Ecosystem Expansion and Contraction in Streams

Desert streams vary in both space and time and fluctuate dramatically in size

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Streams are hydrologically diverse and dynamic ecosystems. Flow may vary between extremes, from high-discharge floods to periods when surface water is absent. Although much is known about the role of floods in shaping ecological processes, far less is known about the biological and chemical changes that occur during periods of water loss in stream ecosystems (Boulton and Suter 1986, Stanley and Fisher 1992). Nowhere is this lack of knowledge more apparent than in desert streams; these lotic ecosystems exist in a setting defined by water limitation, and periods of declining or absent flow are common. However, water loss is by no means unique to desert streams, because intermittent streams are found in many different environments. Moreover, escalating demands on a finite water supply are increasing the likelihood of drying in streams and rivers worldwide. Irrigation, impoundment, diversion, and ground-water abstraction reduce streamflow in mesic and xeric regions alike. In arid and semiarid areas, large rivers that are devoid of water are common, and in more mesic locales, profligate water use decreases the total amount of surface water present

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> **Models of streams highlighting patch structure, rather than gradual transitions from one zone to another, emphasize the importance of spatial patterns of expansion and contraction**

and increases the likelihood that water will be absent at certain times and/or places, leaving the stream bed exposed (Davies et al. 1994, Postel 1992).

Documentation of water loss from streams is a first, vital step toward understanding how drying shapes ecosystem structure and function. Because drying is a spatially heterogeneous process, standard hydrologic measurements, such as discharge (the amount of water moving through a cross-section of the channel per second), are insufficient to describe water loss in streams. Moreover, as we demonstrate in this article, different patterns of drying can drive different ecological changes. We describe changes in surface water distribution during both high- and low-flow conditions in a Sonoran Desert stream drainage. Our analysis shows that streams are spatially

dynamic ecosystems that undergo cycles of expansion, contraction, and fragmentation; that conventional hydrologic measurements of water velocity or volume passing a fixed point represent only one aspect of hydrologic dynamism; and that change in ecosystem size is a fundamental, defining feature, not only of desert streams, but also of all stream and river ecosystems.

Hierarchical approaches to stream studies

The general goals of ecological studies are to identify and describe patterns in nature and to understand both the underlying processes that generate these patterns and their larger-scale consequences. To this end, many ecologists advocate the use of a hierarchical approach to describe and understand patterns in large, complex systems (e.g., O'Neill et al. 1986, Urban et al. 1987). A system, such as a landscape, can be characterized as a series of progressively smaller subunits or patches that have their own distinct structure and function. By dividing a large, heterogeneous entity into smaller, more homogeneous components, complex spatial patterns can be examined at the spatial and temporal scales at which they actually occur, making these patterns easier to understand (Urban et al. 1987).

The complex physical structure of a drainage basin is easily resolved into a hierarchical classification of subsystems (Frissell et al. 1986, Gregory et al. 1991). For example, Grimm
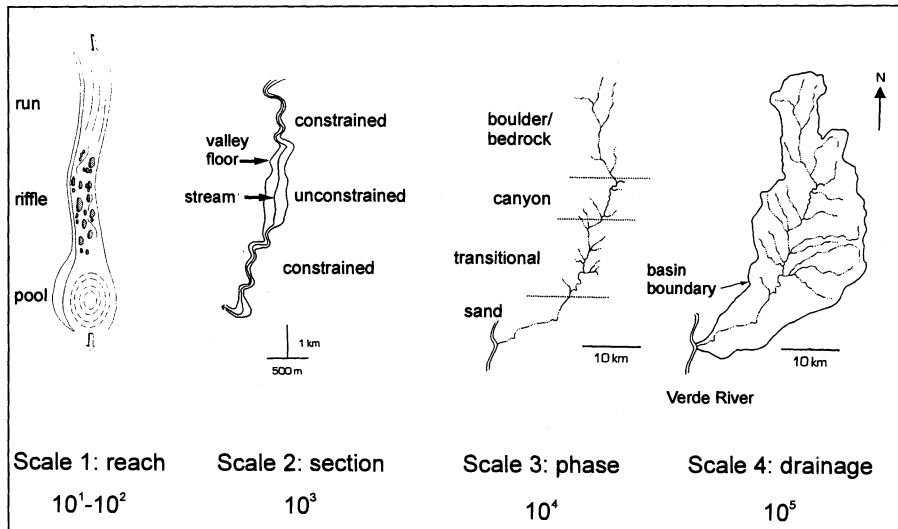
Figure 1. Hierarchical model of stream structure of the Sycamore Creek drainage, showing four spatial scales and their corresponding patch types. (Modified from Grimm and Fisher [1992].) Numbers indicate approximate spatial extent, in meters, of patch types within each scale (e.g., runs, riffles, and pools are 10–100 m in length).

