The Network Dynamics Hypothesis: How Channel Networks Structure Riverine Habitats

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Hierarchical and branching river networks interact with dynamic watershed disturbances, such as fires, storms, and floods, to impose a spatial and temporal organization on the nonuniform distribution of riverine habitats, with consequences for biological diversity and productivity. Abrupt changes in water and sediment flux occur at channel confluences in river networks and trigger changes in channel and floodplain morphology. This observation, when taken in the context of a river network as a population of channels and their confluences, allows the development of testable predictions about how basin size, basin shape, drainage density, and network geometry interact to regulate the spatial distribution of physical diversity in channel and riparian attributes throughout a river basin. The spatial structure of river networks also regulates how stochastic watershed disturbances influence the morphology and ages of fluvial features found at confluences.

Keywords: river ecology, landscape ecology, fluvial geomorphology, river networks, disturbance

Principles of fluvial geomorphology have guided the development of much of riverine ecology over the last half-century. A prominent example is the influential river continuum concept (RCC; Vannote et al. 1980). Based on early principles of fluvial geomorphology (e.g., Leopold et al. 1964), the RCC emphasizes spatially and temporally averaged downstream changes in channel morphology over many orders of magnitude. It predicts gradual adjustments of biota and ecosystem processes in rivers in accordance with the geomorphic perspective of gradual downstream changes in hydrologic and geomorphic properties.

The linear perspective embodied in the RCC has dominated river ecology over the last 20 years (Fisher 1997), although downstream interruptions in channel and valley morphology, caused by alternating canyons and floodplains, tributary confluences, and landslides, have long been observed. Some have viewed these interruptions simply as adjustments to the original RCC (e.g., Bruns et al. 1984, Minshall et al. 1985), whereas others have posited that they serve as the basis for a new view of a river as a "discontinuum" (e.g., Perry and Schaeffer 1987, Townsend 1989, Montgomery 1999, Rice et al. 2001). In essence, river discontinuum perspectives highlight the nonuniform or patchy distribution of habitats and therefore emphasize habitat heterogeneity, expressed at the scale of meters to kilometers. Such heterogeneity also arises because of the human perception of scale, in which fluvial landforms are hierarchically organized from valley segments

to stream bed particles (Frissell et al. 1986). Consequently, the idea of patchy and multiscale habitat formation and its related heterogeneity has imbued much current thinking in riverine ecology (Frissell et al. 1986, Naiman et al. 1988, Townsend 1996, Poff 1997).

Riverine ecology has also recognized the importance of physical disturbance (e.g., storms, fires, and floods) in dynamically creating and maintaining certain attributes of habitats and thus in influencing ecosystem function (e.g., Resh et al. 1988, Swanson et al. 1988, Townsend 1989, Reeves et al. 1995, Poff et al. 1997). Just as habitat patches create discontinuities in space, disturbances create discontinuities in time. Concepts emphasizing disturbance or watershed

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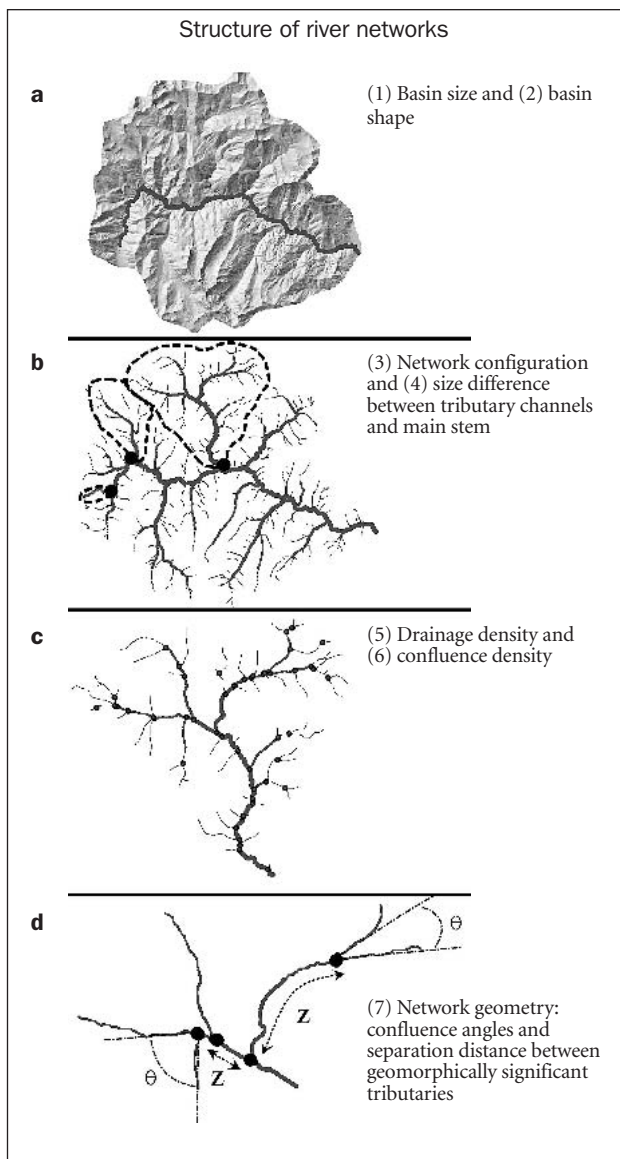
Structure of river networks

a (1) Basin size and (2) basin shape

b (3) Network configuration and (4) size difference between tributary channels and main stem

c (5) Drainage density and (6) confluence density

d (7) Network geometry: confluence angles and separation distance between geomorphically significant tributaries

Figure 1. Seven structural indexes of river networks are considered in this article. (a) Basin size is drainage area, and basin shape is determined by dividing the area of the river basin by the square of the length of the main stem. (b) Confluence effects depend on the overall network pattern and on the size difference between confluent channels (i.e., the size ratio of the tributary basin to the main stem basin upstream of the confluence). (c) Drainage density and confluence density are related measures; drainage density is the total length of channels per unit area of the basin, while confluence density is the number of confluences per unit channel length or basin area. Channel sizes in a basin are distributed according to a power law. (d) Local network geometry (in the vicinity of individual confluences) depends on the tributary–main stem area ratio, on the distance between confluences (Z), and on the confluence intersection angle (θ). Black dots in panels b, c, and d represent tributary confluences.

dynamics are generally applied in the context of a particular location within a watershed. However, recent advances in understanding watershed disturbance regimes indicate how disturbance frequency and magnitude are organized by hierarchical and branching river networks (Benda and Dunne 1997a, 1997b, Gomi et al. 2002).

In sum, although the RCC's predictions of gradual downstream change in river attributes and associated biological processes are valid over orders of magnitude in river size, three other themes have arisen in riverine ecology over the past two decades in the effort to address how deviations arise from the expected mean state in physical attributes along a river profile. These themes are (1) patchiness or heterogeneity, (2) stochastic disturbance, and (3) hierarchical scaling. This suite of concepts has been used to argue that riverine ecology should be guided by principles of landscape ecology, a discipline that incorporates a similar set of ideas (Schlosser 1991). Such a landscape view of rivers has led to the idea of "riverscapes" (Ward et al. 2002) and hence to an emphasis on the importance of studying riverine habitats and their patchiness over multikilometer scales (e.g., Fausch et al. 2002, Wiens 2002).

In a similar vein, a conceptual framework integrating heterogeneity, disturbance, and hierarchical scaling has been advocated for general ecology under the title of "hierarchical patch dynamics" (Wu and Loucks 1995), and this concept may apply well to riverine ecology (Townsend 1989, Poole 2002). While both hierarchical patch dynamics and the landscape view of rivers hold promise for advancing the field of riverine ecology, they are presently limited in doing so because they lack a physical basis for understanding or predicting the morphological implications of rivers as networks (as opposed to "linear features," *sensu* Fisher [1997]) and for understanding how stochastic watershed disturbances are translated into patterns of physical heterogeneity throughout the river network.

