Applicability of ecological theory to riverine ecosystems

J. V. Ward, C. T. Robinson and K. Tockner

Introduction

The conceptual foundations of lotic ecology were derived from diverse sources over a relatively long period (MINSHALL 1988). How do the most influential of the concepts dealing with fluvial systems conform with current knowledge in ecological theory? How effectively is new knowledge incorporated into the thinking of running water ecologists? These questions are important, not only for the further advancement of the discipline, but also to ensure that river conservation and management initiatives are based on a sound theoretical foundation.

The objective of this study was to briefly examine the extent to which current understanding of the structural and functional attributes of riverine ecosystems was consistent with contemporary ecological theory. Length restrictions precluded a detailed analysis of all the concepts that have had an influence on running water ecology. Rather, after addressing relevant historical constraints, concepts considered herein to be particularly influential, especially those with a broad ecosystem perspective, were assessed based on their concordance with ecological theory. Literature citations were used sparingly and selectively.

Historical constraints

Historical constraints have markedly influenced our perspectives of river ecosystems. These include possible biases relating to (1) the types and geographical locations of fluvial systems from which concepts were derived, (2) a long history of river engineering, and (3) a paradigm shift in ecology.

The conceptual foundations of running water ecology emanated largely from European and North American stream ecologists studying small forested streams (a mesic, small forested stream, temperate zone bias). In stark contrast, studies in the tropics occurred later and initially focused on fish communities of large, relatively pristine rivers. Therefore, it is difficult to ascertain whether perceived differences between temperate and tropical running waters are in fact real.

The conceptual foundations of running water ecology formed after most river systems in developed (temperate zone) countries had undergone substantial human-induced modifications. This was especially true in Europe where river engineering began centuries ago (PETTS et al. 1989), but also applies to large rivers in the United States (BENKE 1990). Floodplain reaches have been altered to the greatest extent (WARD & STANFORD 1995a). Because the theoretical foundations of stream ecology were based mainly on geographical regions where riverine reaches had been severely modified, one might expect concepts of lotic ecology to reflect a misconception of the natural condition.

Until quite recently, ecology was typically conducted according to the following unstated presuppositions: that nature is more or less deterministic, homeostatic and spatially homogeneous, that equilibrium conditions generally prevail, and that scale is not a critical variable (WIENS 1999). Of course ecologists of this earlier period were aware that these were simplifying assumptions, but much research was designed and results interpreted accordingly. The 'new paradigm in ecology' (sensu TALBOT 1996), in contrast, views natural systems as open, spatially heterogeneous, non-deterministic, non-equilibrial, and with patterns and processes that are highly scale dependent. Although this contemporary perspective has become firmly ingrained (sometimes to the point of dogma) in the thinking of most ecologists, some of the most influential concepts in run-
ning water ecology contain relicts from the earlier period. However, a note of caution is needed here: rather than an 'either/or' dichotomy (deterministic versus stochastic), the discipline can profit from a balanced view recognizing that various ecological phenomena may dominate under different conditions and at different times.

**Theoretical frameworks**

Herein, selected lotic ecology concepts are considered under the following theoretical frameworks: gradient analysis, disturbance, hierarchy, ecotones, and connectivity (Table 1). Most of the lotic ecology concepts listed in the table relate to more than one of the theoretical frameworks. Figure 1 presents examples, in a lotic ecosystem context, for each theoretical framework.

**Gradient analysis**

Ecology has a long-standing interest in how patterns and processes change along environmental gradients. The term gradient analysis was first applied to changes in mountain vegetation along an altitudinal continuum (Whittaker 1956). Given that unidirectional flow is the defining feature of rivers, it is natural that examining gradients from headwaters to the lower reaches has been a dominant theme in lotic ecology.

The stream zonation concept (Illies & Botosaneanu 1963) envisions a series of distinct communities along rivers, separated by major faunal transition zones (e.g. the rhithral–potamal transition); the river continuum concept (Vannote et al. 1980) is a clinal (rather than zonal) perspective of gradually changing resource gradients along which stream biota are predictably structured; the hyporheic corridor concept (Stanford & Ward 1993) defines an alternating series of constrained reaches and alluvial flood plain reaches, analogous to beads on a string. The zonation and river continuum concepts provide an essentially unidirectional (longitudinal) perspective, whereas the hyporheic corridor concept also includes interactive pathways in the lateral and vertical dimensions within alluvial flood plains. It is proposed herein that the unidimensional perspective of the zonation and continuum concepts reflects situations where the dynamic mul-

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Fig. 1. Examples from lotic systems of the five theoretical frameworks addressed herein. Sources: (A) modified from Gurnell et al. 2000; (B) expansion/contraction of the channel network of an island-braided reach of the Fiume Tagliamento, from Tockner unpublished; (C) modified from Tockner et al. 1998; (D) from Tockner unpublished; (E) modified from Ward et al. 1999b.
tiple channel networks of alluvial flood plains have been engineered into constrained single-thread channels. These models may indeed serve as suitable frameworks for investigating patterns and processes occurring along managed rivers, but they should not be invoked to portray the natural condition.

