

Riverine landscapes: taking landscape ecology into the water

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SUMMARY

1. Landscape ecology deals with the influence of spatial pattern on ecological processes. It considers the ecological consequences of where things are located in space, where they are relative to other things, and how these relationships and their consequences are contingent on the characteristics of the surrounding landscape mosaic at multiple scales in time and space. Traditionally, landscape ecologists have focused their attention on terrestrial ecosystems, and rivers and streams have been considered either as elements of landscape mosaics or as units that are linked to the terrestrial landscape by flows across boundaries or ecotones. Less often, the heterogeneity that exists within a river or stream has been viewed as a 'riverscape' in its own right.

2. Landscape ecology can be unified about six central themes: (1) patches differ in quality (2) patch boundaries affect flows, (3) patch context matters, (4) connectivity is critical, (5) organisms are important, and (6) the importance of scale. Although riverine systems differ from terrestrial systems by virtue of the strong physical force of hydrology and the inherent connectivity provided by water flow, all of these themes apply equally to aquatic and terrestrial ecosystems, and to the linkages between the two.

3. Landscape ecology therefore has important insights to offer to the study of riverine ecosystems, but these systems may also provide excellent opportunities for developing and testing landscape ecological theory. The principles and approaches of landscape ecology should be extended to include freshwater systems; it is time to take the 'land' out of landscape ecology.

Keywords: ecological flows, landscape ecology, river ecosystems, scale, spatial pattern

Introduction

Riverine landscapes. The phrase creates an instant contradiction of terms. How can a river be a *landscape*? Should not we be referring to 'riverscapes' or 'streamscapes' or 'aquascapes'; something that more explicitly recognises that we are dealing with an aquatic system? After all, 'landscape' traditionally refers to an area of land, 'an expanse of natural

scenery that can be seen from a single viewpoint' (Random House, 1999). Landscape ecologists have been even more explicit. For example, Hobbs (1995) defined landscapes as 'heterogeneous areas of land, usually hectares or square kilometers in area, composed of interacting ecosystems or patches'. Dispensing with pretexts altogether, Zonneveld (1995) equated landscape ecology with 'land ecology'. Although his land ecology included aquatic systems, the terrestrial emphasis was clear.

My thesis in this paper, and the theme underlying the following papers from the Riverine Landscapes symposium, is that, although landscape ecology has traditionally focused on land, it has much to offer, and perhaps even more to learn from, studies of aquatic

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systems, especially rivers and streams². Riverine systems are governed by water flows, and because of its density and viscosity, water is a much more effective agent in linking landscape elements, both in space and in scale, than is the air in which terrestrial landscapes are immersed. Consequently, rivers and streams should be ideal settings in which to do landscape ecology.

My purpose here is to establish the elements of a linkage between land ecology and aquatic ecology in the spatial context that is the essence of landscape ecology. I will begin by describing briefly what landscape ecology is about, what various workers take to be its primary focus. I will then consider the ways in which landscape ecologists have included rivers and streams in their studies. Finally, I will develop the major themes of landscape ecology and show how they can be combined in a framework that may apply equally well to terrestrial and to aquatic systems. It will be evident to anyone familiar with freshwater ecology that there is really not much new here, that stream and river ecologists have been doing landscape ecology for some years without recognising it as such. My overall conclusion, however, will be that the traditional distinction in ecology between whether something is happening on land or in water is of minor import in the context of landscape ecology – it is the spatial patterns, relationships and processes that are important, not the substrate or the medium.

What is landscape ecology?

Broadly considered, landscape ecology lies at the intersection of the well-established disciplines of geography, ecology and social anthropology. It incorporates as well elements of the hybrids of these disciplines: spatial ecology (ecology + geography), human geography (geography + social anthropology) and cultural ecology (social anthropology + ecology).

This scope is impossibly large, and different approaches to landscape ecology emphasise different elements of the mix. Landscape ecology began in Europe, with roots in physical geography, aerial photointerpretation (i.e. pattern analysis), and land-use policy

and management. From the beginning, two elements were of central importance: the role of humans as part of the landscape rather than external forces, and the focus on landscapes at a scale relevant to human perception and actions (i.e. Hobbs' 'hectares or square kilometres'). This emphasis is understandable, given the long history of human modification and design of landscapes over most of Europe. As it has developed, this European perspective on landscape ecology has increasingly embraced systems thinking and holistic philosophies in an attempt to integrate humans and landscapes into a 'total human ecosystem' (Naveh, 1994).

As landscape ecology expanded from its European birthplace, it colonised new areas, with different landscapes and different cultures, and it drifted or mutated from this initial perspective. In North America, in particular, the linkages with traditional ecology were especially strong. Here the emergent focus has been on spatial patterns and their effect on ecological processes, often in largely 'natural' landscapes (Turner, 1989). Humans have often been neglected or considered only as a disturbance agent. Landscapes have been considered at multiple scales, from square meters or less to hundreds of square kilometres. Much of the emphasis has been explicitly mechanistic, dissecting *how* landscape patterns influence ecological processes, often through computer modelling or experiments.