The purpose of this article is to develop a geomorphic framework in support of recent advances in river ecology. To create this framework, which we call the network dynamics hypothesis, we developed testable predictions about how the spatial arrangement of tributaries in a river network interacts with stochastic watershed processes to influence spatiotemporal patterns of habitat heterogeneity. We begin with a general review of how tributary confluences modify channel morphology. Then we describe how tributary confluence effects vary in terms of the specific attributes of a network's structure, including basin size, basin shape, network pattern, size difference between confluent channels, drainage density, confluence density, local network geometry, and the power law of stream sizes (figure 1). Next, we describe how stochastic watershed disturbances such as floods, fire, and storms impose temporal heterogeneity on confluence effects, but in a predictable fashion that reflects the controls exerted by the underlying network structure. Finally, we consider how the general principles developed in our hypothesis could

vance the coupled disciplines of geomorphology and riverine biology.

Effects of tributary confluences on channel and valley morphology

By definition, a tributary is the smaller of two intersecting channels, and the larger is the main stem. Strictly speaking, a tributary junction, or confluence, is defined as the point where two different streams meet. In the broader definition used in this article, a tributary junction is the valley floor environment influenced by tributaries and may include alluvial fans, terraces, secondary channels, and wider floodplains. The numerous bifurcations and confluences of distributaries in braided channel systems are not covered here.

Three main types of processes are responsible for transporting sediment and organic material down tributaries to confluences with the main stem. Debris flows transport an unsorted mixture of sediment (including boulders and logs) and often create erosion-resistant deposits; normal runoff floods transport bed load and suspended load and create stratified alluvial deposits; and flash floods transport extremely high sediment loads and create deposits intermediate between debris flows and runoff floods. These sediment transport processes often create depositional fans where tributary channels enter lower-gradient and wider channels or valleys (Bull 1977).

The interaction of two independent sediment transport regimes at channel junctions can produce dramatic changes on the receiving channel and valley floor (see table 1 for a listing of these effects). Morphological effects at confluences, including formation of fans, may be transient or persistent, depending on the rate at which organic material and sediment are transported to tributary junctions and moved by receiving channels. Sediment deposits that form at junctions can impose a topographic impediment to the main channel, often locally constricting valley width and displacing the main channel across the valley floor (figure 2). These topographic effects induce certain morphologic responses in main stem channels, such as a localized flattening of the channel gradient upstream and a corresponding steepening of the gradient downstream (figure 2). Gradient-induced longitudinal variations in sediment transport rate in the vicinity of junctions cause upstream reductions in substrate size, increases in channel meandering, and increases in floodplain and terrace width. These changes are offset by other tendencies on the

Tributary confluence effects

North Fork Boise River

Upstream (zone of interference)

Tributary influx of sediment to alluvial fan

Alluvial fan

Downstream (zone of mixing)

Longitudinal profile

Elevation

Distance

Zone of interference   Tributary   Zone of mixing

Morphological consequences

- Lower gradient
- Wider channel/floodplain
- Increased bank erosion
- Increased wood recruitment
- Finer substrates
- Greater lateral connectivity
- Higher disturbance magnitude

- Higher gradient
- Larger substrate sizes
- Deeper pools
- More bars
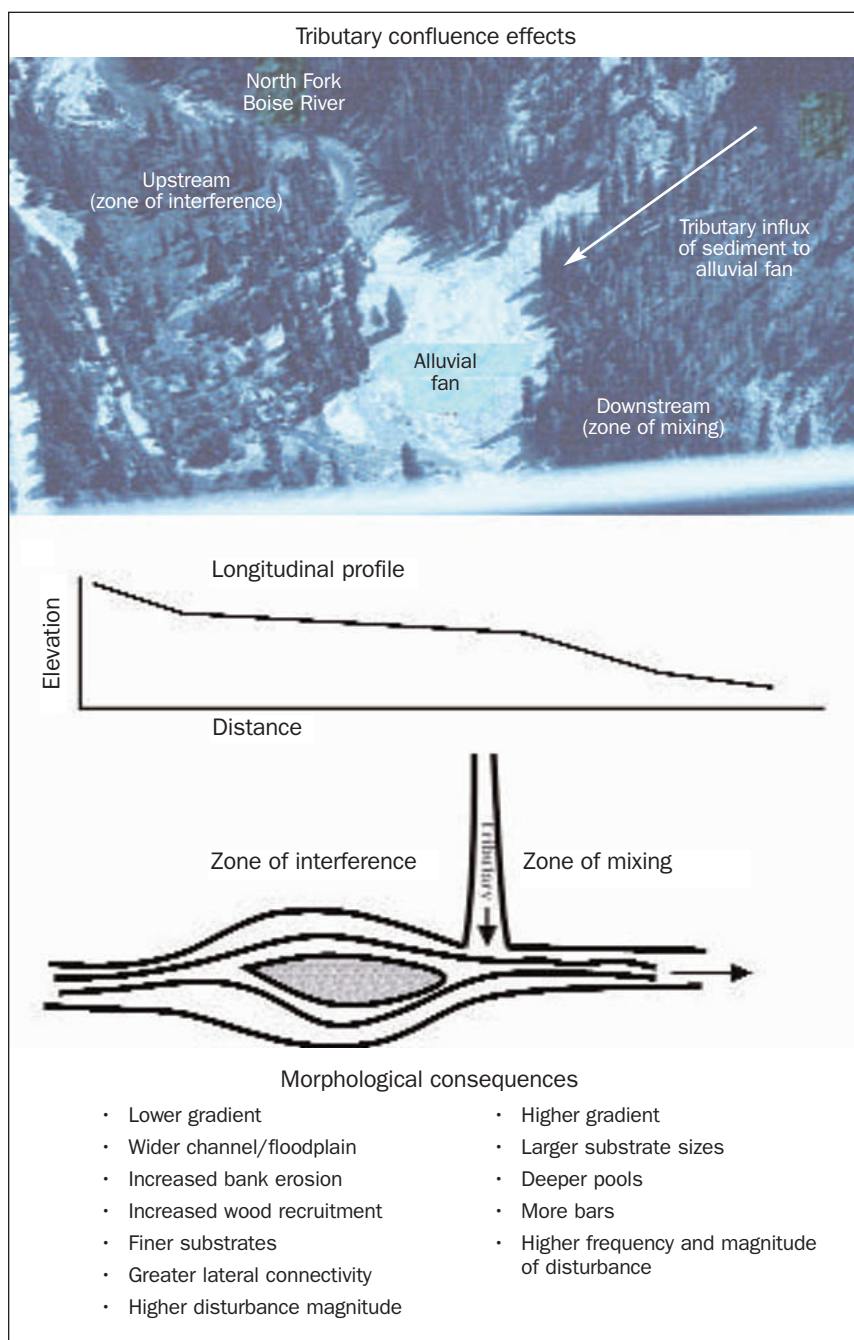- Higher frequency and magnitude of disturbance

Figure 2. An alluvial fan, enlarged after a fire, triggers tributary junction effects in the North Fork Boise River (320-square-kilometer drainage area). Junction effects include expanded floodplain and terrace formation, increased channel meandering and side channels upstream of the fan, and channel steepening downstream (Benda et al. 2003b). Confluence effects include upstream interference in which a lower gradient and wider channel cause a reduction in the transport of sediment and wood and a corresponding increase in channel changes. "Mixing" effects downstream of the confluence, including a steeper channel gradient and a higher frequency and magnitude of disturbance, arise from the abrupt introduction of sediment and wood from the tributary. Photograph: Steven Toth.

Table 1. Fourteen studies documenting tributary confluence effects in 19 nonregulated streams and rivers across the western United States and Canada.