**Disturbance**

The role of disturbance, a topic of long-standing interest in ecology, has undergone a paradigm shift (Pickett & White 1985). Historically, disturbance was viewed as a deviation from the equilibrium conditions prevailing in nature, whereas disturbance is now generally recognized as an agent responsible for sustaining the ecological integrity of ecosystems. For example, the critical role of natural disturbances such as fire, hurricanes and tidal action in maintaining high levels of biodiversity became a central theme in ecology (Connell 1978).

According to the 'new paradigm in ecology', non-equilibrium conditions predominate in nature. It is, in fact, lack of disturbance that suppresses biodiversity, and this is perhaps most apparent in highly managed rivers. In reality, river ecosystems in the natural state are generally more dynamic than terrestrial or marine systems, but in much of the world the natural disturbance regime has been largely eliminated by a variety of river regulation measures.

The serial discontinuity concept (SDC) is a theoretical model for rivers whose natural dynamics have been suppressed by regulation. The original model (Ward & Stanford 1983) had a unidimensional perspective that perceived dams as disruptions of longitudinal resource gradients. The expanded SDC model (Ward & Stanford 1995b) also included alluvial flood plains, thereby encompassing dynamics along the lateral dimension. Both of these models were based on hypothetical reference river ecosystems, in the first case derived from the river continuum concept and in the second case also incorporating the flood pulse.

The flood pulse concept (Junk et al. 1989) is a theoretical framework for examining the adaptive strategies employed by aquatic and terrestrial biota to exploit the dynamics associated with alternating wet and dry phases over annual cycles in large floodplain rivers. The focus is, therefore, on the lateral and temporal dimensions. The flood pulse concept emphasizes the importance of alternating dry and wet phases in enhancing biodiversity and productivity, as well as the dynamic edge effect created by the 'moving littoral'. Perhaps the most important contribution of the flood pulse concept (based largely on pristine tropical rivers) was to make river ecologists of the temperate zone aware of the extent of hydrological extremes possible in flood plains, and the tight coupling of the biota with the flood regime. The views of Welcomme (1995), who believed that temperate rivers in the pristine state probably behaved in a similar manner to tropical rivers, are generally concurred with herein (but see Tochner et al. 2000).

The telescoping ecosystem model (TEM) of Fisher et al. (1998) specifically addressed the differential recovery trajectories within four subsystems (surface stream, riparian, hyporheic, parafluvial) following disturbance (flood, drought). Disturbance/recovery are defined in a biogeochemical context as 'processing length' (i.e. material cycling), with a short processing length reflecting high rates of cycling. Disturbance increases processing length (extends the cylinders of the telescope that represent the four subsystems); recovery involves a return of processing length (contraction of the cylinders) to predisturbance rates. The TEM is an important concept because (1) it recognizes subsystems adjacent to surface waters as integral parts of the stream ecosystem, and (2) it emphasizes that the subsystems may respond differently to a disturbance and may exhibit quite different recovery trajectories. The concept focuses on interactive pathways along vertical, temporal and, to a lesser extent, lateral dimensions. Although developed for relatively small, single-thread, canyon-constrained streams without extensive flood plains, it may be possible to expand the model to encompass floodplain rivers.

Recent studies of relatively pristine alluvial flood plains in the Alps have greatly heightened awareness of the remarkable levels of habitat
heterogeneity and fluvial dynamics possible in natural river systems (e.g. Tockner et al. 1997, Ward et al. 1999a). Based on these studies, it is essential to include the shifting mosaic of lotic, lentic and riparian habitats of fringing flood plains, as well as contiguous alluvial aquifers, as integral parts of the total river ecosystem.

**Ecotones**

Clements (1905) regarded ecotones as tension zones between adjacent communities. Ecotones are now viewed as semi-permeable boundaries between relatively homogeneous patches, transition zones where the rates of change in ecological patterns or processes are increased relative to the surroundings (Wiens 1992). The book on aquatic–terrestrial ecotones edited by Naiman & Decamps (1990) firmly established the ecotone concept in aquatic ecology, yet very little empirical work on ecotones per se has been conducted in river ecosystems. Nonetheless, it is apparent that riverine ecotones, operating across a broad range of spatio–temporal scales, play important roles relating to speciation, evolutionary invasion of fresh waters, biodiversity, bioproduction and nutrient transformation (Ward & Wiens 2001). Ecotones are perhaps most apparent in intact alluvial flood plains, which themselves constitute a large-scale ecotone between the river and the upland. Within flood plains, ecotones are manifest at a variety of scales, including the boundaries between different riparian communities, surface water–groundwater transitions (e.g. upwelling/downwelling zones, springs), lotic–lentic transitions and oxic–anoxic boundary zones in the soil.