and Fisher (1992) described desert streams as a system of patch types, ranging from small particles, such as stones and leaves, to entire drainage systems. We use a modified version of this scheme to demonstrate spatial hydrologic dynamics in the Sycamore Creek drainage, which is in Arizona's Sonoran Desert. We focus on four spatial scales, each composed of its own unique patches of similar size (Figure 1). These scales are (from smallest to largest): *reaches* (10^1–10^2 m), *sections* (10^3 m), *phases* (10^4 m), and finally the entire Sycamore Creek *drainage* itself (10^5 m).

Each spatial scale consists of two or more distinct patch types or channel forms. Reaches occur as sandy, shallowly graded runs, rock- and gravel-filled riffles, or deep pools. Similarly, sections can be either constrained (i.e., with narrow channels and restricted valley floors) or unconstrained (i.e., with valley floors that exceed 100 m in width). The four phases are defined by major changes in channel slope and substrate. The upper boulder–bedrock phase is steep and, as its name suggests, dominated by large stones and bedrock. The canyon phase is extremely narrow, with precipitous hillsides and pools separated by abrupt drops in channel elevation. The stream then opens into the transitional phase, which consists of a mixture of narrow and broad, rocky and sandy channels. The final patch type, the lower allu-

vial phase, is found at the base of the drainage and is characterized by extensive, deep alluvial deposits. At the largest scale, the drainage itself consists of two patches, the mainstem and tributary channels.

Our consideration of spatial scales ranging from tens of meters to several kilometers in the Sycamore Creek drainage not only reveals important hydrologic and ecological information about each scale, but also provides insights into between-scale relationships. For example, hierarchical models predict that patterns occurring at larger spatial scales constrain or control the characteristics of smaller scales (Urban et al. 1987). We examine one such constraint on patterns of water loss and consider how knowledge of constraints may be used to predict future ecological states of the stream.

Desert streams as model systems

Desert streams offer several advantages as model systems for hydrologic and ecological research. First, because they are characterized by extremes in magnitude and variance of discharge (McMahon 1979), hydrology plays a profound and fundamental role in shaping ecological conditions in these streams. Second, warm temperatures and abundant sunlight foster high rates of produc-

tion; thus, changes in variables such as primary production or invertebrate densities are often pronounced and, therefore, easily detected. This combination of extreme hydrology and high productivity of desert streams has been exploited to understand the role of disturbance, such as flash flooding, in shaping population, community, and ecosystem processes (e.g., Fisher et al. 1982, Grimm 1987, Meffe and Minckley 1987). These same features make desert streams equally amenable to understanding the importance of low-flow dynamics in shaping ecological patterns in lotic ecosystems.

A third advantage offered by desert streams is that, unlike their mesic counterparts, they can be examined easily at large spatial scales. Because streams are relatively narrow, they are typically undetectable with high-altitude (satellite) remote-sensing techniques. Average stream widths are often smaller than the resolution of even the most powerful satellites; thus, only riparian corridors can be clearly recognized in remotely sensed images (Muller et al. 1993, Paris 1992). Moreover, streamside vegetation often creates a complete canopy over the channel; as a result, the stream cannot be seen from above, even from low-level aircraft. Although data about characteristics at large spatial scales can be collected by ground-based techniques, these approaches are extremely labor intensive. Consequently, landscape-level research on all but the largest lotic ecosystems is typically restricted to examining processes or activities occurring in the surrounding watershed and then inferring the potential effects of these processes on the stream. Unlike their mesic counterparts, however, desert streams can be seen clearly from a low-altitude aircraft. Productive riparian borders make channels a distinct green feature in a landscape of muted colors. Flash floods carve out broad, sandy channels, and under normal conditions, surface flow occupies only a fraction of the total channel width. Dark bands of water are clearly visible against the lighter sediment background, even from great distances. Hence, these features of desert streams make large-scale investigations feasible.