Location	Climatic region	Type of sediment transport	Contributing stream area (km²)	Receiving stream area (km²)	Morphological effects	Source
Sekiu, Olympic Mountains, Washington	Humid	Debris flow	0.02 to 0.73	0.67 to 4.2	a, b, d, g, k	Benda et al. 2003a
Ash Creek, Arizona	Arid	Flash flood	0.42	9.8	d, f	Wohl and Pearthree 1991
Queen Charlotte Islands, British Columbia	Humid	Debris flow	0.11 to 5.6	0.3 to 12.0	k	Hogan et al. 1998
Matheny and Sitkum, Olympic Mountains, Washington	Humid	Debris flow	0.37	20.3	a, b, d, g, j, k	Benda et al. 2003a
Coast Range, Oregon	Humid	Debris flow	0.08 to 0.27	0.8 to 30	a, b, c, d, e, f, g, h, j, k, l	Everest and Meehan 1981
Sheep Creek, Idaho	Semiarid	Alluvial	26.6	64.6	a, b, c, d, g	Benda et al. 2003b
Oregon Cascades	Humid	Debris flow	0.11 to 3.0	51 to 71	e, f, g	Grant and Swanson 1995
Crooked River, Idaho	Semiarid	Alluvial	3.4	219	a, b, c, d, g	Benda et al. 2003b
Bear Creek, Colorado	Semiarid	Flash flood	5.9 to 23.9	193 to 407	e	Grimm et al. 1995
North Fork Boise River, Idaho	Semiarid	Alluvial	0.6 to 29	322 to 461	a, b, c, d, f, g, h	Benda et al. 2003b
Wenaha River, Oregon	Semiarid	Alluvial	18 to 71	446 to 516	f, g	Baxter 2002
Snoqualmie River, Washington	Humid	Alluvial	85 to 750	712 to 1794	a, b, c, d	Booth et al. 1991
Pine and Sukunka Rivers, British Columbia	Semiarid	Alluvial	23 to 203	1579 to 2145	d	Rice et al. 2001
South Fork Payette River, Idaho	Semiarid	Flash flood	0.55	2470	e	Meyer and Pierce 2003
Bella Coola River, British Columbia	Humid	Alluvial	12.8 to 285	4779 to 5421	m	Church 1983
Middle Fork Salmon River, Idaho	Semiarid	Debris flow/flash flood	2.5 to 295	1176 to 7096	a, b, e	Meyer and Leidecker 1999
Grand Ronde, Oregon	Semiarid	Alluvial	764 to 1342	6953 to 7781	f, g	Baxter 2002
Snake River, Oregon	Semiarid	Alluvial	9137	240,765	g, f	Meyer and Pierce 2003
Colorado River (before dam), Colorado	Arid	Debris flow/flash flood	14.3 to 6076	280,000 to 386,800	a, d, e, i	Melis et al. 1995

a, gradient steepening; b, gradient lowering; c, upstream sediment deposition; d, changing substrate size; e, boulders and rapids; f, terraces; g, floodplains; h, side channels; i, midchannel bars; j, ponds; k, logjams; l, meanders; m, channel instability.

Note: Sites are arrayed according to increasing drainage area of the main stem (in square kilometers). The studies indicate the dominant type of sediment transport, the drainage areas of tributaries and main stems, and the type of morphological effects at confluences indicated by the authors.

downstream side of the junction, including coarser substrates and increases in channel width, pool depth, and occurrence of bars. The same general classes of channel changes occur at confluences regardless of their location in the river network (see table 1), although certain types of changes, such as boulder accumulations leading to rapids, occur predominantly near debris flow or flash flood deposits. The morphological conditions near channel junctions differ from those in reaches located upstream or downstream; confluences are agents of habitat formation and increased morphological heterogeneity (figure 2; Rice et al. 2001, Benda et al. 2003a). In this article, we concentrate on the morphological effects at junctions linked to tributary sources of sediment and wood, although our analysis of the influences of river network geometry should also apply to more flow-related changes in morphol-

ogy at junctions in less erosion-prone landscapes (e.g., Best 1986, Rhoads 1987).

Effects of river networks on the structure of riverine habitats

The physical structure of river networks can be defined by basin size, basin shape, network pattern, size difference between confluent channels, the power law of stream sizes (e.g., Horton 1945), drainage density and confluence density, and local network geometry (figure 1). Our predictions about how river network structure influences spatial patterns of confluence-related morphology (box 1) apply to a range of channel changes (e.g., changes in substrate size, channel width, or extent of floodplains and terraces), although morphological effects can be broadly stratified according to

Box 1. The influence of river network structure on spatial patterns of confluence-related morphology

Testable predictions from the network dynamics hypothesis are listed below. The predictions apply to a range of morphological changes at confluences (including morphological heterogeneity), although they can be broadly stratified according to upstream and downstream position relative to confluences (see, e.g., figure 2). Presently, it is not feasible to make quantitative predictions of channel changes at confluences because of the complexity of channel environments (Rhoads 1987). Confluences that have identifiable morphological effects (including those confluences listed in table 1) are referred to as "geomorphically significant confluences."

Predictions related to network structure

- The likelihood of confluence effects increases with the ratio of tributary to main stem sizes.

- Heart-shaped and pear-shaped basins containing dendritic networks favor increasing tributary size and hence confluence effects downstream, compared with rectangular basins containing trellis or parallel networks, which do not.

- The separation distance between geomorphically significant junctions (and their morphological effects) increases downstream with increasing basin size, particularly in dendritic networks.

- As basin size increases, the channel length and area affected by individual confluence-related channel and valley morphological modifications will increase.

- Closely spaced tributaries will yield valley segments of higher physical heterogeneity, compared with valley segments that do not contain closely spaced geomorphically significant confluences.

- Basins with higher drainage density and corresponding higher junction density will have a higher degree of morphological heterogeneity. Correspondingly, basins of high topographic roughness, in part related to higher drainage density, should contain a higher degree of riverine heterogeneity.

Predictions related to watershed disturbances or dynamics

- Basins with higher punctuated sediment supply and transport will be characterized by greater confluence effects.

- Channelized disturbances (i.e., floods and accelerated sediment and wood supply) will have greater frequency and magnitude proximal to and immediately downstream of confluences, leading to greater physical heterogeneity, including the age distribution of fluvial landforms.

- Channelized disturbances will be magnified immediately upstream of geomorphically significant confluences, leading to greater physical heterogeneity, including the age distribution of fluvial landforms.

- In sufficiently large basins (approximately 102 km^2), the age distribution of confluence-related landforms (i.e., fans, terraces, floodplains) will be skewed toward older geomorphic features in headwaters and toward younger features in downstream portions of the basin.

- Physical heterogeneity (i.e., diversity of forms and ages of channels, floodplains, terraces, and logjams) will be concentrated in certain parts of networks.

upstream and downstream position relative to confluences (e.g., figure 2). We also predict local changes in heterogeneity at confluences, which will usually increase. Heterogeneity is defined by the type, form, and age distribution of fluvial landforms. It is not yet possible to develop quantitative predictions about specific morphological changes at confluences because of the low resolution of data (e.g., table 1) and the complex nature of riverine environments (Rhoads 1987).

The role of basin size. Consistent flow-related morphological changes (i.e., in channel width and depth) occur at junctions where the ratio between tributary size and main stem size approaches 0.6 or 0.7 (Rhoads 1987). We postulate that morphological effects caused by punctuated inputs of sediment and wood at confluences will also scale to the size of the tributary relative to the main stem. We anticipate this result because larger basins typically produce larger quantities of sediment, and because larger tributaries generally have larger fans associated with them (Bull 1977). Moreover, larger and more powerful rivers are more effective at removing tributary inputs of sediment (Benda et al. 2003a).

To evaluate this expectation, we analyzed the results of 14 published field studies that document a range of confluence effects in 19 streams and rivers, caused by the abrupt introduction of sediment and wood (see table 1 for a listing of these
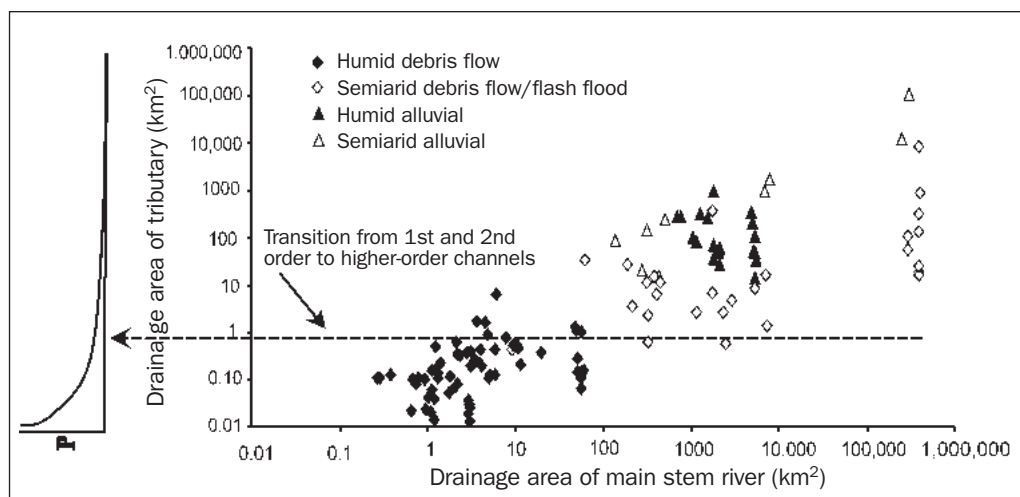
Figure 3. A comparison between tributary basin area and main stem drainage area (in square kilometers), for 168 tributaries where confluence effects (i.e., geomorphically significant confluences) have been documented, reveals that larger main stem rivers require larger tributaries in order to experience confluence effects (table 1; Benda et al. 2004). The dashed line represents the approximate tributary drainage threshold for the first- and second-order streams that comprise the vast majority of stream sizes and for their confluences in networks. Power law distribution of channel (confluence) sizes is shown on the left side of the figure; P refers to the proportion of all channels of a given drainage area.