As landscape ecology has grown, other approaches have emerged. For example, Forman (1995) has advocated a perspective that combines elements of the European and North American views. It links the ecological emphasis on pattern-process relationships with the broad, kilometres-wide scale of human activities and perception of landscapes, and although it does not explicitly embrace holism, it emphasises the importance of humans in landscapes and the relevance of landscape ecology to human land use and resource management.

Which of these approaches is most relevant to rivers and streams? In a sense, the answer is 'all of the above.' Water is an increasingly valuable resource to humans in most parts of the world, and rivers and streams have been the focus of human culture and activities since the dawn of civilisation (Diamond, 1997). Many rivers and streams have been altered by human actions, some dramatically so. At the same time, geomorphological dynamics and hydrological

²I will not attempt to distinguish between rivers and streams, and use the terms more or less interchangeably throughout this paper.

flows in river systems have an overwhelming effect on the spatial and temporal patterns of these systems at multiple scales, and the effects of these physical forces on the spatial dimensions of river ecology are immediate and profound. Stream chemistry and the inputs and distribution of detritus and woody debris are affected by the composition and structure of the surrounding terrestrial landscape. The effects of spatial pattern on ecological processes are everywhere.

My own view of landscape ecology is derived from the ecological perspective. To me, the essence of landscapes is their spatial structure, the form of the mosaics and gradients in space. Because mosaics and gradients are expressed at multiple scales that affect different kinds of organisms or different ecological processes in different ways at different scales, landscape ecology is very much a science of scaling. The central notion of landscape ecology, then, is that where things are located, and where they are relative to other things, can be extremely important to those things and what happens to them. This much is geography (or perhaps spatial ecology). Landscape ecology carries the argument a step further, to emphasise the ways in which the consequences of location and locational relationships are contingent on the characteristics of the landscape in which those locations are embedded. This view leads to a focus on

several central themes of landscape ecology, which I will discuss shortly in the context of riverine ecosystems. First, however, it is important to note the ways in which landscape ecologists have considered aquatic systems in their work.

How have landscape ecologists considered riverine systems?

Despite their traditional focus on 'land', landscape ecologists have not entirely ignored aquatic systems. Generally, they have considered rivers and streams in one (or more) of three ways.

1. Rivers as elements of a landscape mosaic

Most often, landscape ecologists have dealt with rivers as simply one element of a landscape mosaic, equivalent to fields, forests, roadways, or urban centres. This is the view that is fostered by remote sensing, geographical information systems (GIS), or landscape mapping. Although rivers may be mapped with greater or lesser detail, what is generally shown is only the boundary that separates a river from the other elements of the landscape (e.g. Figure 1a).

The elements that are shown in any image or map reflect the level of resolution and the categorisation

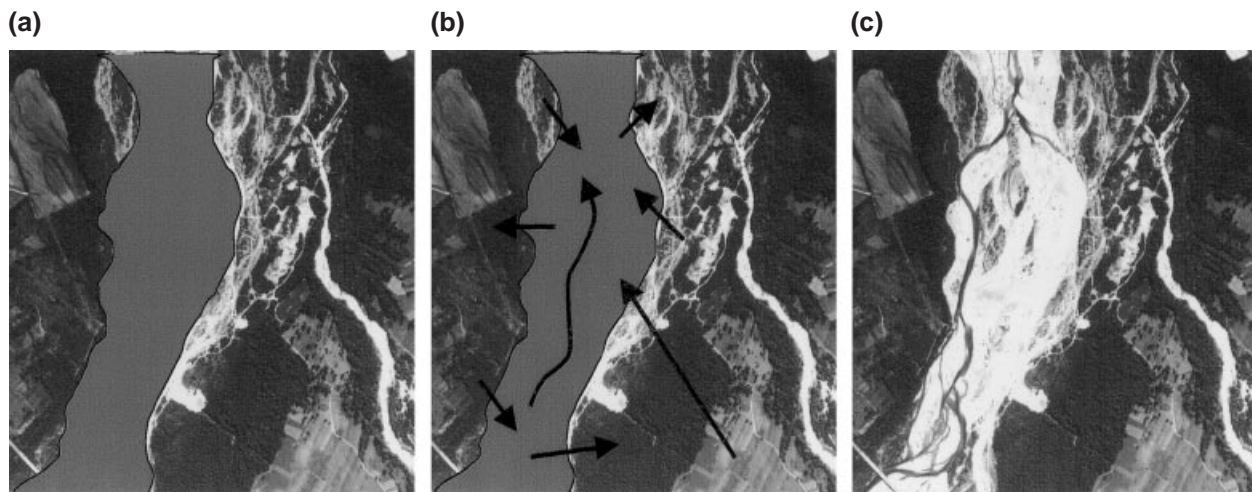


Fig. 1 Three perceptions of rivers as landscapes. (a) The river is an internally homogeneous element contained within a broader terrestrial landscape. (b) The river is connected with the surrounding landscape by a series of flows across the land–water boundary, or longitudinally down the river corridor. (c) The river is a part of a landscape that is internally heterogeneous, and there is therefore a 'landscape' within the river system as well. The images are of the Fiume Tagliamento in Italy, river kilometer 43. The width of the active river corridor is c. 250 m, altitude 300 m, stream order 6. Photo from 17 November 1986, Istituto Geografico Militare, Firenze, courtesy of Klement Tockner.

