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What is hydrologic connectivity and why is it ecologically important?

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Introduction

Hydrologic connectivity (*sensu* Pringle, 2001) is used here in an ecological context to refer to water-mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle. Hydrologic connectivity is essential to the ecological integrity of the landscape, and reduction or enhancement of this property by humans can have major negative environmental effects. Some of these effects are immediate, localized and, therefore, obvious. For example, with respect to migratory fish, a given dam may act to *reduce* hydrologic connectivity (by preventing or impeding migration up or downstream), whereas interbasin river transfers *enhance* this property by allowing the dispersal of fish into river basins outside of their range. Less obvious, are alterations in hydrologic connectivity that exhibit a time lag and manifest themselves at geographic locations far from the source of disturbance. An example concerns the cumulative effect of dams on transport of the inorganic dissolved solute silica. Dams and associated impoundments can reduce the transport of this compound, which becomes deposited in the bottoms of reservoirs (Humborg *et al.*, 2000). The cumulative effects of many dams along a river can potentially result in a reduction in the amount of silica delivered to coastal waters, with consequent negative effects on coastal food web structure that contribute to eutrophication (Justic *et al.*, 1995; Turner *et al.*, 1998).

Management and policy decisions regarding land-use activities and hydropower development are often made in the absence of adequate information on hydrologic connectivity in the landscape. Our current knowledge of how this property maintains the ecological integrity of 'natural' ecosystems is poor due to: (1) the inherent complexity of water movement within and between the atmosphere and surface–subsurface systems; and (2) the extent and magnitude of human alterations, which often occur before we understand how hydrologic connectivity affects ecological patterns in the landscape (Pringle and Triska, 2000).

Hydrologic connectivity is being altered at a rate unprecedented in geologic history, contributing to dramatic losses in global aquatic biodiversity and associated ecosystem integrity (e.g. Dudgeon, 2000; Pringle *et al.*, 2000; Rosenberg *et al.*, 2000). Humans have already appropriated one-half of the accessible global freshwater runoff and this could climb to 70% by 2025 (Postel *et al.*, 1996).

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Of the 3.2 million miles of streams in the USA (i.e. lower 48 states), only 2% remain free-flowing and relatively undeveloped. Less than 42 free-flowing rivers of over 125 miles in length exist; the remaining 98% of US streams have been fragmented by dams and water diversion projects (Benke, 1990). The USA has also lost over half the wetlands that existed at the time of the American Revolution. Accordingly, the World Wildlife Fund's species population index (which measures the average change over time in populations of almost 200 species of freshwater birds, mammals, reptiles, amphibians, and fish) has declined by 50% globally over the 30 year period from 1970 to 1999. Current rates of extinction of many freshwater taxa are more than 1000 times the normal 'background' rate and, as a whole, in the USA the freshwater species are more imperilled than terrestrial species (Master *et al.*, 1998). In this invited commentary, I discuss hydrologic connectivity in terms of: (1) its historical antecedents; (2) species- to ecosystem-level consequences of alterations of this property; and (3) emerging ecological patterns of global concern.

Historical Antecedents of Hydrologic Connectivity

It is instructive to consider how connectivity has been studied in the past to understand the context in which it is used here. As pointed out by Moilanen and Nieminen (2002), connectivity (or its inverse, isolation) has long been recognized as a fundamental factor in determining the distribution of species (MacArthur and Wilson, 1967; Levin, 1974; Merriam, 1984; Fahrig and Merriam, 1985). Merriam (1984) first introduced the concept of *landscape connectivity* to emphasize the interaction between species attributes and landscape structure in determining movements of biota among habitat patches.

Connectivity is often used in different contexts by different ecological disciplines. Among conservation biologists it is commonly used with respect to landscape corridors and landscape linkages between patches (Noss, 1991; Bennett, 1999), strategies that are often put forth to counter the challenge of habitat fragmentation. Accordingly, connectivity is a fundamental concept in both metapopulation biology and landscape ecology.

In metapopulation ecology, which is concerned with gene flow between spatially distinct subpopulations of a larger metapopulation, connectivity is often considered as an attribute of a given habitat patch (Moilanen and Hanski, 2001). Although original metapopulation models were designed and tested on terrestrial biota (typically insects and small mammals), metapopulation theory has more recently been applied to riverine biota such as fish and mussels (e.g. Stoeckel *et al.*, 1997; Policanski and Magnuson, 1998; Gotelli and Taylor, 1999; Fagan, 2002).

From a general landscape ecology perspective, connectivity can be defined as the degree to which a landscape facilitates or impedes movement of organisms among resource patches (e.g. Tischendorf and Fahrig, 2000). Connectivity has been used extensively to describe spatial connections in riverine landscapes (e.g. Amoros and Roux, 1988; Ward and Stanford, 1989a,b; Ward, 1997; Amoros and Bornette, 1999). Rivers can be defined as having interactive pathways along one temporal dimension (time scales) and three spatial dimensions (longitudinal (headwater–estuarine); lateral (riverine–riparian/floodplain), and vertical (riverine–groundwater); Ward and Stanford, 1989a). Consideration of dynamic interactions along these four dimensions (i.e. as defined by Ward and Stanford (1989a)) has proven to be a very effective conceptual spatial framework to understand human impacts on river ecosystems (e.g. Boon *et al.*, 1992; Pringle, 1997, 2000). Ward's (1997) definition of riverine connectivity (i.e. as energy transfer across the riverine landscape) stimulated Pringle (2001) to define hydrologic connectivity from a broader perspective that considers hydrological connections on regional and global scales: i.e. water-mediated transfer of matter, energy, and/or organisms within or between elements of the hydrologic cycle. Pringle (2001) discusses the vulnerability of biological reserves throughout the world to cumulative alterations in hydrologic connectivity. The location of a reserve within a river basin (relative to regional aquifers wind and precipitation patterns, and even oceanic currents) can play a key role in its response to disturbance transmitted through the hydrologic cycle.