Patterns of drying at different scales

In this section, we describe patterns of water loss at each of the four spatial scales under consideration. Although there are obvious physical and biological differences between hierarchical levels, patterns of drying share certain common features regardless of scale.

Scale 1: reaches. The most common scale at which researchers examine streams is the reach. Runs, riffles, and pools are easily recognizable and exist on a spatial scale that is tractable to study (10–100 m). In desert streams, such as Sycamore Creek, drying in runs begins with the development of discontinuous flow at the downstream end of the reach; water margins subsequently retreat upstream for a period of days to weeks (Figure 2). This pattern of drying results from complex flows between the stream surface and deeper sediments; water often emerges from the sediments (known as the hyporheic zone) at the upstream end of runs and re-enters the hyporheic zone further downstream (Valett et al. 1994). The most obvious ecological effect of this drying pattern is the stranding of biota at the downstream end of the run. For example, in the drying sequence shown in Figure 2, the blue-green bacterium *Nostoc* was exposed to the atmosphere long before upstream mats of the filamentous green alga *Cladophora* experienced desiccation. Such differential stranding of cyanobacteria could potentially change nitrogen cycling in desert streams, which are strongly nitrogen limited. Biological nitrogen fixation is the only source of this limiting nutrient during interflood periods (Grimm 1987), and the loss of nitrogen-fixing taxa, such as *Nostoc*, would therefore reduce nitrogen inputs during periods of drought.

In the final stages of drying in runs, surface water is reduced to a single isolated pool, typically at the head of the run. Because some aquatic organisms are able to keep pace with retreating stream margins in Sycamore Creek (Stanley et al. 1994), these pools are often filled with dense populations of mobile animals. For
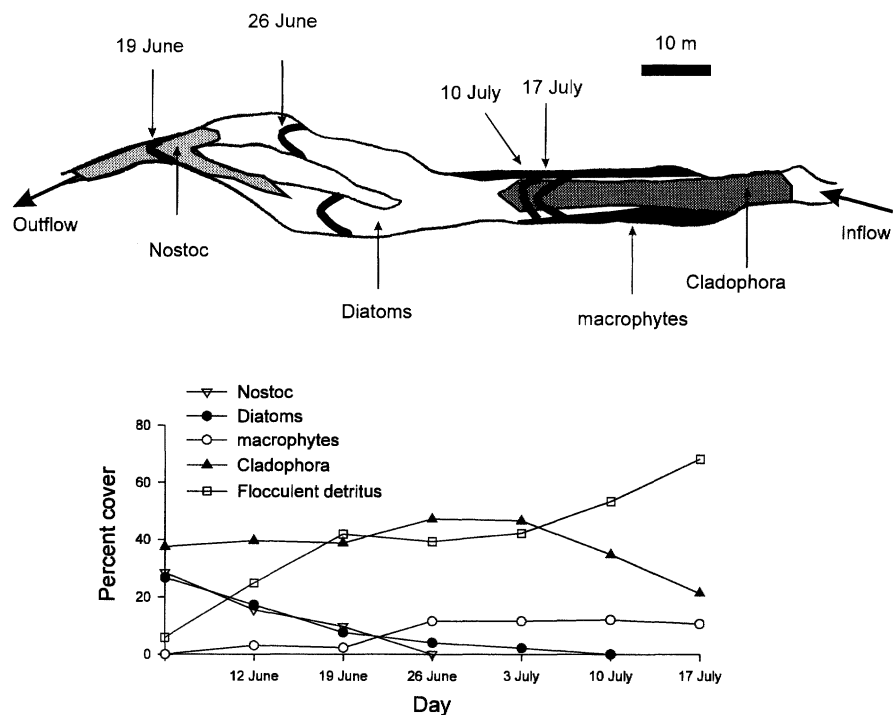

Figure 2. Drying pattern and algal distribution and abundance within a run of Sycamore Creek for several dates in 1989. Progressive drying in an upstream direction (thick black lines) results in differential stranding of downstream algal mats (top), which, in Sycamore Creek, are often nitrogen-fixing cyanobacteria. Changes in the percent of the wetted stream channel covered by each mat type over the course of drying are shown in the bottom panel. In the final stages of drying (after 3 July), the increased densities of invertebrates in the remaining surface water hasten the decline of the filamentous green alga *Cladophora* and the accumulation of flocculent detritus.

example, when one such isolated pool had been reduced to less than 0.3 m², the entire pool was completely filled with snails (*Physella virgata*; Stanley et al. 1994). As drying became acute and invertebrate densities increased, algae senesced and declined and were transformed into flocculent detritus (Figure 2).

