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Flowpaths as Integrators of Heterogeneity in Streams and Landscapes

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Abstract

Streams are heterogeneous in both space and time. Hydrologic flowpaths along which biogeochemical processing occurs integrate different patches of the stream. Disturbance events (flood and drying) change these patches, alter connectivity, and reinforce spatial heterogeneity. Heterogeneity within patches (surface stream, hyporheic zone, sand bars, and riparian zone) is generated by the interaction of nitrogen (the limiting nutrient) in transport and organisms such as algae and bacteria. These organisms store nitrogen as they grow, alter N forms and concentrations in transport, and in some cases (e.g., denitrification) export it to the atmosphere. Changes in nitrogen in transport can be large, as are community responses to nitrogen availability, thus reinforcing spatial heterogeneity in successional time. Flowpaths connect patches as well and generate changes in recipient patches as a function of nitrogen delivery rate. This is especially evident at patch boundaries. In streams, flow is markedly linear and inexorably downstream in orientation; however, landscapes are drained by coalescing, dendritic networks that intimately connect stream channels with terrestrial flowpaths over and beneath soils. We propose that a unified theory of landscapes will require a focus on spatial linkage, a consideration of both spatial and temporal heterogeneity, and a blurring of distinctions between terrestrial and aquatic elements.

Introduction

The concept of heterogeneity has been used variously in stream ecology to describe habitat variability (e.g., sediments) and effects on invertebrate communities (Palmer et al. 1997) or more broadly as patch structure and dynamics at multiple scales (Pringle et al. 1988). Poff et al. (1989) considered heterogeneity of forcing variables such as flood and drought in shaping stream function, again with an emphasis on invertebrates. Dent and Grimm

(1999) considered spatial heterogeneity of nutrient concentration using spatial autocorrelation analysis in a desert stream and applied this approach at three scales to deduce scale-specific causation of resultant patterns (Dent et al. 2001). Results of this approach lend insight into stream structure and function and permit an objective determination of operant hierarchical scales. Fractal analysis has been used to determine patterns of algal distribution in streams (Sinsabaugh et al. 1991) and to infer causes of spatial heterogeneity of invertebrate communities resulting from biotic interactions (Cooper et al. 1997).

Many stream ecologists have acknowledged that streams are spatially variable and have considered how these subsystems interact. Stanford and Ward (1993) have shown how the stream channel interacts with flood plains and how this variability and connectivity are central to stream function and biodiversity. Poole (2002) used a hierarchical approach adapted from Frissell et al. (1986) to examine longitudinal changes in solutes and community organization in streams and to thereby define an integrative approach to fluvial landscape ecology. Fisher et al. (1998a) developed a model of lateral interaction of stream elements in disturbance time to show how subsystem interactions shape whole system function, in that case, in terms of nutrient retention and spiraling.

Although these efforts represent substantial progress in understanding streams as spatially complex ecosystems, the field is still struggling with the challenge of linking heterogeneity with whole ecosystem functioning (Palmer and Poff 1997), determining how and when heterogeneity, in all its manifestations, matters.

Objectives

The purpose of this paper is to examine the consequences of heterogeneity for ecosystem function using streams as an example; in particular, results of our work in Sycamore Creek in Arizona. We will attempt to develop a concept of patch integration to determine when heterogeneity generates higher order properties by virtue of patch interaction. Several terms are essential to this discussion. First, *structure* refers to the configuration of the ecosystem in space. *Patch structure* refers to a situation in which variance changes abruptly at boundaries that enclose patches that are themselves relatively homogeneous. Gradients may occur within patches or may characterize entire ecosystems wherein boundaries do not exist (although they may be arbitrarily imposed). Patch *integration* refers to an interaction among patches and may take several forms (hydrology, organismal movements, wind action) and involve several distinct *currencies* such as nitrogen, caribou, bird song, pheromones, and visual images (Reiners et al. this volume). We think of *integrator* as the mode of connection among patches and currency as the entity moved by the integrator. More broadly, an integrator can be viewed as a set of rules or an algorithm for summing patch influence on the whole. In this paper, we will emphasize integration via hydrologic *flowpaths*.