Natural disturbances, by forming a variety of patch types and successional stages, play an important role in maintaining a diversity of ecotonal habitats in riverine flood plains. The suppression of disturbance (fluvial dynamics) in managed rivers undoubtedly reduces ecotone diversity and affects their functional properties (e.g. permeability), although few data are available. It is likely that the importance of ecotones in sustaining ecological integrity has been underestimated because of their reduced diversity/function in managed rivers. Rigorous investigations into the role of ecotones in material and energy flux are required, in order to provide insight into the major determinants of biodiversity and productivity in river ecosystems. Clearly a holistic perspective would include various interactive pathways between land and water, surface water and ground water, and instream transition zones. Preliminary evidence suggests that management of ecotones should be an integral part of river protection and restoration programs.

**Hierarchy**

Recognition that ecological phenomena manifest across a diverse array of scales led to the development of the nested hierarchical model (Allen & Starr 1982). Perhaps its most important aspect is recognizing that phenomena structuring one hierarchical level may or may not be operative at another level. This was well exemplified by the investigation of Arscott et al. (2000) of the spatio–temporal heterogeneity at three hierarchical levels (corridor, floodplain and habitat scales) in six geomorphic reaches along a dynamic alluvial river system. This work clearly demonstrated that the patterns of variation were scale- and variable-dependent.

Frisse1 et al. (1986) presented a rather elegant hierarchical framework for stream networks, in which they identified the spatial extent of subsystems (from microhabitat to catchment) and their corresponding temporal persistence. This catchment hierarchy concept, despite its utility and influence, has severe limitations. The model was based on small headwater streams and does not address interactions with flood plains or alluvial aquifers. Minshall & Robinson (1998) demonstrated that measures of habitat heterogeneity influenced biota differentially among streams of different size. Ward et al. (1999b) formulated a framework for examining alpha, beta and gamma diversity at hierarchical levels ranging from physiographic region (e.g. Alps) to habitat patches. The views of Townsend (1996), who proposed that various concepts in river ecology “be meshed together into the broad spatio–temporal context of the catchment hierarchy of an entire river”, are concurred with herein.
Connectivity

The concept of connectivity originally referred to gene flow between subpopulations of a metapopulation (MERRIAM 1984). Connectivity is a relatively new concept in ecology and has only recently caught the attention of lotic ecologists. Hydrological connectivity (sensu AMOROS & ROUX 1988) refers to the exchange of matter (including organisms) and energy via the aqueous medium between different units of the riverine landscape. Floodplain water bodies differing in connectivity with surface waters of the main channel exhibit different successional trajectories and contain different biotic communities. In a Danubian flood plain, each of the faunal and floral groups examined exhibited maximum species richness at a different point along a connectivity gradient (TOCKNER et al. 1998). The degree of connectivity between ground waters and surface waters also is an important determinant of functional processes in aquatic and riparian systems (BRUNKE & GONSE 1997, WARD et al. 1998).

However, as stressed by AMOROS & BORNETTE (1999), connectivity is a complex phenomenon that “cannot be reduced to a simple gradient”. This is well exemplified by the biphasic relationship between hydrological connectivity (defined as length of channels with an upstream surface connection with the main channel/total channel length) and channel length in a braided glacial flood plain (WARD et al. 2002). The initial period of expansion in early summer, in which channel length more than doubled, was not accompanied by a substantial increase in connectivity because snow melt recharged aquifers via subsurface pathways. Initial channel expansion mainly involved groundwater-fed channels that did not form upstream connections with the main channel. However, once a

Fig. 2. A modular framework for developing an integrated model of dynamic river ecosystems.
certain threshold was exceeded (a channel length of about 15 km), there was a strong positive relationship between connectivity and total channel length. Exactly how the epigean and hypogean biota are influenced by connectivity patterns in this glacial flood plain remains to be seen. Rigorous analyses of the role of connectivity in river ecosystems hold considerable promise for furthering the understanding of functional processes and biodiversity patterns.

Conclusions
In general, concepts of riverine ecosystems are only partially concordant with current ecological theory. This reflects (1) misconceptions of what constitutes the natural state of river ecosystems, (2) failure to fully recognize the major interactive role between fluvial dynamics and geomorphic structure in sustaining ecological processes and biodiversity patterns in river corridors, and (3) not including flood plains and contiguous groundwater aquifers as integral components of rivers. In addition, (4) the ‘new paradigm in ecology’, that nature is non-deterministic, non-equilibrium, highly heterogeneous and scale-dependent, has not been fully integrated into theoretical developments in lotic ecology. In Fig. 2, a modular framework is presented for developing an integrated model of dynamic river ecosystems that builds upon the major contributions of different concepts. A more holistic understanding of ecological processes, founded on a strong conceptual base, will not only advance the discipline, but also will enhance the effectiveness of conservation and restoration initiatives.

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