In contrast to runs, water loss from riffles follows a different pattern. Drying starts with previously submerged rocks breaking through the water surface. Taxa that attach to large rocks, such as pyralid moths (*Petrophila confusalis* and *Petrophila jaliscalis*) and herbivores that feed on the algae growing on these rocks, are the first to be affected by drying. Eventually, water becomes trapped in depressions throughout the riffle, creating a series of isolated fragments of surface water (Figure 3). As drying progresses, each fragment has distinct and often extreme limnological properties (Table 1). For example, a pool filled with thick mats

of filamentous green algae may be located within a meter of another pool, dominated by fishes. In the former, high rates of primary production deplete nutrients and elevate dissolved oxygen; in the latter, intense feeding by omnivorous fishes removes filamentous algae and favors taxa, such as the filamentous cyanobacterium *Calothrix*, that adhere tightly to rocks and are resistant to grazing. Similar divergence of physicochemical conditions and community structure has been observed in intermittent streams in Texas, tropical Australia, and Costa Rica (Chapman and Kramer 1991, Meyerhoff and Lind 1987, Smith and Pearson 1987). This heterogeneity poses difficult challenges to the biota; survival in these isolated pools requires physiological flexibility to deal with many possible chemical and biological conditions.

Water loss from pools is typically a gradual process. In most cases, pools slowly decrease in length, width, and depth. However, this patch type is

Figure 3. Drying pattern within a Sycamore Creek riffle during summer 1991. Dashed lines outline two rocks to provide a frame of reference. Dark areas represent distribution of surface water; white areas denote dry stream bed. This figure shows how riffles dry to produce a fragmented habitat of isolated pools, which subsequently diverge dramatically in water chemistry and community structure (e.g., see Table 1).

8 June   16 August

1 meter

20 August   23 August
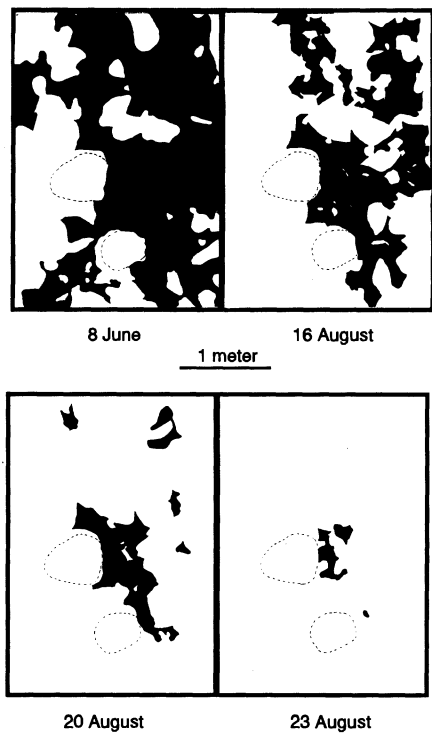
more buffered from drying than runs or riffles. Stream size change in a 12-km stretch of Sycamore Creek was mostly attributable to loss of water from riffles, whereas the total surface area of pools remained relatively constant, and runs were intermediate in their susceptibility to drying (Figure 4). Because pool and riffle communities differ in their species composi- tion (Wood et al. 1992), drying tends to shift the entire section toward a more pond-like community at the expense of riffle assemblages. The patterns of community divergence that are associated with drying may have prolonged effects on community structure after rewetting and stream re-expansion. In Sycamore Creek, postflood recovery of benthic invertebrates during drought years is characterized by low densities and pronounced shifts in community composition—an apparent historical legacy of reduced total numbers and taxonomic diversity during drying (Boulton et al. 1992).

At the small scale of the reach, the spatial patterns of drying differ in riffles, runs, and pools; the ecological consequences of these patterns appear to differ as well. However, drying does not necessarily progress inexorably and inevitably to a desiccated end. The larger 12-km study section of Sycamore Creek never dries completely; some surface water is always present. The drying process may also be interrupted at any stage by rewetting associated with precipitation and runoff.