effects). We refer to confluences that have observable morphological effects as "geomorphically significant." Together, these studies describe 168 junctions along 560 kilometers (km) of river, spanning 7 orders of magnitude in drainage area in the western United States and Canada (see Benda et al. [2004] for a more detailed analysis). These data reveal that as the size of the main stem increases, geomorphically significant confluences are associated with increasingly larger tributaries (figure 3). For example, debris flows that originate from small basins (up to 1 km^2 in drainage area) create tributary-junction effects in basins of only 1 to 50 km^2. By contrast, tributary-junction effects in larger rivers (1000 to 300,000 km^2) are associated with larger tributaries (10 to 10,000 km^2).

The data in figure 3 also reveal a threshold below which tributary basins less than approximately 1 km^2 do not affect main stem rivers larger than approximately 50 km^2. This is significant because it indicates how the "law of stream numbers" (Horton 1945), the universal power law regarding the distribution of channel sizes (and, by analogy, of the confluences linked to those channels), constrains confluence effects at the scale of entire networks. In humid landscapes, for example, the vast majority (80% to 90%) of tributary basins are first or second order, with less than 1 km^2 in drainage area (Benda and Dunne 1997a). On the basis of the threshold identified in figure 3, only 10% to 20% of tributary confluences (i.e., those of third order or higher) are available to significantly affect main stem rivers of a size greater than approximately 50 km^2. This finding has important ramifications for the increased downstream spacing of confluence effects as the size of the main stem increases.

The variability of the data in figure 3 is probably due to factors such as basin geology (e.g., the durability and size distribution of sediment), sediment transport processes (e.g., debris flows and flash floods that transport boulders and are more likely to cause confluence effects), and local valley width (e.g., wide valleys that limit fan formation and the associated confluence effects). Temporal variation in the history of storms, fires, and floods that create or rejuvenate confluence effects should also cause the waxing and waning of confluence effects. A more detailed analysis of the data in figure 3 allows for probabilistic predictions of confluence effects (Benda et al. 2004). For example, in humid environments, a range of 0.6 to 0.9 for the probability of a confluence effect corresponds to a range of 0.04 to 0.8 for tributary–main stem drainage area ratios.

The role of network pattern and basin shape. The scaling relationship between tributaries and main stem channels (figure 3) allows us to consider how the factors that control the spatial distribution of tributary sizes in river networks influence spatial patterns of confluence-related morphology and heterogeneity. Downstream trends in junction effects are influenced by network patterns and hence by drainage basin shape. Two common types of network patterns are dendritic and trellis networks. Dendritic networks, which resemble the hierarchical branching pattern of a tree, often form in homogeneous and gently sloped geologic beds and create heart-shaped or pear-shaped basins. In contrast, trellis networks, characterized by small tributaries intersecting main stem channels, are often associated with elongate landforms in dipped and folded sedimentary rocks or in areas of parallel fractures; they create narrow, rectangular basins.

The spatial configuration of tributaries within a watershed changes the likelihood of confluence effects downstream in river networks. Since larger tributaries are required to create geomorphic effects as the size of the main stem increases (e.g., figure 3), dendritic networks in heart-shaped or pear-shaped basins should promote confluence effects throughout the watershed (figure 4; see Benda et al. [2004] for more details). These effects occur because increasing the basin width downstream promotes the coalescing of hierarchically branched channels, resulting in larger tributaries forming

downstream. In contrast, narrow, rectangular basins containing trellis networks lack the formation of larger tributaries and therefore discourage confluence effects as main stem size increases. Consequently, network configuration related to basin shape should strongly influence the downstream sequence of confluence effects (figure 4; see also the testable predictions in box 1).

In addition to dendritic and trellis networks, other network types include parallel networks, which form in conjunction with parallel landforms, and rectangular networks, which form where numerous faults and joints converge at high angles. Region-specific types of geology and hillslope topography should influence network patterns and hence the spatial distribution of confluence-related channel morphology and associated physical heterogeneity. For example, the young and porous rocks of the high Cascade Mountains in Oregon are characterized by trellis networks, while older and less permeable rocks nearby exhibit dendritic networks (Grant 1997).

Drainage density and confluence density. The cumulative effect of confluences within a basin should be proportional to the total number of geomorphically significant channel confluences. This number is related to drainage density (defined as channel length per unit watershed area) and to network shape, which either promotes or inhibits the occurrence of confluent channels (see figure 5). The corresponding confluence density (the number of geomorphically significant confluences, per unit area or per unit channel length) should provide a simple measure of the net morphological effect of confluences in rivers (box 1). Drainage densities in humid to semiarid landscapes range from 2 to 12 km channel length per square kilometer watershed area, primarily reflecting variations in precipitation, landscape age, and bedrock porosity (Grant 1997). This large range in drainage density translates to a correspondingly large range in the density of channel confluences, with implications for the degree of channel heterogeneity found in different landscapes (figure 5).

Local network geometry. A river's geologic structure and tectonic and erosional history create specific patterns of intersecting tributaries over kilometer scales. Local network geometry can be used to describe the kilometer-scale variation of tributary effects in rivers, including the longitudinal sequence of tributary–main stem size ratios (figures 3, 4), tributary intersection angles, and distance between geomorphically significant confluences (figure 1d). The tributary–main stem intersection angle is the upstream angle formed at a confluence. Intersection angles are almost always acute, and as they become less so and approach 90°, the likelihood of a geomorphic effect at a confluence increases. For instance, in a series of river studies and in flume experiments, Mosley (1976) and Best (1986) showed how bar size, bar location, and scour depth vary with confluence angle. Lateral bars are more likely to form at acute angles; scour depth, by contrast, increases with increasing confluence angle and approaches an asymptote at
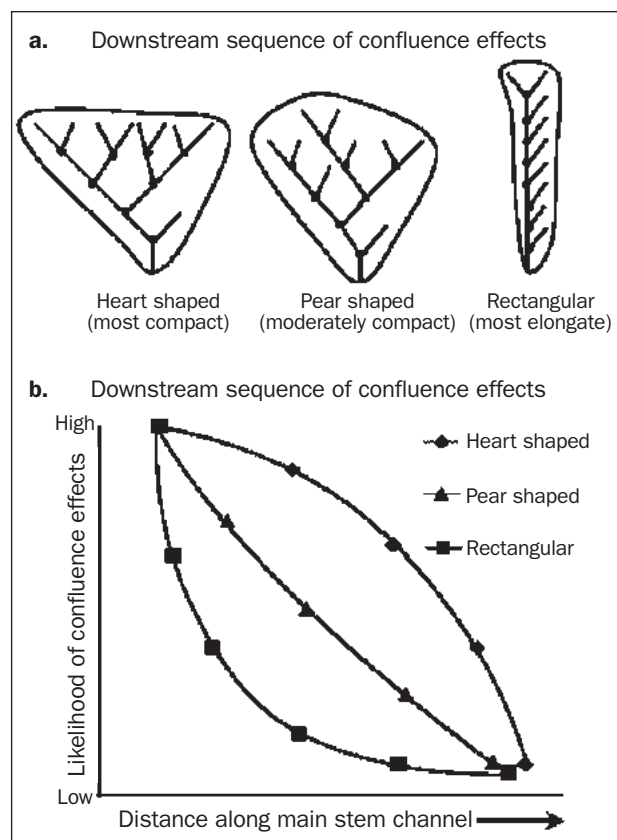

Figure 4. (a) Network patterns and the associated basin shapes affect the downstream sequence of confluence effects. Common network patterns include dendritic networks, within heart-shaped and pear-shaped basins, and trellis networks, within narrow, rectangular basins. (b) The anticipated downstream sequence of confluence effects (ranging from high to low likelihood) is based on the size of the tributaries relative to the main stems. Dendritic networks in heart-shaped basins promote the greatest likelihood of confluence effects downstream, while trellis networks in rectangular basins promote the fewest effects downstream. Modified from Benda and colleagues (2004).

angles approaching 90°. Moreover, in headwater areas, confluence angles greater than 70° encourage debris flow deposition and consequent junction effects (table 1), while deposition is discouraged at junctions with more acute angles (Benda and Cundy 1990).