rules that are followed. Thus, vegetation may be mapped as broad categories (e.g. forest vs. fields), as finer categories (e.g. coniferous versus deciduous forest), or as yet finer categories (e.g. *Tsuga* forest versus *Pseudotsuga* forest versus *Pinus* forest), and so on (see Alexander & Millington, 2000; or, for cautionary examples, Monmonier, 1996). So it is also with rivers. The level of resolution of an image or map determines whether or not rivers or streams of particular sizes even appear as landscape elements, and stream order provides a widely accepted framework for categorising different streams as different landscape elements. Because their focus is generally on the land, however, landscape ecologists do not normally make such distinctions.

The humanistic focus of European landscape ecology emphasises another way to categorise rivers as landscape elements, in terms of their importance to human activities and culture. Rivers are used as transportation corridors, as water sources for settlements or farmlands, as fisheries, as waste disposal conduits, and so on, and rivers in a landscape can be differentiated according to these differing uses. But again, the view of a river is as a channel separated from the other elements of the landscape by its edges. The river has neither dynamics nor internal structure of its own.

2. Rivers linked with their surroundings by boundary dynamics

Another view of rivers considers them as functional parts of landscapes that are connected by boundary flows, by exchanges of materials, organisms, energy, or information across boundaries between adjacent landscape elements (Hansen & di Castri, 1992). Although terrestrial ecologists may think of such flows in rivers simplistically, in terms of downstream hydrology alone, any riverine ecologist knows that a wide array of exchanges occur across river boundaries (e.g. Figure 1b). Moreover, many of these flow pathways occur across boundaries that are not evident from the vertical view provided by remote sensing. Exchanges through the hyporheic zone, for example, are related to properties of the substratum such as sediment type or bedrock geology that rarely appear in landscape images. As a consequence, the static 'mapable element' view of landscapes shown in Fig. 1a not only fails to consider the dynamic and

differential exchanges that occur across the riverine boundary, but neglects some important boundaries of the river system entirely.

3. Rivers as internally heterogeneous landscapes

Of course, rivers are not homogeneous entities. Rivers have an internal structure of their own, whether it is the pattern of pools and riffles of a small tributary stream, the channels and vegetated islands of a braided river in a floodplain (e.g. Fig. 1c), or the main stem, backwaters, and oxbows of a large river. The spatial pattern of this heterogeneity *within* rivers constitutes a landscape in its own right. All of the structural and functional features that can be used to characterise a river as a part of a broader terrestrial landscape also apply to the landscape within a river. In many cases, this within-river landscape is also quite dynamic, varying in patch composition and configuration in response to changes in hydrologic flow regimes (Malard *et al.* 2002).

These three ways of viewing riverine landscapes reflect gradients of increasing sensitivity to detail, in two dimensions. The first represents a progression from thinking about rivers as parts of broader terrestrial landscapes to considering the details of landscape structure of the rivers themselves. The second is a change from depicting landscapes as relatively static spatial patterns to considering the dynamics of those patterns – time becomes important. In a sense, the scale of resolution in both space and time (the 'grain' with which the system is viewed) becomes progressively finer, and as a consequence more and more detail is revealed. These gradients also represent a shift from thinking terrestrially to thinking aquatically, from 'black-boxing' rivers to considering their internal structure and dynamics. It is my thesis that the former approach is relatively sterile and is unlikely to produce interesting insights. It is in the latter arena, that of rivers *as* landscapes, that landscape ecology may have something to offer to riverine ecologists, and studies of riverine systems may contribute to the development of landscape ecology.

The central themes of landscape ecology as they relate to riverine ecosystems

The notion that landscape ecology is concerned with the influence of spatial pattern on ecological processes

contains several more specific themes. These themes can provide a unifying way of thinking about riverine landscapes in ways that parallel our thinking about terrestrial landscapes, and in the process contribute to the broadening of landscape ecology to consider the structural and functional texture of aquatic systems. Here I will briefly discuss these six themes, illustrating each with a few examples from stream and river systems. In no way do these examples represent a review of the relevant literature; instead, they reflect the non-random browsings of a terrestrial ecologist. The following papers provide many more examples.

1. Patches differ in quality

Although there is an increasing recognition of the importance of gradients and fuzzy or indeterminate boundaries in geography and landscape ecology (Burrough & Frank, 1996), most visualisations of landscapes are as patchwork-quilt arrays of elements ('patches') that comprise a mosaic. It is perhaps telling, in this regard, that Forman (1995) titled his book on landscape ecology 'Land Mosaics', thereby emphasising both the land and the discrete-patch aspects of conventional landscape ecology.