Heterogeneity exists when the ecosystem is not uniform and patches are present. This is virtually always the case. However, if the whole-system consequence of this heterogeneity is merely additive, the result is arguably less interesting than if whole-system consequences "emerge" as more than the sum of parts and are not deducible from patch structure alone. By integration we mean lateral interaction among patches sensu Turner and Chapin (this volume). Integration occurs when patches interact in a nonadditive way, resulting in nonlinear interaction among patches. The resulting nonlinear function may be contingent upon patch configuration and arrangement as well as specific routing of the integrator among various structural patches. Integration algorithms may change over time at different temporal scales and may themselves vary with time. Furthermore, integration varies as a function of currency, thus hydrologic integration for nitrogen may have a different influence on ecosystem function than for phosphorus. Migration (an integrating mechanism) of wildebeest will affect ecosystem function differently than will swarms of locusts. Ecosystem function is the holistic property that integrated patches of heterogeneous systems influence. In our stream research, material retention is an ecosystem function (emergent property) of special interest, but other ecosystem properties such as primary production or biodiversity or carbon processing efficiency can be influenced by patch structure and integration as well.

In the sections below, we will describe how hydrologic integration acts through the currency of nitrogen to integrate patches in Sycamore Creek, a well studied stream of the Sonoran desert of central Arizona (Fisher et al. 1982). The ultimate issue is nitrogen retention in arid landscapes. We know that only a small fraction of nitrogen entering desert landscapes is hydrologically exported (Grimm and Fisher 1992). In this paper, we define any process preventing hydrologic export to be retention. This includes both storage (e.g., as soil organic nitrogen) and loss to the atmosphere (e.g., ammonia volatilization and denitrification). We do not know where in this heterogeneous landscape the nitrogen is lost or retained, nor do we know the relative importance of various processes operating to retain or export it. Our goal below is to illustrate several issues that arise from attempts to apply heterogeneity-integrating ideas to streams at the level of surface stream, hyporheic zone, sand bars, riparian zones, drainage networks, and catchments (Figure 15.1). In each of these, nitrogen is transported in various chemical forms along hydrologically defined flowpaths.

Multiple disturbances, most notably drying and flooding, influence Sycamore Creek. Successional changes between disturbance events are pronounced. Thus patch structure, flow (integrator force and pattern), and nitrogen concentration (currency magnitude) change rapidly. Sycamore Creek has been described in detail elsewhere (Fisher et al. 1998b).

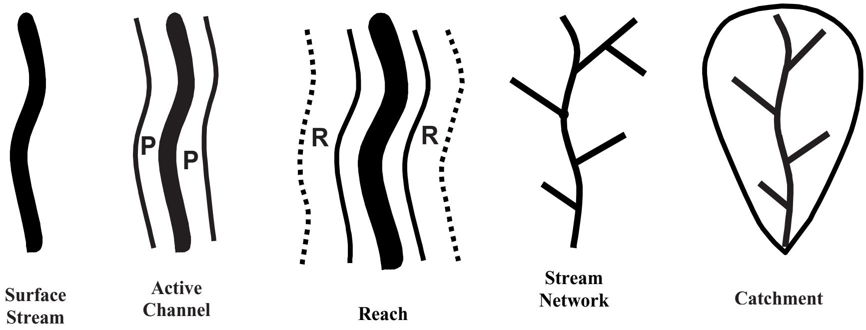

FIGURE 15.1. Depiction of aquatic ecosystem components as a function of increasing spatial extent: surface stream, defined as the wetted perimeter; active channel, comprised of the surface stream and parafluvial zone (P) or sand and gravel bars; stream reach, comprised of the active channel and adjacent riparian zone (R); stream network; and catchment, which includes all nested stream segments in a given area, as well as the land area they drain.

Surface Stream

At the level of the surface stream channel, defined as the wetted perimeter, water flows on the sediment surface and connects patches represented by different substrates (cobbles and sand, for example) and superimposed benthic communities of algae and cyanobacteria mixed with organic detritus and assorted invertebrates. Hydrologic flowpaths connect these patches, and nitrogen in transport is removed or augmented by organismal uptake, assimilation, growth, excretion, or decomposition.

Flash floods obliterate and then restore patch structure. In postflood successional time, benthic algae recolonize sediments at a rate determined by the availability of inorganic nitrogen (largely nitrate), the limiting element in this system. As growth requires nitrogen, concentration declines in a downstream direction (Grimm 1987). Eventually, nitrogen is so low that N-fixing cyanobacteria gain a competitive advantage and replace green algae, gradually dominating the stream bottom in a downstream to upstream direction (Figure 15.2; Grimm 1994). In this case, patchiness in terms of algal coverage develops and changes over time as a function of the flowpath integrator. Changes in the form of the currency (NO_3^- to atmospheric N_2) shifts community composition to cyanobacteria. In this manner, ecosystem function (N retention) simultaneously causes and responds to patchiness (heterogeneity). Interestingly, a positive rate of nitrogen accretion continues after hydrologically supplied N is depleted. Diffusion of atmospheric N_2 supplants hydrology as the integrator controlling nitrogen uptake later in successional time. This dynamic at the scale of 100 m and 100 days is both a cause and consequence of heterogeneity and involves a shift in integrators in time (hydrologic to atmospheric), both operating on the same currency (N).