Network geometry also describes the distance separating geomorphically significant confluences. For example, a concentration of large tributaries in a central, sediment-producing region is characteristic of watersheds along mountain fronts abutting depositional plains (figure 6a). Alternatively, tributaries that are separated by canyons can lead to clumped distributions of geomorphically significant tributaries and associated physical heterogeneity (figure 6b). Large tributary junctions that are closely spaced may have con-

fluence effects that overlap, particularly during watershed disturbances such as floods and concentrated basin erosion. Confluence effects may also be less pronounced in wide valley floors, where fans are isolated from the main stem by broad terraces or floodplains.

Scaling properties of confluence effects. The finding that larger tributaries are required in order to affect the morphology of larger rivers reveals two scaling effects on habitat patches
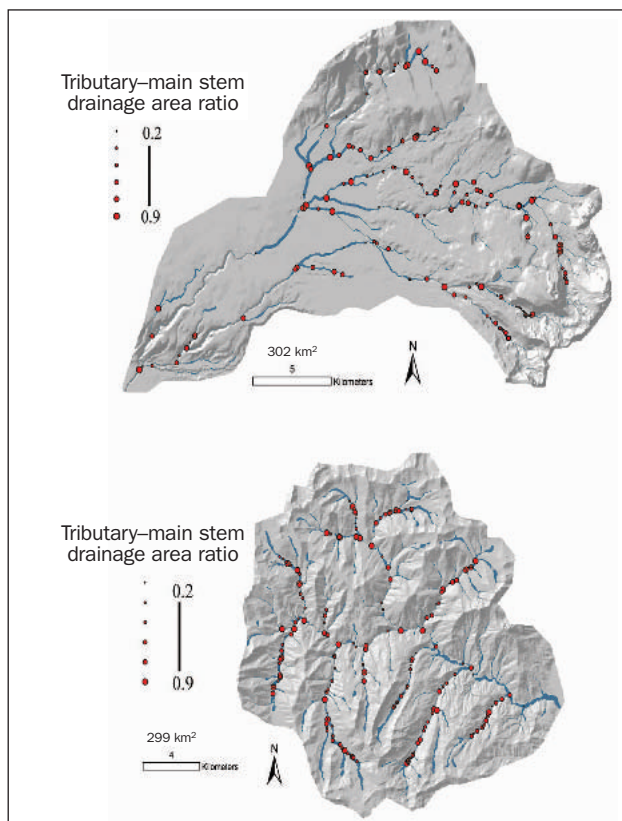

Figure 5. Two basins in northern California illustrate variation in confluence densities. Black dots represent confluences, with tributary–main stem ratios indicated by dot size. A watershed formed in relatively young and homogeneous lava flows (top) has a drainage density of 3 kilometers (km) channel length per square kilometer drainage area and a corresponding confluence density of 4.7 junctions per square kilometer. A watershed located in the older and geologically heterogeneous terrain (bottom) has a drainage density of 5 km channel length per square kilometer and a corresponding confluence density of 12 junctions per square kilometer. On the basis of the difference in confluence density, the second watershed is predicted to have higher confluence-related habitat heterogeneity (box 1). The probability of confluence effects depends on the increasing size ratio of tributary to main stem drainage area, as indicated by the size of the dots (Benda et al. 2004). Estimation of drainage density or confluence density should be sensitive to map scale and to the method of depicting channel networks.

that develop near confluences. First, geomorphically significant confluences should be separated by increasing distances downstream in watersheds where tributary basins downstream increase in size (e.g., dendritic networks in pear-shaped and heart-shaped basins; figure 4, box 1). This increasing separation occurs because tributary length is related to tributary drainage area (Hack 1957), and thus the length and width of a basin increase with increasing tributary length. This spacing pattern is reflected in the field data (figure 7). In the upper portions of humid drainage basins, morphological effects are spaced on average hundreds of meters apart (Benda 1990, Hogan et al. 1998, Benda et al. 2003a), reflecting the spacing of low-order tributaries. By contrast, in larger basins (up to 300,000 km^2), the distances separating junction effects are on the order of several kilometers to tens of kilometers (Baxter 2002, Benda et al. 2003b).
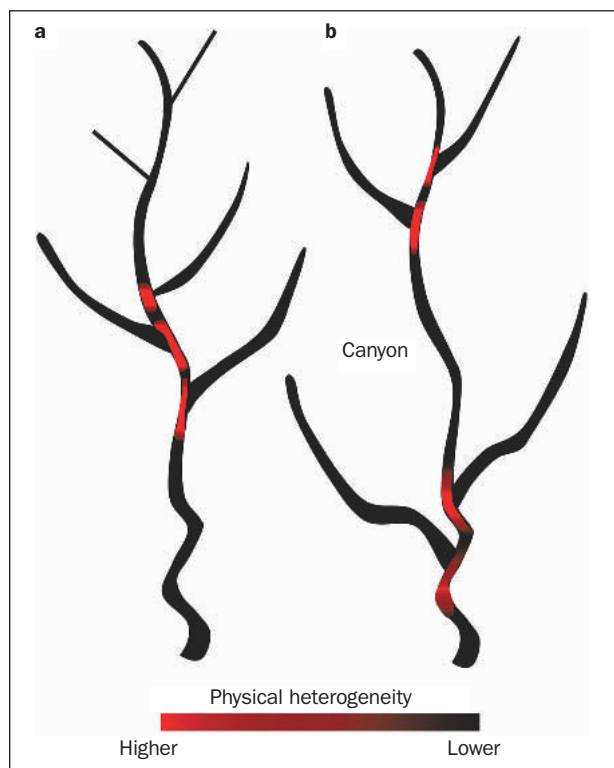

Figure 6. Local network geometry (kilometer scale) varies in response to the size, spacing, and confluence angles of intersecting tributaries, which reflect underlying geologic structure, topography, and erosion history. Different local geometries are expected to lead to different patterns of physical heterogeneity, linked to tributary confluences. (a) With a number of large tributaries near the center of the network, confluence-related heterogeneity is concentrated in a central, sediment-producing region. This pattern is characteristic of watersheds located along mountain fronts and abutting depositional plains. (b) When major tributaries are separated by canyons, the associated areas of physical heterogeneity are divided as well.
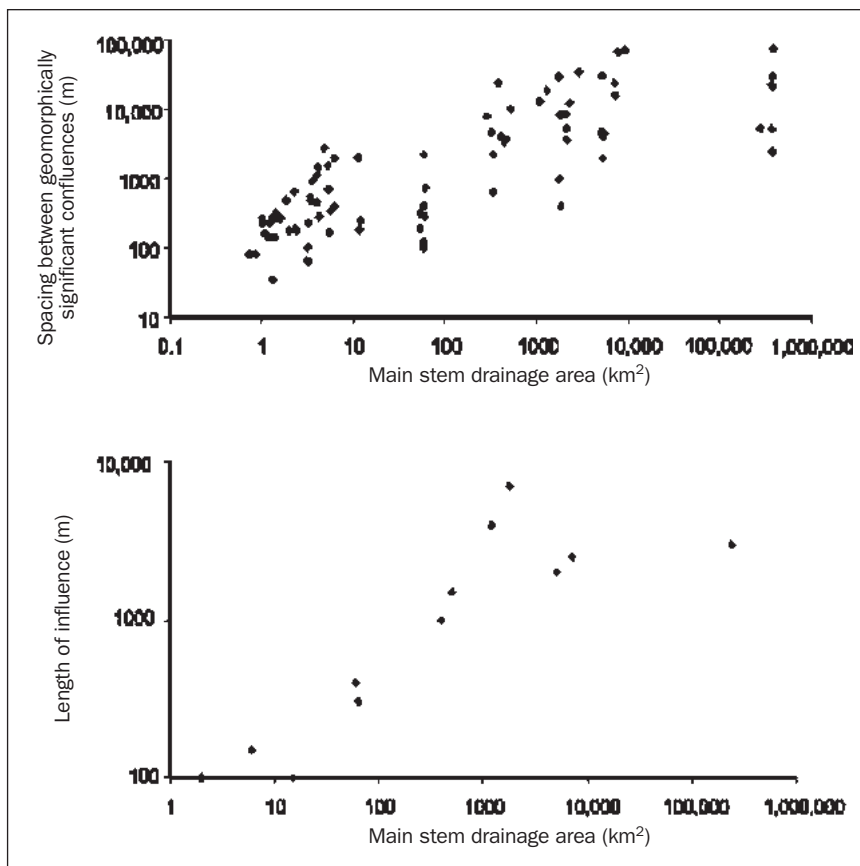
Figure 7. Confluence effects in rivers (e.g., changes in substrate, floodplains, or channel morphology) reveal two scaling properties. First, the distance separating geomorphically significant confluences (shown in meters) increases downstream, particularly in dendritic networks (top). Second, the length of altered habitat patches associated with geomorphically significant confluences (also in meters) increases downstream (bottom).