Indeed, many landscapes do exhibit a distinct patch structure, especially if they have been subjected to human modification (e.g. Fig. 1). The elements within a landscape can be categorised and described as different patch types, and often the differences among patch types can be quantified. To the organisms occupying a landscape, however, these differences may reflect differences in patch quality, in the costs or benefits of being in a particular patch type (Wiens, 1997). Recognising that patches differ in quality is the first step in transforming a descriptive map of a mosaic into something that can represent the spatial component of ecological processes.

Several studies in streams and rivers illustrate the effects of variations in patch quality. For example, Palmer *et al.* (2000a) documented that larval chironomids and adult copepods were more abundant in patches of leaves than in sand patches in a fine-scale streambed mosaic. They went beyond this direct observation of patch 'preference' to conduct field experiments, which revealed that these organisms colonised leaf patches composed of rapidly decomposing leaves more rapidly than leaf patches containing more refractory leaves. These differences were

tied to food resource availability: rapidly decomposing leaves contained higher abundances of bacteria and fungi than did the refractory leaves. In another study, Hughes (1998) modelled the distribution and growth rates of arctic grayling (*Thymallus arcticus*) in Alaskan streams. In this case, invertebrate drift density and water temperature (which differed in different parts of the stream) affected individual growth rates and body size, which in turn affected the position of fish in a spatially defined dominance hierarchy. As a consequence, there was a size-dependent distribution of individual fish among resource patches of differing quality (as measured by growth rates). The recognition that patches in a stream differ in quality and that organisms respond to these spatial variations is not new, of course: in the 1920s, Dodds & Hisaw (1924) and Ruttner (1926) noted the selection of patches of high velocity, where respiration is facilitated, by lotic invertebrates.

Patch quality changes over time, especially in such dynamic systems as streams and rivers. Lancaster (2000) documented the shifting nature of patch quality by experimentally determining how the distribution of stream invertebrates among patches varied under different flow regimes. Invertebrates accumulated in refugium patches during high flow disturbances, but there were no differences between the refugium and control patches at low flows. The magnitude of the effects under high flows varied among taxa, as well as among patches of different sizes. Collectively, these (and many other) studies show that not all patches are equal, nor do they remain the same over time.

2. Patch boundaries affect flows

Patches, by definition, have boundaries, and any interactions or exchanges among patches must therefore be mediated by the boundaries. Traditionally, boundaries have been thought of as ecotones, areas of rapid change in environmental features and, frequently, enhanced biodiversity (Malanson, 1993; Ward & Wiens, 2001). Boundaries are also zones in which flows or exchanges of materials, energy, or individuals among patches in a landscape are regulated. Boundaries differ in their permeability to these flows, and these differences can create spatial patterns in the abundance of organisms, concentrations of nutrients, or deposition of materials (Wiens, Crawford & Gosz, 1985; Hansen & di Castri, 1992). What

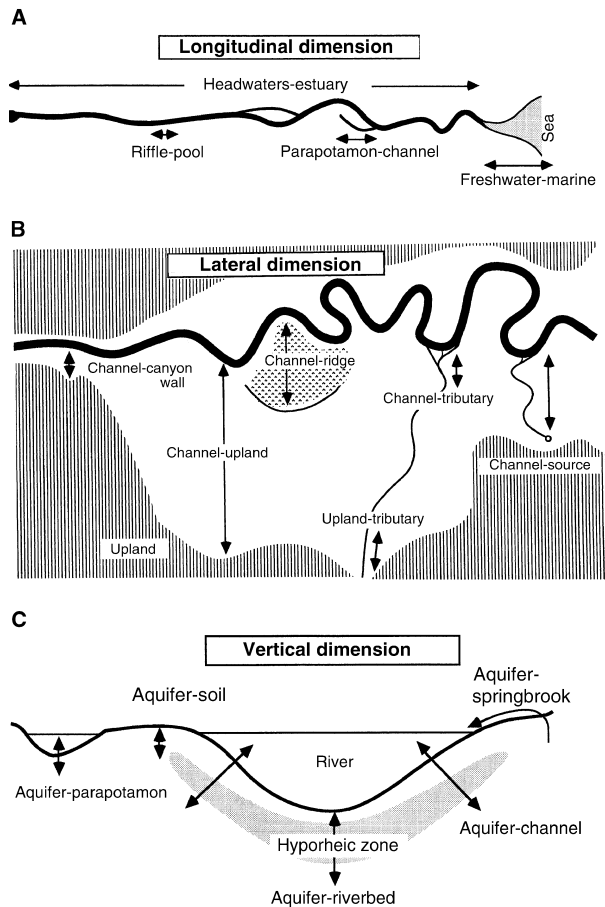


Fig. 2 Major ecotones and pathways of exchanges of materials, energy, and organisms in the longitudinal (A), lateral (B), and vertical (C) dimensions of a riverine system. From Ward & Wiens (2001).

happens, ecologically, in any patch in a landscape is a function of the patterns and magnitudes of across-boundary exchanges with its surroundings; no patch is an island.