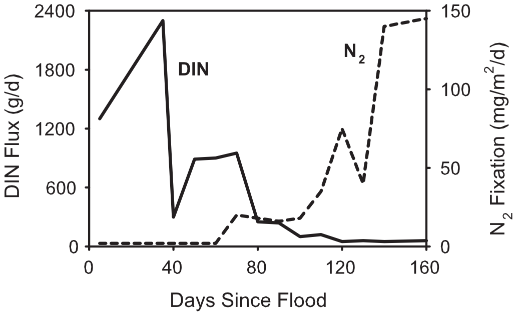

FIGURE 15.2. Temporal shifts in stream water DIN flux (g/d) and N_2 fixation ($mg/m^{-2}d^{-1}$) by cyanobacteria in the surface stream as a function of days post flood (Grimm 1994). Stream water DIN concentration is typically high immediately after floods; however, as algae begin to recolonize and take up nitrogen, DIN concentration declines, often to undetectable levels. When DIN concentration is low, cyanobacteria, which can fix atmospheric N, have a competitive advantage, and cyanobacterial biomass begins to increase over other green alga species. This leads to a shift in the integrator linking patches from hydrologic to atmospheric and a shift in producer community composition from green algae to cyanobacteria. In stream segments, nitrogen is depleted first in downstream reaches, thus space can be substituted for time on the X-axis (Grimm 1994 and Dent et al. 2001).

During periods of drought, surface flow may be lost as the stream dries (Stanley et al. 1997). Although the larger desert landscape may continue to be connected hydrologically, flow occurs deeper and more slowly in fluvial sediments. Mortality is high among stream organisms. At the scale of the catchment, surface drying represents a structural patch dropping out of the integration. In this case, the physical structure of the landscape does not change; rather, the integrator shifts horizontally and vertically over time as the surface stream shrinks and then dries completely. Any model of heterogeneity and ecosystem function must be able to deal with patches that come and go (algae) but also with patches that remain but lose connections with others (the surface stream as a whole during drought). At a variety of scales, the relationship between heterogeneity and ecosystem function will change in time as well as space. Heterogeneity can have a strong temporal component.

Hyporheic Zone

Even when drying eliminates the surface stream, hyporheic flow continues. Water always moves beneath stream sediments whether surface flow is present or not. Vertical up- and downwelling zones exist, due to geomorphology, in particular the run-riffle sequence (Dent et al. 1999). Upwelling

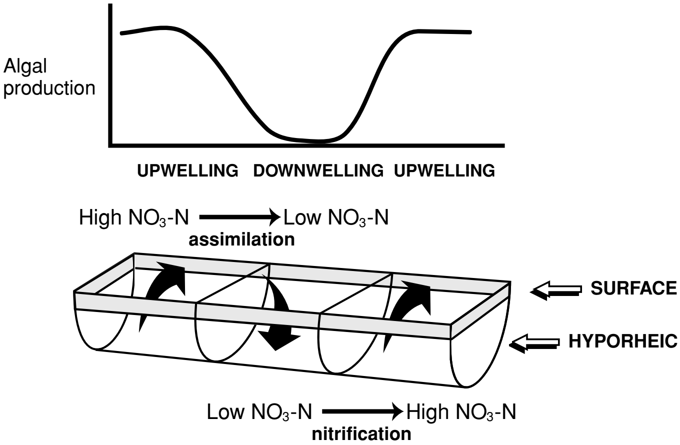

FIGURE 15.3. Patterns in algal production and nitrate concentrations in hyporheic upwelling and downwelling zones. When stream water DIN concentration is low, patterns of algal production in the surface stream are tightly linked to zones of hyporheic upwelling and downwelling. Water downwelling into the hyporheic zone from the surface stream is low in DIN and thus algal production is low in these areas. However, downwelling water is often high in DON (dissolved organic nitrogen), and mineralization and subsequent nitrification of organic nitrogen in the hyporheic zone increases nitrate concentrations in subsurface water. Where this high nitrate water upwells into the surface stream, algal production is high (Valett et al. 1994). Patterns of upwelling and downwelling are hydrologically driven and may lead to positive (net uptake and storage of N) retention or negative (N-fixation and increased N export), depending on their configuration. (Valett et al. 1994).

zones terminate hyporheic flowpaths of usually tens of meters and, because nitrification is high in stream sediments, contribute water high enough in nitrate to stimulate algal growth (and nutrient retention) on stream bottom sediments there (Figure 15.3; Valett et al. 1994). Downwelling zones receive surface water low in nitrate, and algal growth is much lower there and often is dominated by cyanobacteria that fix nitrogen rather than sequester inorganic nitrogen in transport. This pattern of up and down welling is hydrologically driven and, depending on its configuration, may result in nutrient retention by algae and a decrease in transported nitrogen or in nitrogen fixation and atmospheric linkage.

