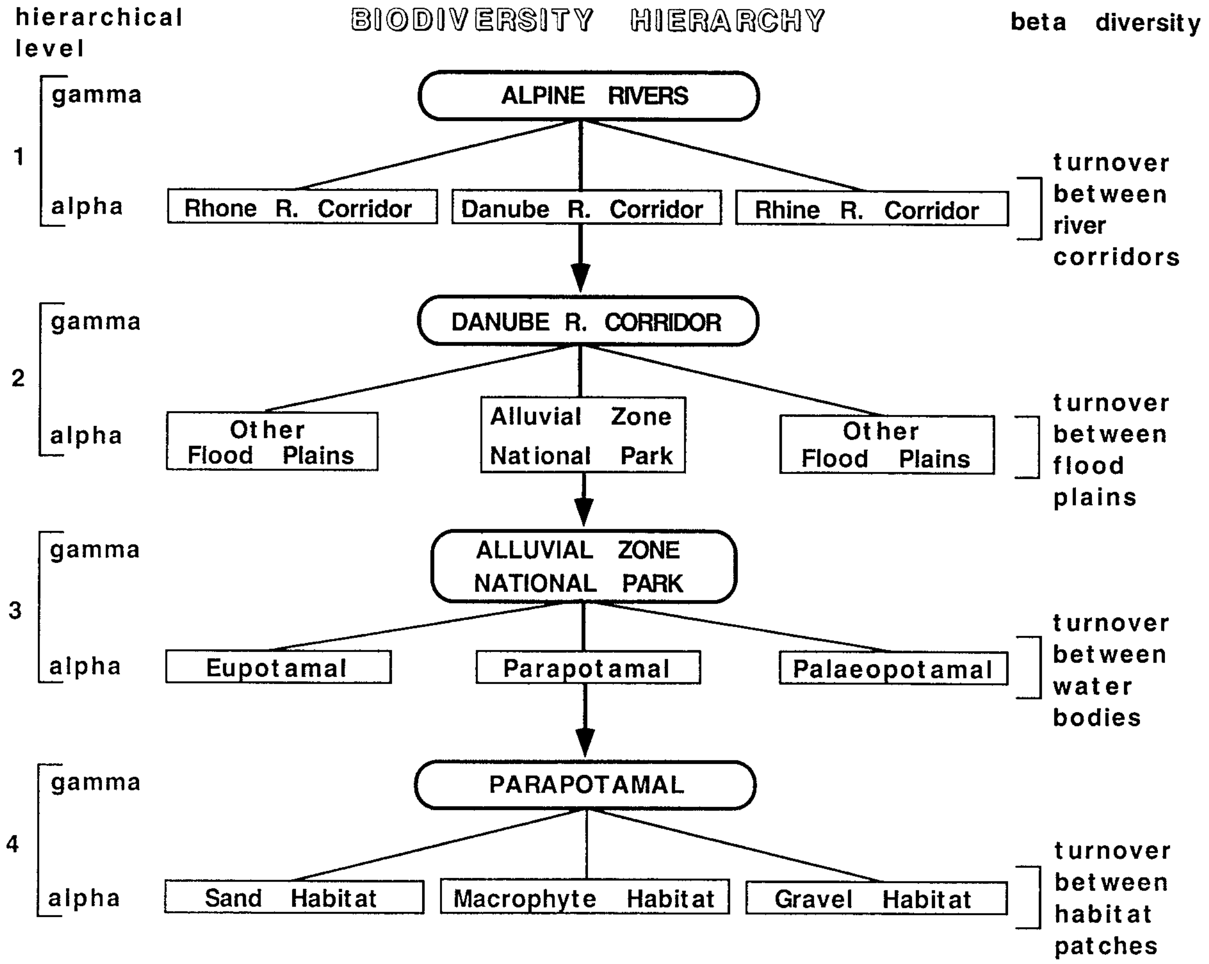

Figure 8. A hierarchical framework for investigating biodiversity in river corridors (modified from Ward et al. 1999c). This framework illustrates the hierarchical nature of biodiversity, showing how biodiversity in river corridors may be examined at different scales (e.g., from a physiographic region such as the Alps to the habitat patch scale). See Ward et al. (1999c) for species richness values of fishes, gastropods, and amphibians at each of these scales.

scape elements, rather than focusing restoration efforts on protecting individual species.