Boundaries (or ecotones) have received considerable attention from river and stream ecologists. Riverine systems are characterised by a multiplicity of longitudinal, lateral and vertical boundaries, and therefore of potential exchange pathways (Fig. 2). Of all these boundaries, studies have focused especially on the riparian zone and its effects on land–water interchanges (e.g. Naiman *et al.*, 1988; Nilsson, 1992; Malanson, 1993; Naiman & Décamps, 1997; Naiman, Bilby & Bisson, 2000). The width and composition of riparian vegetation bordering a river, for example, can influence such things as the amount of shading that the stream receives, the transfer rates of nutrients,

pollutants, litter, or coarse woody debris to the river, the occurrence and rate of predation by terrestrial predators on aquatic organisms, or the movement of aquatic insects into the riparian zone (e.g. Nakano, Miyasaka & Kuhana, 1999; Nakano & Murakami, 2001). Less obvious, but perhaps no less important, are exchanges that occur across the boundaries beneath a river or stream, into and out of the sediments or the hyporheic zone (Stanford & Ward, 1988; Ward, 1989, 1997; Palmer *et al.*, 2000b; Ward & Wiens, 2001; Fig. 2C).

Of course, these boundary dynamics, like all else in riverine ecosystems, are strongly affected by hydrology. Floods or droughts raise or lower water levels and alter boundary locations and configurations, and thus the direction and magnitude of exchanges across the boundaries (e.g. Bendix & Hupp, 2000). Schlosser (1995), for example, documented how variations in flow discharge could affect the permeability of boundaries created by beaver (*Castor canadensis*) dams and ponds to both upstream and downstream movement of lotic fish, and therefore of fish predation effects on invertebrate colonisation of riffle or pool patches in the stream. Both the variety of boundaries and their strong and shifting dynamics in riverine landscapes contrast with the relatively stable and two-dimensional view of boundary exchanges that has developed among terrestrial landscape ecologists (e.g. Wiens *et al.*, 1985; Forman, 1995).

3. Patch context matters

Although a boundary or ecotone may have properties of its own, the nature of a boundary is largely determined by what is on either side of the boundary. The various boundaries shown in Figs 1 and 2 differ not only in their locations, but in their context. What enters a stream or river system across the land–water boundary, for example, may depend on the vegetational characteristics of the terrestrial landscape. What lies across the boundary will have a powerful effect on what happens within the riverine ecosystem. Linkages between properties of a catchment and stream functioning and integrity have been recognised for some time (e.g. Cummins, 1974; Likens & Bormann, 1974; Hynes, 1975). More recently, Cresser *et al.* (2001) conducted a model analysis of cation fluxes into a Scottish river that demonstrated that water chemistry was influenced not only by the soils and bedrock

geology of the adjacent area, but by the vegetational cover of the riparian zone and the forms of human land-use in the surrounding landscape. Evapotranspiration from the riparian vegetation may also affect the overall water balance of a riverine system (Dahm *et al.* 2002), and alterations in the composition or extent of the riparian zone may thus have a profound effect on overall hydrology, at least in arid environments. In a desert stream, Fisher *et al.* (1998) demonstrated that nitrogen dynamics are dependent on the composition and temporal dynamics of the spatial mosaic of interacting patches, as a consequence of both internal patch properties (i.e. nutrient retention or release) and patch interactions (i.e. boundary fluxes). The linkages between the biota of streams and that of the underlying sediments are dependent not only on the inputs of nutrients, litter, and detritus (all of which relate to the upstream landscape composition), but to the shading effects of adjacent terrestrial vegetation as well (Palmer *et al.* 2000b). In some cases, there may be considerable time lags involved in these patch-context effects. In examining invertebrate and fish diversity in a series of streams in North Carolina, Harding *et al.* (1998) found that contemporary diversity was best predicted by the land-use history in the watershed during the 1950s, whereas riparian and whole-catchment land use in the 1990s were comparatively poor predictors. There was a legacy of past patch context, a 'ghost of land use past'.

4. Connectivity is critical

Movements of individuals, materials, nutrients, energy, or disturbances through a landscape involve more than boundary configuration, permeability, and context. If a landscape is indeed a mosaic of patches of different types, then these movements are affected by how the patches are arrayed in the mosaic. The probability that an organism or an ion in one location in a landscape will move to some other location is a function of the complex of patch types and boundaries that separate those locations. In a landscape, the shortest distance between two points may well be a straight line, but the actual movement pathways between those points may be much longer and more convoluted. Although landscape connectivity is often thought of in terms of corridors – roughly linear strips of habitat connecting otherwise isolated habitat

patches – connectivity is in fact a complex product of patch quality (e.g. resistance to movement or patch-residence time), boundary properties and patch context. It is also affected, obviously, by the distance between locations (e.g. distance–decay diffusion) and by the movement characteristics of the features of interest.