Surface stream–hyporheic interaction is an example of integration of heterogeneous patches by hydrology and a quantitative change in currency (N concentration), resulting in uptake or augmentation. In this example, activity is localized at the interface between subsystems. Vertical connectivity both generates heterogeneity (in algae and in nitrogen cycling) and is accentuated by it, thus is a positive feedback. We argue that simply adding hyporheic and surface rates to determine system function would miss this important interfacial property. Instead, knowledge of their connection is needed to fully understand the fluvial system as a whole.

Sand Bars and the Parafluvial Zone

Main channel sand bars also exchange water and nutrients with the surface stream but they do so laterally rather than vertically, as is the case with the hyporheic zone. Transformations of nutrients are similar, and outwelling edges of sandbars support dense algal communities, which may retain up to 80% of outwelling nitrogen (Henry and Fisher 2003). Nitrogen fixers dominate inwelling and nonwelling zones, at least during low flow when dissolved inorganic nitrogen in stream water is below limiting levels. This generates a spatial pattern—"hot" spots of nitrogen retention and "cold" spots of nitrogen fixation (Fisher et al. 1998b). In postflood successional time, the streambed is a mosaic of N-fixing and N-retaining photosynthesizers. Relative abundance of these patches will determine whole system N retention of the active channel subsystem (surface stream plus hyporheic zone plus sand bars). Again, ecosystem function is determined by flow-path dynamics.

As it turns out, nitrification across sand bars is nonlinear (Figure 15.4a) presumably because dissolved organic nitrogen derived from the surface stream is depleted by microbes, whereas mineralization of phosphorous (from apatite minerals in sand) is linear (Figure 15.4b; Holmes et al. 1994; Holmes 1995). As a result, long flowpaths through sand bars decrease N:P ratios and have the capacity to shift potential nutrient limitation from N to P. We have not yet seen N:P drop below Redfield ratios wherein phosphorus limits productivity, but were this to happen, algal growth and nitrogen removal could be controlled by phosphorus concentration, not nitrogen.

Distribution of sand in bars may affect the outcome (consequence) of heterogeneity because of the change in nutrient concentration along the flowpath. Many small bars will increase N:P while the same amount of sand in one large bar will decrease N:P in comparison (Figure 15.5). This is an example of the same integrator (water) working on multiple currencies (N and P) simultaneously but in different ways owing to their chemical properties. The question is, how does their interaction influence an ecosystem property (e.g., N retention), and the answer is through control via stoichiometry involving a shift in the limiting nutrient.

Riparian Zone

Riparian zones are important in that they represent an interface between upland areas and streams and may serve as a filter (via uptake or transformation). Riparian zones thereby influence the rate of input of nutrients into

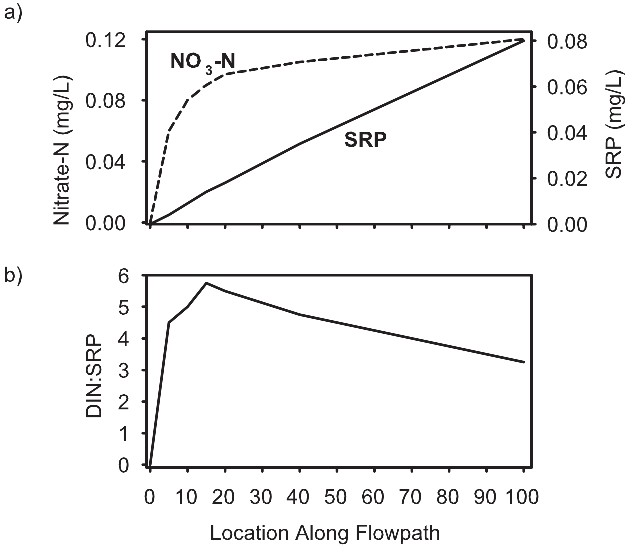

FIGURE 15.4. Changes in sand bar subsurface water (a) nitrate and soluble reactive phosphorus concentrations and (b) DIN:SRP ratio, as a function of location along the flowpath. Adapted from Holmes 1995. (a) Increases in SRP are linear along the flowpath while increases in nitrate are nonlinear, reaching a plateau. (b) As a result, long flowpaths through sand bars decrease N:P ratios and have the capacity to shift potential nutrient limitation from N to P.