But how does one accurately assess the success of river conservation measures? What is needed is a means to quantify ecological integrity in river corridors, enabling comparisons of different landscape configurations and different conservation strategies. In a general review of the methods used to quantify spatial patterns in landscapes, Gustafson (1998) concludes that *'spatial heterogeneity indices represent a link between pattern and process'*; he also states that methods to relate spatial heterogeneity to ecological function have not been adequately developed. We propose that two phenomena hold promise for integrating the relevant ecological processes at the landscape scale: (1) beta diversity and (2) the diversity of successional stages (for both hydrarch and riparian systems). Several indices of beta diversity are already available, but have not been used to assess ecological integrity in river corridors. Indices of successional diversity suitable for this purpose have not yet been developed, to our knowledge.

Conclusions

River ecologists are just beginning to fully comprehend the great extent by which rivers in much of the world deviate from the natural state. It is crucial to preserve as far as possible those rivers and river segments that retain some of their natural functional attributes. In conclusion, we wish to stress the following points: (1) flood plains and alluvial aquifers are integral functional components of river corridors, (2) river corridors are non-equilibrium systems the functional processes of which depend on natural disturbance regimes, (3) natural river corridors are characterized by multidimensional environmental gradients, (4) connectivity between landscape elements is crucial for sustaining functional processes, (5) hydrarch and riparian successional processes increase habitat heterogeneity, thereby contributing to the high levels of species diversity in intact river corridors, (6) effective conservation and restoration efforts require a strong conceptual foundation and a thorough understanding of natural processes, (7) ecosystem management of damaged river corridors involves reconstituting disturbance regimes and reconnecting landscape elements, and (8) once functional processes are re-established, the river itself becomes the agent of restoration (let the river do the work).

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References

Amoros C. and Petts G.E. (eds) 1993. Hydrosystemes Fluviaux. Masson, Paris, France.

Arscott D.B., Tockner K. and Ward J.V. 2000. Aquatic habitat structure and diversity along the corridor of an Alpine floodplain river (The Fiume Tagliamento). Archiv für Hydrobiologie 149: 679–704.

Decamps H. 1984. Towards a landscape ecology of river valleys. In: J.H. Cooley and F.B. Golley (eds), Trends in Ecological Research for the 1980s, Plenum, New York, NY, USA, pp. 163–178.

Edwards P.J., Kollmann J., Gurnell A.M., Petts G.E., Tockner K. and Ward J.V. 1999. A conceptual model of vegetation dynamics on gravel bars of a large Alpine river. Wetlands Ecol. Manag. 7: 141–153.

Forman R.T.T. and Godron M. 1981. Patches and structural components for a landscape ecology. BioSci. 31: 733–740.

Gustafson E.J. 1998. Quantifying landscape spatial patterns: What is the state of the art? Ecosyst. 1: 143–156.

Gurnell A.M., Petts G.E., Hannah D.M., Smith B.P.G., Edwards P.J., Kollmann J., Ward J.V. and Tockner K. 2001. Riparian vegetation and island formation along the gravel-bed Fiume Tagliamento, Italy. Earth Surface Processes and Landforms 26: 31–62.

Johnson W.C. 1994. Woodland expansion in the Platte River, Nebraska, Patterns and causes. Ecol. Monogr. 64: 45–84.

Klein B. and Tockner K. 2000. Biodiversity in springbrooks of a glacial flood plain (Val Roseg, Switzerland). Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 27: 704–711.

Kollmann J., Vieli M., Edwards P.J., Tockner K. and Ward J.V. 1999. Interactions between vegetation development and island formation in the Alpine river Tagliamento. Appl. Veget. Sci. 2: 25–36.

Malard F., Tockner K. and Ward J.V. 1999. Shifting dominance of subcatchment water sources and flow paths in a glacial floodplain, Val Roseg, Switzerland. Arct. Antarct. Alp. Res. 31: 135–150.