Rivers and streams are often seen as the epitome of connectivity, as so much of what goes on is tied to water flow and hydrology, and water (generally) flows downhill. The river continuum concept (Vannote *et al.*, 1980) emphasises the longitudinal linkage of ecosystem processes in streams and rivers through the downstream flows of water and materials, but it is a simplistic view of the actual patterns of connectedness and variations in flows and deposition that occur in a river. The serial discontinuity concept of Ward & Stanford (1983) recognises the importance of zonal structure along a water course (as, at a finer scale, does the riffle-pool distinction). Both the river continuum concept and the serial discontinuity concept, however, consider the river as a single channel flowing through a constrained reach bordered by a narrow strip of riparian vegetation that includes all of the important linkages with the surrounding terrestrial landscape (Ward, 1997; but see Ward & Stanford, 1995a). In fact, there is a rich texture of spatial heterogeneity both within streams and rivers and in the surrounding terrestrial landscape (Fig. 1c), and this patchiness alters the movements of water, organisms and everything else in a riverine system. The downstream dispersal of riparian plant propagules or of aquatic insects, for example, may be affected by the spatial arrangement of dead-water zones (backwaters, pools, eddys) in a reach (Johansson, Nilsson & Nilsson, 1996; Bond, Perry & Downes, 2000). In a system of serially linked lakes and streams in arctic Alaska, Kling *et al.* (2000) found that downstream movement of materials is affected not only by altitude and position in the catchment (i.e. stream order), but by the particular longitudinal configuration of the stream-pond sequence. Processing of materials within the lakes altered water chemistry, and thus the nature of inputs to a stream at a lake outlet. In-stream processing of materials generally resulted in opposite changes, altering the nature of inputs to a downstream lake. At a finer scale, the occurrence and development of debris islands in streambeds or floodplains (e.g. Gurnell, Gregory & Petts, 1995;

Edwards *et al.*, 1999; Kollmann *et al.*, 1999; Naiman *et al.*, 2000; Ward *et al.*, 2000) creates new patches and boundaries and alters water-flow pathways and the movement and retention of materials in the river system.

Connectivity in riverine system occurs laterally as well as longitudinally, of course (Fig. 2B). The most obvious and most dynamic linkages are those between the main channel of a river or stream and the floodplain (Amoros & Roux, 1988). Here, connectivity is a seasonal phenomenon, subject to the occurrence and magnitude of flooding. In the tropical and subtropical savannahs of northern Australia or the llanos of Venezuela, for example, the wet season may bring metres of rainfall and vast areas may be submerged. With the onset of the long dry season, the flooding abates and much of the floodplain becomes part of the terrestrial landscape, leaving only isolated remnant ponds (oxbows and billabongs) that have little connectedness with the riverine system (Junk Bayley & Sparks, 1989). River regulation, in the form of dams or levees, restricts both the lateral connectivity between the river and the floodplain and the temporal and spatial variance in connectivity in the main stem of the river (Ward & Stanford, 1995b; Kingsford, 2000). Although the changes in the floodplain that accompany flow regulation are traditionally thought of in terms of disturbance and vegetational succession, a landscape perspective draws attention to the importance of altering the seasonally pulsed connectivity between the aquatic and terrestrial ecosystems.

5. Organisms are important

Clearly, variations in stream flow, invertebrate drift, boundary exchanges, patch context, or riverine connectivity affect different organisms differently. Any natural historian or fisherman knows this. Moreover, because different organisms have different movement capacities and different expressions of patch or habitat selection, their responses to the heterogeneous structure of a landscape mosaic will differ. The overall patterns of biodiversity that occur within riverine systems reflect these organismal responses to landscape structure. Biodiversity may be greater at ecotones or boundaries between patches in the riverine landscape (Amoros, Gibert & Greenwood, 1993; Ward & Wiens, 2001; Ward & Tockner, 2001), perhaps

as a consequence of the attraction of some organisms to the boundary and the accumulation of others at the interface between hospitable and inhospitable patches. Because different taxa may respond differently to landscape properties, the spatial patterns of diversity may also vary among groups. For example, Tockner, Schiemer & Ward (1998) documented a peak in fish diversity in portions of the Danube floodplain that had high connectivity to the main river channel, whereas amphibian diversity peaked where connectivity was low, in isolated floodplain ponds.

These broad diversity patterns are ultimately founded on the ways in which particular organisms or species relate to landscape structure. Palmer *et al.* (2000a) found that larval chironomids and adult copepods responded differently to the spatial arrangement of patches of leaves and sand in a streambed landscape. Likewise, Lancaster (2000) documented differences among stream-invertebrate taxa in their response to refugium patches during high streamflow disturbances. Drift of stream invertebrates varies among taxa in relation to their life-history traits and settling responses and varies among portions of a stream in relation to stream connectivity, hydrological flows and boundary configurations. As a consequence, the distribution of invertebrate drift in a stream is a non-random consequence of the intersection of organismal traits and stream landscape structure. All of these examples lead to the general conclusion that 'landscapes' must be viewed from an organismal rather than an exclusively anthropocentric perspective (Wiens *et al.*, 1993; Mac Nally, 1999).