The second scaling property of confluence-related morphology is that the size of habitat patches associated with tributaries increases downstream (figure 7). Although the data are sparse, the length of channels affected by confluences ranges from tens or a few hundreds of meters (in basins less than approximately 100 km^2) to several kilometers (in basins between approximately 1000 and 300,000 km^2). We expect the size of habitat patches to increase farther downstream because the channel gradient declines with increasing river size; therefore, any vertical obstruction in a channel that backs up sediment (e.g., fans, logjams, boulders) should influence a channel distance upstream at least equivalent to the obstruction height divided by the tangent of the underlying stream gradient.

Interaction of river networks with stochastic watershed processes

A river network can be thought of as the landscape template within which climatically induced stochastic fluctuations in the supply and transport of water, sediment, and organic material occur. The structure of a river network (basin size, shape, network configuration, and so on; figure 1) can be used to help understand the role of stochastic watershed processes in shaping riverine environments.

Disturbance. The role of tributary confluences on longitudinal patterns of riverine heterogeneity, and the dependence of this heterogeneity on basin scale, basin shape, network pattern, drainage density, and network geometry, can be framed as a general set of testable predictions (see box 1). The spatial configuration of a network thus provides a template for organizing the transport and deposition of sediment, wood, and water through a watershed, but the supply and transport of material that creates confluence effects varies dynamically over time because of climate-driven events (storms, floods, and fires). The watershed disturbance regime (Miller et al. 2003)—the frequency, magnitude, and spatial extent of episodic climatic and geomorphic processes—can vary within and among watersheds and thus contribute to variation in heterogeneity at confluences, including the waxing and waning of effects over time.

Moderate to large disturbance-driven, landscape-scale fluctuations in the supply and storage of in-channel sediment and organic material create many of the morphological changes observed at confluences. For example, the fluctuating supply of sediment storage at confluences creates fans, floodplains, terraces, logjams, secondary channels, and fans (table 1; Small 1973, Benda et al. 2003b). The episodic nature of sediment-related disturbances creates the form and age mosaic of the erosional and depositional landforms characteristic of valley floors, ultimately contributing to physical heterogeneity and potentially to biological diversity and increased productivity (Swanson et al. 1988). Although biological recovery processes, such as vegetation succession, can also influence patterns of physical heterogeneity in the channel and valley floor (Gregory et al. 1991), that topic is beyond the scope of this article. For more comprehensive discussions of the role of disturbances in riverine environments, see Resh and colleagues (1988), Reeves and colleagues (1995), Poff and colleagues (1997), and Nakamura and colleagues (2000).

Amplification of disturbances at confluences. The channel disturbance regime can be altered at tributary confluences. First, tributaries represent abrupt increases in the supply of water, sediment, and wood, and therefore channel responses related to those inputs should have a higher frequency and magnitude near or immediately downstream of confluences.
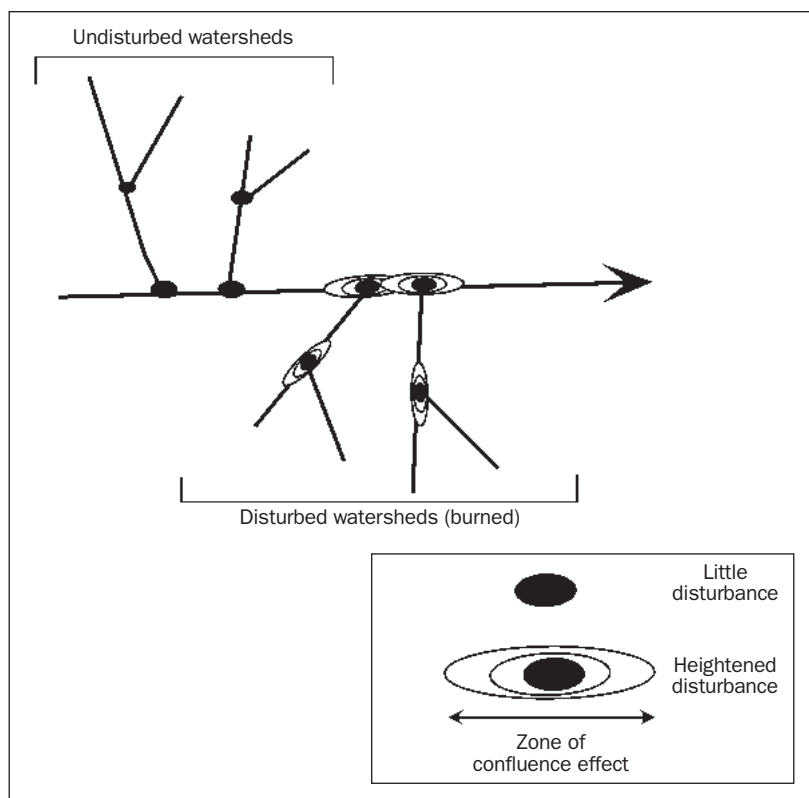
Figure 8. Channel disturbances (from fires, storms, or floods) are amplified at confluences, because tributary basins are point sources of water, sediment, and wood, and because the topographic knick points created by confluences (e.g., shallowing of stream gradient) can interfere with the transport of sediment and wood from upstream. (Black dots represent tributary confluences.) Because of the timing of disturbances, confluence effects expand and contract over time, and these effects could overlap with one another during periods of heightened watershed disturbance.

Second, reductions in channel gradient, and expansion of valley floors upstream of confluences (e.g., figure 2), can interfere with the downstream and fluctuating transport of sediment and wood. Where increased sediment and wood storage occurs upstream of confluences that lead to wider and lower-gradient (i.e., more responsive) channels, the magnitude of flow-related disturbances can increase. These interactions have been observed in the field and predicted by simulation models (Benda and Dunne 1997a). For example, Church (1983) noted that the highest rates of channel meandering occurred in the vicinity of tributary junctions in coastal British Columbia. Similarly, Jacobson (1995) documented that the greatest fluctuations in sediment storage occurred at and near confluences.

Since the supply and transport of significant amounts of sediment is episodic, depositional areas at confluences, including fans (e.g., figure 2), should expand and contract over time in response to storms, fires, and floods (Benda et al. 2003b). Consequently, the spatial extent of these areas' upstream and downstream zones of influence should vary over time (figure 8). Moreover, a disturbance that originates from one tributary (i.e., a flash flood) is more likely to affect a downstream area of a confluence if the two tributaries are relatively close together.

River network organization of disturbance regimes. The locally altered disturbance regime at a confluence is embedded within a larger pattern of disturbance frequency and magnitude, dictated by the hierarchical nature of branching river networks. Periods of flooding (and thus of accelerated sediment supply and transport) should increase in frequency and decrease in magnitude downstream, because of several features of the coupled climate–landscape system (figure 9). First, the typical inverse relationship between storm size and intensity causes flood hydrographs to be most spiked and erosion events to be most concentrated in small subbasins (Church 1998, Miller et al. 2003). Second, as river size increases downstream (on the order of 100 km^2) through the intersection of tributaries, the number of potential sources of erosion rises abruptly at each confluence, increasing the tempo of sediment supply and transport (Benda and Dunne 1997a). As channels widen and sediment storage capacity increases downstream, however, it becomes more difficult to create large sediment-related disturbances (e.g., figure 9). Consequently, although the frequency of sediment-related disturbances should increase downstream, specifically at confluences, their magnitude should decline (Benda and Dunne 1997b).