the stream channel just as sand bar edges and hyporheic-surface interfaces influence fluxes across ecosystem components. In many areas, riparian surfaces intercept water and solutes as they move into the stream for the first time and thus represent a lateral filter. In arid streams such as Sycamore Creek, water enters stream channels first via tributaries and then moves into

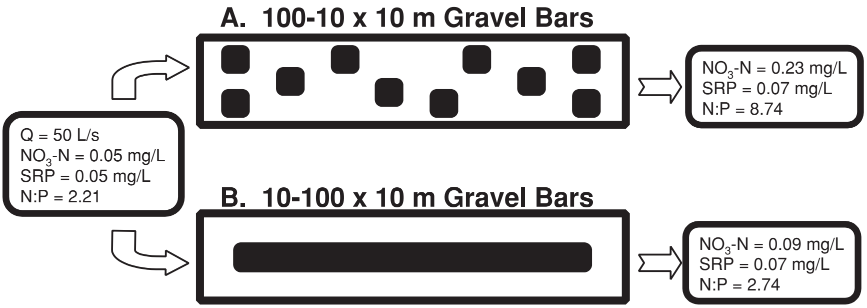

FIGURE 15.5. Consequences of sand bar configuration on reach-scale nitrogen retention. Adapted from Holmes 1995. Many small bars (A) will increase N:P while the same amount of sand in one large bar (B) will decrease N:P in comparison.

riparian zones (and back) from the stream side. While water and its load move back and forth with flowpaths determined by geomorphology, desert streams are net hydrologic "losing reaches," and much stream flow is lost by transpiration of riparian trees (Culler et al. 1982). Biologically active nutrients are stored long term in riparian trees. Nitrogen may be lost via denitrification at these interfaces (Schade et al. 2001). Because net flow occurs out of the stream most of the time, the riparian zone is a sink for nutrients at base flow. During floods, however, exchange can be large as water inundates riparian terraces, mobilizes nutrients accumulated there by soil processes such as nitrification, and transports them back to the stream channel (Marti et al. 2000; Schade et al. 2002; Heffernan and Sponseller 2004). This exchange is punctuated in arid lands but is important in all streams and has been called ROSS (region of seasonal saturation) by Baker et al. (2000).

We see then that riparian zones represent another patch contributing to heterogeneity and integrated by hydrology in a manner dictated by the interaction of geomorphology and hydrology. Depending on the regime of exchange during base flow or flood stage, nutrients vary, stoichiometric changes can occur, and nitrogen may be retained in biomass or lost to the atmosphere. The magnitude of landscape level nutrient retention is thus a function of spatial and temporal patterns of flowpaths and associated currencies.

As stated earlier, water enters larger desert streams not underground across the riparian zone at base flow but down tributary channels during storms. These tributary channels form networks wherein flowpaths in the form of surface flow are highly organized as a convergent, branched network. Depending on climate, this network may itself be highly intermittent, as is integration of heterogeneity at this scale.

Network Structure

Up to this point we have discussed streams as if they were linear systems with longitudinally and laterally (and in some cases vertically) dispersed subsystems connected by flowing water and its load. Heterogeneity exists within each subsystem and in the larger stream of which they are a part. This linear view of streams has been productive in helping us understand upstream-downstream linkages, lateral connections, and size-related changes in stream segment function (Vannote et al. 1980). Only recently have stream ecologists begun to treat streams as branched structures (Osborne and Wiley 1992; Fisher 1997; Nakamura et al. 2000; Power and Dietrich 2002), a view prevalent among geomorphologists for more than a half century (Horton 1945; Strahler 1952).

Stream flow in channels coalesces in a convergent network, the structure of which can vary considerably depending on geomorphology, hydrology, slope, and catchment age. The stream network perfuses the terrestrial watershed and integrates ecosystem properties from headwaters to the sea, should the catchment be large enough. Clearly at the landscape scale, the stream network, through transport and processing, reflects whole ecosystem function, especially in the case of material retention, as small watershed budgets have shown (Likens et al. 1970). Depending on climate and geomorphology, low-order stream channels may be dry most of the time. This is especially true in arid land streams such as Sycamore Creek where small streams may transport water for only a few hours a year.

Storm size, intensity, and duration influence the extent of flow in intermittent networks, and the majority of events generate runoff that is "absorbed" by this component of the landscape—only large, rare events generate flow that extends into large perennial streams. In addition, storm events may generate flow in some segments of the network, whereas others remain dry and hydrologically unconnected. In a sense, the network is variously integrated from storm to storm by a set of meteorologic and hydrologic variables that were largely irrelevant to integration at the level of stream segments (discussed earlier). Hydrologic models exist of stream network operation in terms of water flows (Tague and Band 2001; D'Odorico and Rigon 2003). We are suggesting that these transport functions be combined with order-specific processing rates to generate a holistic picture of material retention at the network level.