Because all species are different from one another in at least some respects, the logical outcome of advocating an organismal-based approach to landscapes is that the analysis of riverine landscapes and their ecological effects will inevitably degenerate into a series of idiosyncratic, situation-specific findings with little emergent generality. Describing broad patterns of biodiversity is one way to deal with this problem, but much important information is lost under the umbrella of 'diversity.' Several aquatic ecologists (e.g. Townsend & Hildrew, 1994; Resh *et al.*, 1994; Rader, 1997; Poff, 1997) have suggested instead that general patterns in the distribution and abundance of species or in the assembly of communities might be derived by aggregating taxa into 'trait groups' based on

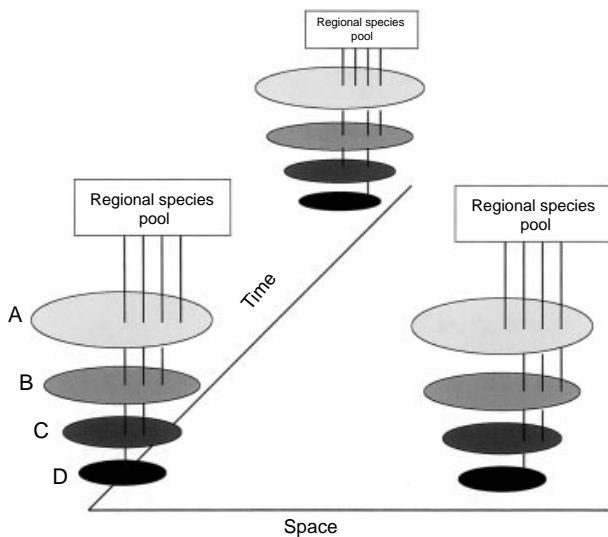


Fig. 3 The 'filtering' of species with certain traits among hierarchical spatial scales. Environmental or landscape filters at the watershed/basin scale (A) restrict the occurrence or abundance of species lacking particular traits at the valley/reach scale (B), and so on to the channel/unit scale (C) and micro-habitat scale (D), as indicated by the truncation of the vertical lines. Because riverine systems are dynamic, the ways in which the environmental filters restrict community membership at different scales will change in space and time. Modified from Poff (1997).

shared combinations of ecological and life-history features. Poff (1997) envisioned these traits interacting with landscape or environmental 'filters' within a riverine system to determine which taxa might pass through the filters (by virtue of their ecological traits) to constitute the river or stream community at a particular scale (Fig. 3). Of course, riverine systems vary in both time (as a result of streamflow variations and seasonal changes) and space (because of landscape structure). These variations can be conceptualised as alterations in the nature of the environmental filters (i.e. as opening or closing 'pores' in the filters; Fig. 3). Lancaster's (2000) documentation of differential accumulation of stream invertebrates in refugium patches under high versus low streamflow conditions provides an example. To the degree that species sharing similar suites of traits will respond to important features of landscape in similar ways, aggregating taxa into such functionally defined groups may provide a way to develop an organism-centred landscape ecology without becoming mired in a mass of species-specific details.

6. The importance of scale

'Scale' is perhaps the overarching theme of landscape ecology (Wiens, 1989, 2001; Peterson & Parker, 1998). All of the factors discussed above – patch quality, boundaries, context, connectivity and organism responses – change with changes in scale. The size of the 'window' through which an organism views or responds to the structure of its landscape (its *extent*), for example, may differ for organisms of different body sizes or mobility, and organisms may discern the patch structure of the landscape within this 'window' with differing levels of resolution (*grain*). As a result, the organism-defined 'landscape' is scale-dependent. In Colorado mountain streams, for example, larvae of a caddisfly (*Agapetus boulderensis*; high hydrodynamic profile, low mobility) responded to the streambed mosaic of riffles and cobbles at different scales than did mayfly nymphs (*Epeorus* sp.; low hydrodynamic profile, high mobility) (Wellnitz *et al.* 2001). A salmonid fish that moves over much larger sections of a stream would likely respond to patch-mosaic configuration at still different scales, yet its responses to stream structure would still be scale-dependent. For example, Fukushima (2001) documented that an association between the distribution of salmonid redds in Japanese streams that was evident at a 50-m scale of resolution disappeared when considered at broader scales.

It has become commonplace to consider landscape scaling hierarchically, and such an approach dovetails nicely with the hierarchical classifications of river and stream systems adopted by many aquatic ecologists (e.g. Frissell *et al.*, 1986; Townsend & Hildrew, 1994; Ward & Palmer, 1994; Pahl-Wostl, 1998; Habersack, 2000; see Fig. 4). Poff's 'landscape filter' concept (Fig. 3) is explicitly hierarchical, envisioning different environmental factors acting to determine the occurrence of species at different spatial scales. Such multiscale filtering is evident in the experiments of Downes, Hindell & Bond (2000), which showed that lotic macroinvertebrate density and diversity depended on both patch substratum type (i.e. patch quality) at a local scale and site-to-site differences in faunal composition at a broader scale.