Species- to Ecosystem-Level Effects of Alterations in Hydrologic Connectivity

Reductions in hydrologic connectivity have some fairly well documented species- to ecosystem-level effects in river ecosystems. Species-level effects of dams on migratory salmonid fishes have received much attention (Pacific Rivers Council, 1993). Over 100 major salmon and steelhead populations or stocks have been extirpated on the West Coast of the USA and Canada, and at least 214 more are at risk of extinction (Nehlsen *et al.*, 1991). Less is known about species-level effects on biota of less economic importance (nongame fishes, freshwater shrimps, crayfish, and other invertebrates), yet increasing evidence indicates that they are significant.

We are just beginning to acknowledge the magnitude of ecosystem-level consequences of migratory faunal depletion caused by dams (Freeman *et al.*, 2003). As just one example, populations of bald eagles and grizzly bears that depend on salmonids as a food source may decrease dramatically if this food source is eliminated (Spencer *et al.*, 1991). Faunal components that are vulnerable to river fragmentation can also play key roles in determining ecosystem-level properties/ processes, such as water quality and nutrient cycling. It is well documented that anadromous fish, such as salmon, can provide major input of nutrients and energy to freshwater systems when spawning adults return from the sea (Ben-David *et al.*, 1998; Gresh *et al.*, 2000). Consequently, when dams block salmonid migration routes, patterns of nutrient cycling in entire riverine ecosystems can be altered.

The loss of mussel species from streams, where they were once diverse and abundant, is yet another legacy of reduced hydrologic connectivity. Some 90% of the world's freshwater mussel species are found in North America, and 73% of all mussel species in the USA are at risk of extinction or are already extinct. The prognosis is not good: in 1990, 90% of the listed mussels were still declining, and only 3% were increasing (Master, 1990). Given that mussels filter an enormous amount of water and that they were once plentiful, landscape consequences of their elimination likely include substantial losses in system productivity, decreased local retention of nutrients and alterations in the structure and stability of the benthic stream environment (Strayer *et al.*, 1999).

Establishment of new hydrologic connections in the landscape (e.g. interbasin transfers) and restoration of connectivity in highly modified human-dominated landscapes (e.g. dam removal) can also have species- to ecosystem-level effects. For example, dam removal (or provision of fish-passage devices around hydroelectric dams) in tributaries of the Laurentian Great Lakes can result in the transport of bio-accumulated toxic chemicals and also nonnative species into upstream habitats (summarized by Freeman *et al.* (2002)). Consequent cascading ecological effects throughout the food chain include impaired reproduction of bald eagles feeding on fish contaminated with polychlorinated biphenyls (PCBs) and other persistent organic chemicals (Giesy *et al.*, 1995).

Emerging Ecological Patterns of Global Concern

Cumulative human alterations of hydrologic connectivity are currently affecting ecosystems on a large scale, resulting in emergent ecological patterns of global concern. Although some direct ecological effects of altered hydrologic connectivity in stream ecosystems are increasingly well understood (e.g. local effects of dams and river regulation), indirect biogeochemical effects are more elusive and difficult to identify. Pringle (2003) summarizes information on interacting effects of altered hydrologic connectivity and contaminant transport, focusing on three emerging ecological patterns of global concern: (1) regional declines in migratory birds and wildlife resulting from wetland drainage and contaminated irrigation drainage; (2) bioaccumulation of methylmercury in fish and wildlife in newly created reservoirs; and (3) deterioration of estuarine and coastal ecosystems that receive the discharge of highly regulated silicon-depleted and nutrient-rich rivers.

The hydrologic transport, bioaccumulation and associated ecological effects of endocrine-disrupting chemicals is another emergent ecological pattern that is receiving increasing attention.

Knowledge of hydrologic connectivity on global scales is paramount in understanding how persistent organic compounds such as PCBs ultimately become very highly concentrated within arctic food chains. As summarized by Colburn *et al.* (1997), ocean currents are ultimately key vectors that act to transport biota that have sequestered PCBs into the arctic food web, where they undergo further biological magnification within long-lived animals. PCB levels in seals and predatory polar bears are, respectively, 384 million and 3 billion times the PCB concentration in ocean water, potentially affecting the long-term reproductive capacity of these animals and the humans that eat them.

It is clear that human activities are exerting ecological effects via increasingly broad feedback loops in the hydrologic cycle that ultimately include alteration of climate. Predicted effects include increases in global average precipitation, changes in regional patterns of rainfall, snowfall and snowmelt, rising sea levels, and saltwater intrusion into coastal aquifers and river mouths (e.g. Firth and Fisher, 1992; Gleick, 1998).

In conclusion, an important area of collaborative study between hydrologists and ecologists is to understand how cumulative human alterations of hydrologic connectivity influence ecological patterns on regional and global scales. Such interdisciplinary research is fundamental for land-use decisions, which are often made in the absence of adequate information on how hydrological connections in the landscape structure ecosystems.

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