At Sycamore Creek, spatial and temporal patterns of surface runoff for a summer storm in the low-order network are illustrated in Figure 15.6a. Hydrographs show substantial change in the runoff signal from order to order and its complete loss (presumably by absorption in sediments) in some cases (fifth and seventh order). DOC, NH_4^+, and NO_3^- concentrations are quite high in transport (Figure 15.6b), and when flow stops, these materials stop as well and produce a legacy of materials that may jump-start biological processes with the advent of water associated with the next storm.

Potential denitrification in channel sediments reflects this legacy. Rates vary with order and sediment depth and indicate maximum activity that might occur in networks after storms (Welter 2004). The network-specific rates of denitrification will be a complex function of order-specific rates; mobilization and deposition of raw materials fueling denitrification; the geometry of the network, which will determine how and when water and materials are routed; and drying rate, which will limit the duration of biological activity. We developed a hot-spot index that takes into account the potential for gaseous loss of N and the time that each site is wet or active (Figure 15.7). According to this scheme, potential for N loss is highest in deep sediments of intermediate orders. Surface activity is depressed by comparison, probably due to more rapid drying and lower potential for denitrification, although transport-related legacies may also play a role. As we continue to move down the network into progressively larger channels, we will eventually reach perennial streams. Although the intermittent upland networks experience more discrete flow

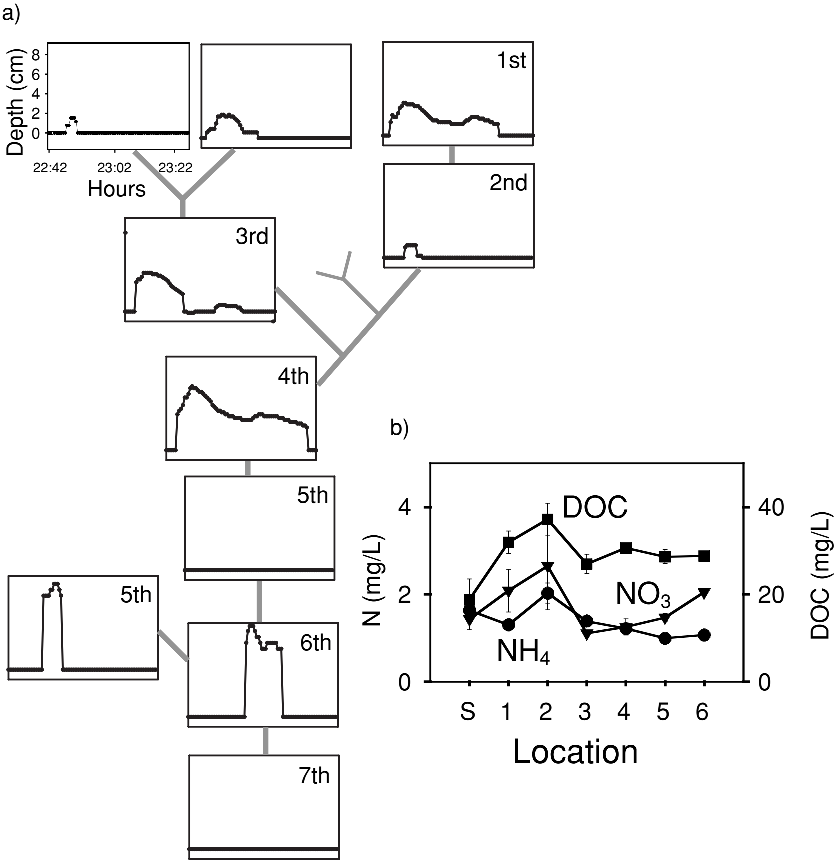

FIGURE 15.6. Temporal patterns in (a) surface runoff (depth in cm) and (b) runoff chemistry (NO_3-N, NH_4-N, and DOC mg/L) for a single 1-cm storm event in July 2000. (a) Runoff signal changes with location and from order to order in the network. X- and Y-axis scales are identical for all depth panels, indicating that runoff water is "absorbed" in some locations (fifth- and seventh-order channels). (b) Inorganic N and DOC concentrations (mg/L) also change with location (S indicates sheetflow collected directly from terrestrial hill slopes, and 1–7 represent different stream orders). Concentrations are quite high and represent a significant source of carbon and nitrogen for microbes in channel sediments. Thus, hot spots of microbial metabolism are likely to occur where flow is "absorbed" in the network. These materials may also produce a legacy of available resources that may jump-start biological processes with the advent of water associated with the next storm.

events, they dry quickly. Perennial stream-riparian systems remain wet or active most of the time. Further research is needed to determine how these different network positions compare in terms of their contribution to net N retention seasonally, annually, or on longer temporal scales.