This pattern of sediment-related disturbance frequency and magnitude throughout a network (figure 9) has implications for confluence-related morphology. Large-magnitude sediment pulses originating from concentrated floods and erosion, in the upper regions of networks affected by large storms and fires, have a frequency on the order of many decades to a couple of centuries (Swanson et al. 1982, Meyer et al. 2001). Hence, any snapshot of the age distribution of fluvial landforms in headwaters at the mouths of small basins is likely to be skewed toward older, eroded features whose effects on main stem channels are minor and dependent on the time since the last episodic input (Benda et al. 2004). In contrast, at the tributary mouths of larger basins characterized by more frequent and lower-magnitude sediment pulses during floods, the fluvial landforms should have a higher proportion of younger features with more persistent effects in main stem rivers (box 1).

Concentration of heterogeneity in river networks. The increased morphological heterogeneity at confluences is controlled by the size ratios of confluent tributaries, by the power law of stream and confluence sizes, by network patterns, by local network geometry, and by the river networks' organization of

disturbance regimes. Because of these controls, it is likely that riverine heterogeneity (linked to confluences) is nonuniformly distributed across watersheds, and it may even be concentrated in certain regions of networks. For example, in topographically uniform watersheds, there may be a zone of maximum physical heterogeneity located in the central network. Relatively close spacing of geomorphically significant tributaries (e.g., figure 6a), interacting with a moderate disturbance frequency (and disturbance magnitude; figure 9), could maximize physical heterogeneity between headwaters and basin mouths (box 1). This has been predicted using a simulation model (Benda and Dunne 1997b). Moreover, dendritic networks in heart-shaped basins may promote the highest likelihood of confluence effects in the central network, where confluencing tributaries are largest (e.g., figure 4).

Watersheds that have sharply declining valley gradients as they transition from mountains to depositional plain, in combination with large tributaries converging near the area of transition, could create a zone of concentrated heterogeneity between the mountain uplands and lowlands. For instance, in the unregulated Queets River basin (1170 km^2), the highest rate of channel meandering and the largest number of gravel bars and side channels occurred in an area approximately midway between the headwaters and the mouth (O'Connor et al. 2003). The localized convergence of large tributaries in watersheds with heightened erosion may also focus channel dynamics and associated heterogeneity. In the Ozark Plateau, for instance, Jacobson (1995) found that the stream bed elevation changed more frequently in midsize watersheds (1400 to 7000 km^2), where "sediment waves combined additively at confluences," than in channels located in smaller (< 1400 km^2) or larger (8000 to 10,000 km^2) watersheds, where the frequency and magnitude of perturbation were lower.

Ecological implications

New concepts in riverine ecology are focusing on river attributes at landscapes scales (e.g., riverscapes), on their heterogeneity, and on the role of stochastic disturbances in shaping them. Yet the prevailing perspective is of a river network as a linear feature, hobbling new concepts in riverine ecology (Fisher 1997). Viewing rivers as networks is fundamental to the new landscape view of rivers.

The network dynamics hypothesis: A physical foundation in riverine ecology.
New conceptual frameworks in riverine ecology emphasize the importance of habitat heterogeneity, stochastic disturbances, and scaling issues (Townsend 1989, Schlosser 1991, Fausch et al. 2002, Poole 2002, Ward et al. 2002). Although the new conceptual
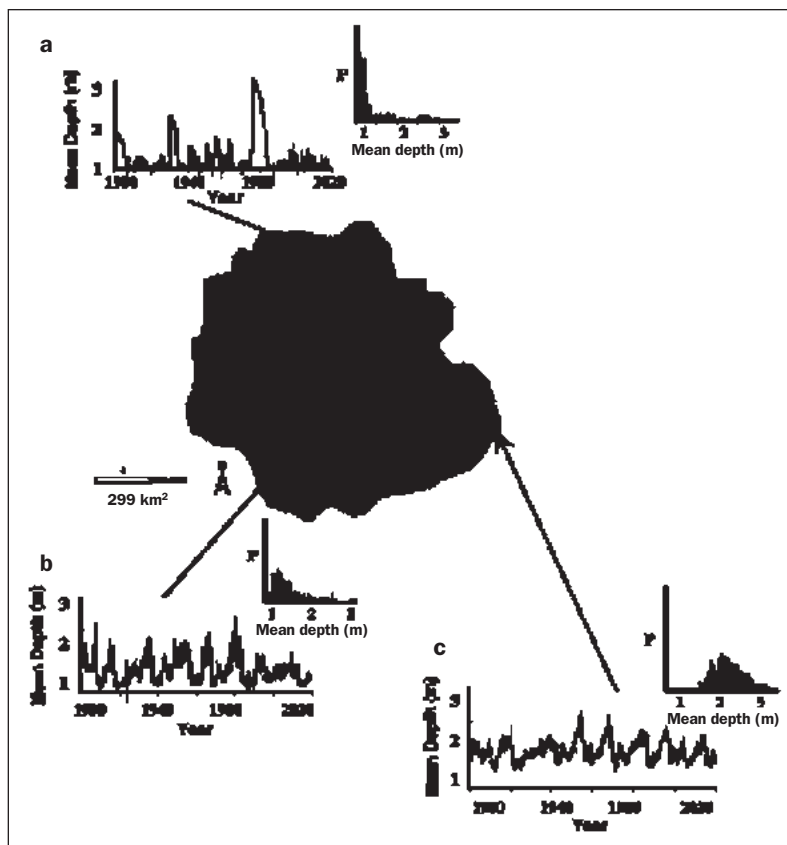

Figure 9. Because watershed dynamics (the frequency and magnitude of sediment-related disturbances) vary with basin size, they influence the age distribution of confluence-related landforms and consequently the effects of these landforms in channels. (a) Disturbances are large but rare in headwaters (as indicated by the time series of channel sediment storage), leading to a higher proportion (P) of older confluence-related landforms in headwater channels. (b, c) Disturbances are more frequent but of lower magnitude farther downstream in a network. This should create a higher proportion of younger confluence-related landforms and hence more persistent confluence effects. The highest frequency of intermediate-size disturbances is predicted to occur in the central network (b), contributing to a zone of heightened channel disturbance and maximum physical heterogeneity. The relationship between disturbance frequency and magnitude can be represented in the form of probability distributions (insets for a, b, and c; modified from Benda and Dunne 1997b), the shape of which evolves downstream from skewed to more symmetrical forms. Black dots on the map represent confluences.