Malard F., Tockner K. and Ward J.V. 2000. Physico-chemical heterogeneity in a glacial riverscape. Landsc. Ecol. 15: 679–695.

Osterkamp W.R. 1998. Processes of fluvial island formation, with examples from Plum Creek, Colorado and Snake River, Idaho. Wetlands 18: 530–545.

Petts G.E., Moller H. and Roux A.L. (eds) 1989. Historical changes of Large Alluvial Rivers, Western Europe, Wiley, Chichester, UK.

Schiemer F., Baumgartner C. and Tockner K. 1999. Restoration of floodplain rivers: 'The Danube Restoration Project'. Regul. Riv. Res. Manag. 15: 231–244.

Schumm S.A. 1985. Patterns of alluvial rivers. Ann. Rev. Earth Planet. Sci. 13: 5–27.

Stanford J.A., Ward J.V., Liss W.J., Frissell C.A., Williams R.N., Lichatowich J.A. and Coutant C.C. 1996. A general protocol for restoration of regulated rivers. Regul. Riv. Res. Manag. 12: 391–413.

Tockner K., Malard F., Burgherr P., Robinson C.T., Uehlinger U., Zah R. and Ward J.V. 1997. Physico-chemical characterization of channel types in a glacial floodplain ecosystem (Val Roseg, Switzerland). Archiv für Hydrobiologie 140: 433–463.

Tockner K., Schiemer F. and Ward J.V. 1998. Conservation by restoration: The management concept for a river-floodplain system on the Danube River, Austria. Aquat. Conserv. 8: 71–86.

Tockner K., Pennetzdorfer D., Reiner N., Schiemer F. and Ward J.V. 1999. Hydrological connectivity and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). Freshwater Biol. 41: 521–535.

Tockner K., Ward J.V., Arscott D.B., Edwards P.J., Kollmann J., Gurnell A.M., Petts G.E. and Maiolini B. The Tagliamento River: A model ecosystem for Alpine gravel-bed rivers. In: H. Plachter and M. Reich (eds), Ecology and Conservation of Gravel Bed Rivers and Alluvial Floodplains in the Alps. Springer, Berlin, Germany (in press).

Tockner K., Malard F. and Ward J.V. 2000. An extension of the flood pulse concept. Hydrol. Proc. 14, 2861–2883.

Turner M.G. and Gardner R.H. 1991. Quantitative methods in landscape ecology: An introduction. In: M.G. Turner and R.H. Gardner (eds), Quantitative methods in landscape ecology, Springer Verlag, New York, NY, USA, pp. 3–14.

Ward J.V. 1997. An expansive perspective of riverine landscapes: Pattern and process across scales. GAIA 6: 52–60.

Ward J.V. 1998. Riverine landscapes: Biodiversity patterns, disturbance regimes, and aquatic conservation. Biol. Conserv. 83: 269–278.

Ward J.V., Malard F., Tockner K. and Uehlinger U. 1999a. Influence of ground water on surface water conditions in a glacial flood plain of the Swiss Alps. Hydrol. Process. 13: 277–293.

Ward J.V., Tockner K., Edwards P.J., Kollmann J., Bretschko G., Gurnell A.M., Petts G.E. and Rossaro B. 1999b. A reference river system for the Alps: The Fiume Tagliamento. Regul. Riv. Res. Manag. 15: 63–75.

Ward J.V., Tockner K. and Schiemer F. 1999c. Biodiversity of floodplain river ecosystems: Ecotones and connectivity. Regul. Riv. Res. Manag. 15: 125–139.

Ward J.V., Tockner K., Edwards P.J., Kollmann J., Bretschko G., Gurnell A.M., Petts G.E. and Rossaro B. 2000. Potential role of island dynamics in river ecosystems. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 27: 2582–2585.

Wiens J.A. 1995. Landscape mosaics and ecological theory. In: L. Hansson, L. Fahrig and G. Merriam (eds), Mosaic Landscapes and Ecological Processes, Chapman & Hall, London, UK, pp. 1–26.