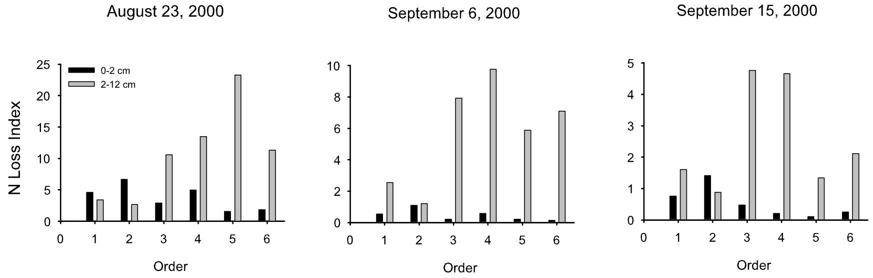

FIGURE 15.7. N loss hot-spot index values as a function of channel order and depth based on areal rates of potential denitrification and percent soil moisture after a single storm in August 2000. Potential denitrification rates were measured in the lab using a method similar to the assay of denitrification enzyme activity (DEA; Smith and Tiedje 1979). Samples were collected separately for soil moisture over time following the storm. Hot-spot index values were calculated by multiplying potential denitrification rates by percent soil moisture on each of three dates after the storm and used as an index of potential loss at each site. Upon wetting, index values closely resemble patterns in potential rates; however, *in situ* rates would likely vary depending on storm-specific delivery of DOC and NO_3^- to different locations in the network. As sediments begin to dry, index values shift across orders and depths, with higher rates maintained where sediments remain wet for the longest period of time. Index values change dramatically over time (note shift in Y-axis scale) as a result of drying. Hot spots for denitrification in intermittent networks turn on and off in the landscape in response to moisture and may shift spatially from storm to storm based on patterns in legacies of DOC and NO_3^- availability.

Some Overarching Issues

By discussing how the heterogeneous stream-riparian landscape is connected (integrated) by flowpath and how fluxes of the currency (nitrogen) changes as a function of connectivity in space and time, we can begin to understand how heterogeneity can influence ecosystem functioning (nutrient retention) in a manner not evident by simply adding up patch-specific processes. These interactions are of course complicated and ever changing, but several conceptual issues have emerged from our examination of the several subsystems of which streams are composed. We will summarize these general issues briefly below in hopes that they are general enough to apply widely to a range of landscapes, integrators, and currencies.

First, heterogeneity may apply to integrators as well as structural patches. In our studies of desert streams, we see that many patches are involved in net function, yet hydrologic connectivity also varies greatly, and in time of drought may be absent. Flood and drought can change the nature of the relationship among patches as much or more as changing the array of patches themselves. The nature of integration changes seasonally to be sure but may also respond to longer term schedules such as climate change or geologic cycles.

Second, in the fluvial system water is a primary integrator and is undoubtedly the major force connecting patches of the landscape. Other integrators may operate simultaneously in parallel, interacting networks. For example, in some fluvial systems, fish and invertebrate movements connect patches. Salmon migrations are famous for moving nutrients (Bilby et al. 1996; Helfield and Naiman 2001), but insect emergences may represent substantial terrestrial subsidies; for example, with the riparian zone via bird or spider predation (Sanzone et al. 2003). It would be interesting to compare the relative effects of multiple integrators such as hydrology and animal movements (and their interactions) in other landscapes that experience substantial migrations.

Material movement by spatial fluxes of animals and water can take many forms—as many as there are elements. Because the vector (water) moves many things, an opportunity exists to compare patch integration in the context of different currencies (chemical elements, diseases, or propagules, for example).

With chemical elements moving across the landscape in a single integrator, water, a lucrative opportunity for application of stoichiometric concepts and models (Sterner and Elser 2002) exists at the landscape level. Our example of N:P changes across sand bars is a simple one, and more work using multiple elements is needed. It is likely that landscape integrator interactions adjust nutrient ratios in such a way that shifting control will occur. Rather than thinking of control by a single key element, a better question is when, where, and under what conditions are elements X, Y, and Z key? The answer to this question will not only vary in space and time, but shifts in key elements will *determine* patterns in space and time.