Whether one views scale variation hierarchically or continuously (e.g. Wiens, 1989), it is apparent that both the physical and cultural processes that produce

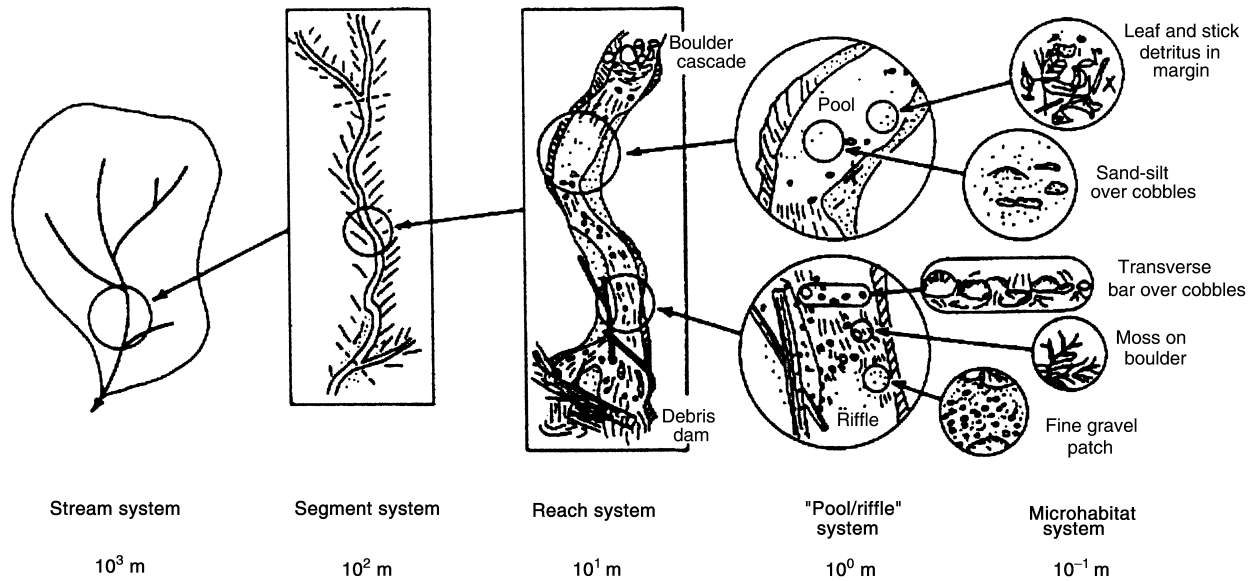


Fig. 4 The hierarchical classification of stream habitats of Frissell *et al.* (1986); from Townsend & Hildrew (1994).

landscape patterns and the responses of organisms to those patterns are scale-dependent. As a consequence, relationships that are apparent at one scale may disappear or be replaced by other relationships at other scales. Thus, Roth, Allan & Erickson (1996) found that measures of stream biotic integrity for stream fish were strongly correlated with the extent of agriculture, wetlands, and forest in the surrounding terrestrial landscape at a catchment scale, but were weaker or non-significant at a local scale. Local-scale riparian vegetation was only a weak, secondary predictor of stream biotic integrity. Here, then, regional land use overwhelmed the contributions of local streamside vegetation in enhancing stream conditions for fish. In other situations, associations that are evident at a local scale may disappear when the scale is expanded. Evidence of a preference of riffle-dwelling stream invertebrates for gravel of a particular size, for example, may disappear when the scale is expanded to include pools as well as riffles in the analysis.

This scale-dependency of ecological patterns and processes poses formidable difficulties to both observation and experimentation in riverine systems. One way to determine how patch structure in a stream landscape affects the distribution of organisms, for example, is to array patches of different types and sizes in a stream following an experimental design

(e.g. Lancaster, 2000; Palmer *et al.*, 2000a). Such experiments have contributed to our understanding of the importance of patch quality, context, boundaries and connectivity in riverine landscapes. Inevitably, however, experiments are constrained to relatively fine scales in time and space (Kareiva & Andersen, 1986), as are observations (i.e. samples) as well. This creates two problems. First, fine-scale experiments in aquatic systems are likely to be influenced by landscape effects at broader scales, if only because of hydrology (Cooper *et al.*, 1998). As a result, the results of the experiments contain a broader scale effect, which is generally unknown. Because riverine landscapes are heterogeneous, circumventing this problem through replication and controls may be only partially successful. Secondly, because patterns and processes do change with scale, the results of experiments or observations at fine scales cannot readily be extrapolated to broader scales, or *vice versa* (Lodge *et al.*, 1998; Wiens, 2001). In particular, the scales on which river management is applied are often quite different from the scales on which the ecological information that should inform such management is collected. Translating from information to management without considering scaling effects is likely to be risky.

The problem of scaling is produced by variation – variation in riverine systems in time (i.e. seasonal or

help to advance landscape ecology as well. It is time to take the 'land' out of landscape ecology, to put landscape ecology into the water.

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