frameworks hold the potential to advance the discipline of river ecology, they are hindered in doing so because they lack a physical basis for predicting how stochastic disturbances, or watershed dynamics, interact with the spatial structure of river networks to generate patterns of heterogeneity in the habitat along river profiles and throughout entire watersheds. Framed as a set of testable predictions in box 1, the network dynamics hypothesis (NDH) contributes a physically based framework to underpin new conceptual frameworks in the coupled fields of geomorphology and aquatic biology.
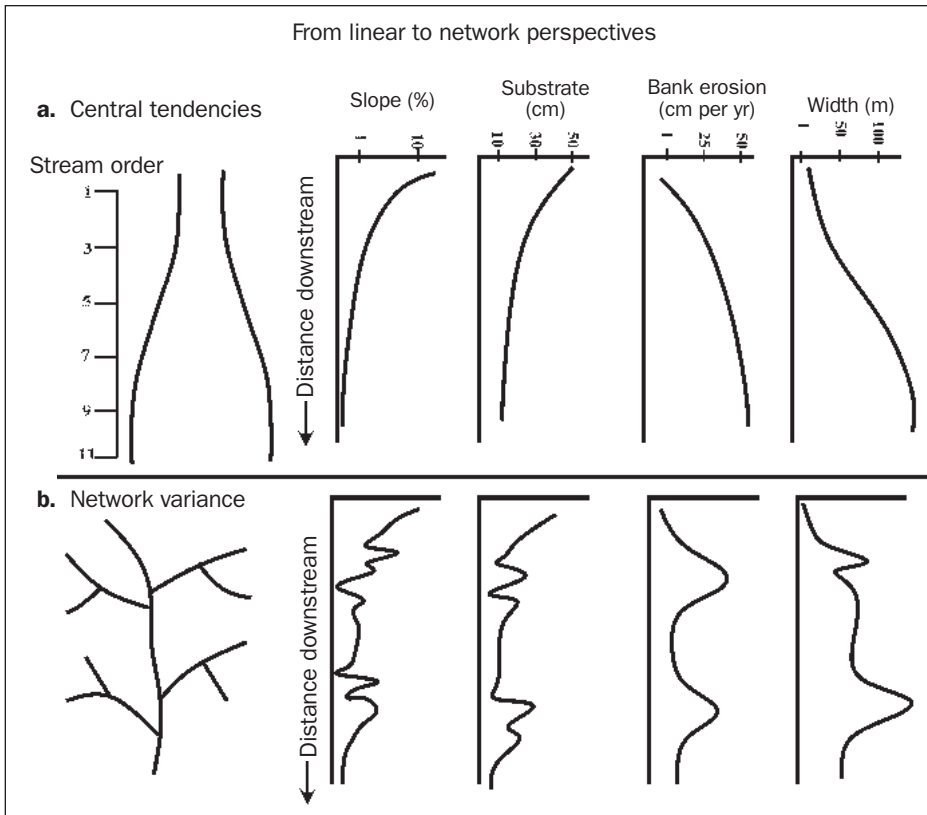
Figure 10. (a) The river continuum concept (RCC), some predictions of which are shown for a main stem river, exemplifies the prevailing linear perspective on riverine ecology. Linear approaches such as the RCC predict gradual and continuous downstream change, with central tendencies, in physical and biological processes. (b) In the nonlinear, network-variance model, the branching character of river networks, coupled with stochastic watershed disturbance, interrupts downstream continua of physical and biological processes to generate hypothetical deviations from downstream central tendencies in the geomorphic properties along the main stem of the network. For some variables, the central tendency shown in panel a may be retained, but with elevated variance around tributary junctions (e.g., slope, substrate), whereas for others the confluence effect of tributaries may eliminate the pattern of central tendency downstream (e.g., bank erosion, width) within certain sizes of drainage basins.

By focusing on variation rather than on expected mean states in fluvial geomorphic features, the NDH complements the emphasis on habitat heterogeneity in landscape views of rivers and in hierarchical patch dynamics. This focus on variation allows for understanding the degree of deviation in channel geomorphic attributes and habitat heterogeneity, caused by punctuated inputs of water, sediment, and organic material from tributaries, along the longitudinal profile of any stream channel. Thus, proceeding down a river, investigators can predict that deviations from the expected mean state (i.e., patchy heterogeneity) will occur in response to network geometry (figure 10). Because the NDH also addresses the stochastic dimension of sediment flux and storage in a drainage network, it can lay a foundation for emerging paradigms in river ecology concerning the regulation of local disturbance regimes according to their position in a network, especially at confluences.

This physical foundation has important implications for much-needed generalization in riverine ecology. Because of differences in basin size, shape, network pattern, channel-type sequencing, basin topography, and disturbance regimes, the variation in riverine environments is virtually infinite. This has led some researchers to conclude that all river networks are uniquely individual (Poole 2002). Although this is certainly true in some absolute sense, the NDH indicates that some generalities can nonetheless be deduced on the basis of certain universal properties of river networks.

Tributary confluences as biological hotspots and their organization by river networks. Tributary junctions represent locations in a network where channel and valley morphology can change and where local heterogeneity can be enhanced relative to the central tendency expected under the river continuum concept (figure 10). Spatial and temporal heterogeneity in resources and habitat may, among other things, contribute to increased local species richness (Huston 1994); therefore, tributary junctions may represent biological hotspots within a river network.

There is limited empirical evidence demonstrating the ecological importance of morphologically diverse tributary junctions. Rice and colleagues (2001) discovered changes in the abundance and composition of macroinvertebrate species in association with sediment size differences at confluences in British Columbia. Kupferberg (1996) found that a native frog species (*Rana boylii*) focuses its breeding nonrandomly near tributary junctions along a 5-km stretch of a fourth-order stream in a relatively steep California river. This species selected shallower and slower areas of stream bed within this zone. Furthermore, recent and extensive river surveys in the Delaware River (Pennsylvania, New York, and New Jersey) suggest that the average abundance of unionid mussels is greater in reaches above tributary junctions than in reaches below them, a difference that may be driven by differential sediment sorting and bed stability during high river flows (William Lellis, Chesapeake Watershed Cooperative Ecosystem Studies Unit, University of Maryland, Frostburg, MD, personal communication, December 2002).

Despite the lack of biological studies focusing on confluences, general ecological principles allow us to infer other likely effects. For macroinvertebrates and fish, increasing the heterogeneity of habitat conditions, including channel width and depth, bed substrate, wood storage, and water velocity, should increase total species richness (Allan 1995). For example, increased channel-wide habitat diversity above significant tributary confluences should create habitat opportunities, such as side channels during flood events, for specialized aquatic species or for life stages that require low-energy environments (e.g., Swales and Levings 1989, Reeves et al. 1995). This has been documented in the Oregon Coast Range, where increased wood storage and pool formation at low-order confluences resulted in increased salmonid rearing (Everest and Meehan 1981). In the Olympic Mountains, Washington, correlations among low-order confluences—which are prone to debris flows, large pools, gravel deposits, and accumulation of wood—promoted increased availability of fish habitat. Likewise, for riparian communities, greater topographic variation in floodplains and terraces should create local variation in inundation and soil moisture regimes, thereby increasing plant diversity (e.g., Kalliola and Puharta 1988, Pollock et al. 1998), or provide interannual variation in riparian plant recruitment (Cooper et al. 2003). Such enhanced floodplain and terrace topography has been documented upstream of alluvial fans (e.g., figure 2; Small 1973, Benda et al. 2003b).

Other ecosystem processes may also be amplified at tributary junctions. For example, the localized flattening of stream gradient and slowing of water velocity upstream of a tributary fan can increase hydraulic head and enhance hyporheic flow through wedges of gravel substrate (Edwards 1998). In this environment, dissolved organic nitrogen can be chemically transformed while in hyporheic transit and emerge in surface water as dissolved nitrate, which can support increased primary productivity (Sedell and Dahm 1984). Similarly, emerging hyporheic flow typically exhibits a smaller range of temperature extremes, which is favored by certain fish (e.g., see Baxter and Hauer 2000).

Of course, tributaries can also modify environmental conditions other than the sediment and morphology of receiving rivers. The details of these modifications will be complex and will depend on the relative sizes and geochemical characteristics of the main stem and tributary streams. Higher inputs of nutrients and invertebrates from tributaries have been shown to promote primary and secondary productivity in receiving streams (e.g., Kiffney and Richardson 2001, Wipfli and Gregovich 2002). Fish may also use tributary mouths as thermal refugia (e.g., Scarnecchia and Roper 2000) or as dispersal corridors that support higher than expected species diversity (Osborne and Wiley 1992).

Conclusions

Starting with the basic observation that the likelihood of morphologically significant perturbations to main stem channels increases with the ratio of tributary to main stem size,

we deduced a set of predictions relating the degree and spatial distribution of physical heterogeneity in a river system to general features of branching river networks (figure 1, box 1). This set of testable predictions—known collectively as the network dynamics hypothesis—provides a new framework for considering how the spatial structures of river networks, combined with time-varying watershed disturbances, create and maintain habitat heterogeneity and thus potentially promote biological diversity and productivity in riverine ecosystems.

The network dynamics hypothesis can serve as a physically based framework for recent advances in watershed-scale geomorphology and aquatic biology, namely, hierarchical patch dynamics (Townsend 1989, Wu and Loucks 1995, Poole 2002) and the application of landscape ecology to river systems (Schlosser 1991, Fausch et al. 2002, Ward et al. 2002, Wiens 2002). Consequently, this hypothesis could provide a foundation for new research in riverine ecology. It also has ramifications for land management and for conservation or restoration strategies. For example, network maps, based on the location of geomorphically interesting confluences, could be generated to identify the highest likelihood of physical heterogeneity (Benda et al. 2004). Putative biological hotspots could thus be identified on the basis of network configuration and watershed disturbance regimes. Also, land management practices that alter the spatial and temporal distribution of sediment and organic matter (e.g., dams, dikes, and forestry practices) could be examined in terms of their effects on downstream habitat heterogeneity, as mediated through confluences in specific network structures. Such analyses could contribute to the development of strategies for targeted restoration efforts in a whole-watershed context.

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