There are a host of ecosystem functions that can be examined as well and no reason to think these will respond in parallel even to a single integrator and a single currency. In Sycamore Creek, for example, movement of nitrogen through sand bars by water results in an increase in nitrogen uptake without a concomitant increase in productivity (a second ecosystem function). The reason for this is cyanobacteria were able to grow just fine at inwelling edges using atmospheric nitrogen and thereby not retaining N in transport (Henry and Fisher 2003).

Connectivity among the patches that confer heterogeneity at any hierarchical level is itself heterogeneous in time and, as a result, movement of water and materials through the stream network is halting and saltatorial. The intermittent, uneven movement generates a spatial pattern that reflects this transport history and is therefore a legacy of events past. Legacies may provide insight into past episodic transport dynamics, but more importantly, they influence future ecosystem functioning when flow, and biological activity, resume. Because of the temporal separation of deposition and restored activity, functional lags are characteristics of this system.

Finally, our consideration of the interaction of flowpath and spatial heterogeneity suggest to us that patch shape and configuration may be crucial descriptors of heterogeneity when the integrator impinges on patches in a spatially oriented way. Not only would geometry of single patches relative to flow direction be relevant but also the sequence or order of patches linked by flow. Landscape ecology has provided a rich toolbox and lexicon for dealing with patch shape. With the addition of the concept of integration, can a science of shape be far behind?

Flow-Integrated Landscapes

Although networks are the true shape of streams, (as depicted in Figure 15.1), they are not planar, but three-dimensional (Figure 15.8). Taking this view, we can see that these are flowpath-integrated landscapes—including both the terrestrial and aquatic components of the watershed. From ridge tops to valley bottoms and within the stream network, all landscape elements are integrated by hydrology via flowpaths. Thus, in many ways, the separation between terrestrial and aquatic landscape elements is artificial.

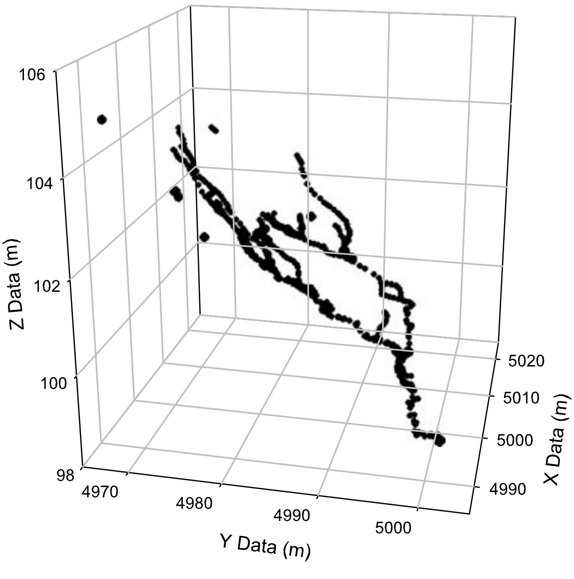

FIGURE 15.8. Three-dimensional image of network structure. Although stream ecologists focus on hydrologic integration of aquatic patches in the landscape, hydrology connects all landscape patches (both terrestrial and aquatic) via flowpaths. These elements lie along a terrestrial-aquatic continuum; varying in the directionality of flow, vertical *versus* horizontal. Resulting hydrologic flows likely result in nonlinear patch interactions in all catchments and motivate study of flow-integrated landscapes and a blurring of distinctions between terrestrial and aquatic elements.

These elements lie along a terrestrial-aquatic continuum; varying in the directionality of flow (vertical *vs.* horizontal) and time wet (and therefore biologically active). But all of these elements are linked via hydrology. This is an example of a common perspective borrowed from one field (stream ecology) and used to "capture" conceptually a larger whole. The influence of terrestrial-aquatic linkages on material transport and retention has been considered from both terrestrial (Peterjohn and Correll 1984; Giblin et al. 1991) and aquatic (Hynes 1975; McDowell and Likens 1988; Boyer et al. 2000) points of view.

Although terrestrial ecologists have primarily focused on vertical fluxes (e.g., percolation, soil development) and stream ecologists have historically emphasized horizontal fluxes, merging of the two approaches may be fruitful. To understand factors that influence material transport and retention in flow-integrated landscapes would require integration of vertical and horizontal flows, calculation of resulting vectors (vertical *vs.* horizontal), determination of residence times and process rates, dissection of flowpaths to determine control points, and assembly via modeling to determine higher level emergent effects of network structure and segment/node configuration. To do this we need to borrow from soil science, hydrology, biogeochemistry, fluvial dynamics, and geomorphology. We think that separation of aquatic and terrestrial ecology is counterproductive in this context and for these reasons.

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