Scale 2: sections. Channels and terraces that support riparian vegetation make up the valley floor. In desert streams, valley floor morphology varies from extremely narrow canyons, in which the channel is highly constrained and terraces are absent, to expansive, unconstrained channels that spread over low-gradient landscapes (Graf 1988). Streams in the Cascade Mountain region of the Pacific Northwest share a similar morphology of constrained and unconstrained sections. In the latter setting, unconstrained channels are physically and, hence, biologically diverse, whereas constrained sections show little habitat diversity and lower biotic diversity. Not surprisingly, these differences have a range of ecological consequences, such as enhanced fish productivity and nutrient retention in unconstrained channels as compared with constrained channels (Gregory et al. 1991).

As in Cascade streams, channel complexity is pronounced in unconstrained sections of desert streams, such as Sycamore Creek. In both regions, deep alluvial deposits can absorb large volumes of water. In contrast to the Pacific Northwest, however, the limited amount of water contained within a desert stream may not completely saturate these sediments, and thus the stream is particularly prone to drying as it passes through an unconstrained section. Surface water distribution in a 12-km length of Sycamore Creek during February, May, and September 1989, demonstrates the progression from wet to extremely dry conditions, showing both differential susceptibility to and patterns of drying among the constrained and unconstrained patches that comprise this spatial scale (Figure 5). Drying started in the center of the largest unconstrained section. Water loss progressed rapidly in both upstream and downstream directions, leaving a long, continuous stretch of dry channel. In a single month, more than half of the 3-km unconstrained channel in Sycamore Creek may dry (Stanley 1993). Water loss in the broad channel areas of desert streams is so rapid that whole runs, riffles, and pools dry in a single day. The effect of

Table 1. Limnological features of four isolated pools during midday in a drying riffle of Sycamore Creek. These pools, located only a few meters from one another, vary significantly in nutrients and algal composition.

Isolated pool	Dominant biological features	Dissolved oxygen (mg/L)[a]	Total inorganic nitrogen (μg/L)[a]	Soluble reactive phosphorus (μg/L)[a]	Chlorophyll$a$ (mg/m^2)[b]	Ash-free dry mass (g/m^2)[b]
1	High fish density; Calothrix growing on rocks	3.74	39	78	134.5	43.3
2	Moderate fish density; Calothrix growing on rocks	11.10	2	42	364.2	91.7
3	Moderate fish density; dense Cladophora mats	12.54	26	50	564.2	596.2
4	Frogs; mixed diatoms	5.31	56	50	183.7	76.3

[a]For each pool, n = 3.
[b]For each pool, n = 5.

a wide valley floor on drying is so pronounced that it overrides reach-specific patterns of drying and therefore can be considered a constraint on reach-level hydrology.

Continuous flow persists in constrained sections unless drying becomes severe, as in September 1989 in Sycamore Creek (Figure 5). Drying patterns in these narrow channel areas are characterized by short lengths of dry channel interspersed with short wetted stretches, resulting from drying of individual runs and riffles. Thus, in contrast to unconstrained sections, where larger-scale drying occurs so rapidly that there are no apparent differences in smaller-scale (reach-level) patterns of water loss, drying in constrained sections reflects patterns occurring at the smaller scale of individual runs, riffles, and pools.

These two drying patterns have distinct ecological consequences. As a result of the extensive lengths of channel lacking surface flow in uncontrained sections, water travels exclusively in the hyporheic zone below the stream surface for hundreds to thousands of meters, where its chemistry can change substantially. In constrained patches, by contrast, subsurface flow paths are short and changes in water chemistry are less pronounced (Stanley and Valett 1992). Nitrification is an important hyporheic process, and high-nitrate water emerging from sediments at the ends of unconstrained sections stimulates algal primary production, often for hundreds of meters below these emergence points (Grimm et al. 1981). This phenomenon occurs in constrained reaches as well, but because chemical changes are less pronounced, production is stimulated over shorter distances.

In addition to between-patch differences in pattern and susceptibility to drying seen in both reaches and sections, the expanded extent of the larger section scale highlights another critical feature of drying: its magnitude. The overall size of Sycamore Creek ranges from 12 km during the continuous flow along the entire study area to a minimum of 4 km during periods of extreme drought. Long lengths of the stream commonly lack surface flow for weeks or months at a

Figure 4. Regression of water surface areas in all riffles, runs, and pools within a 12-km section of Sycamore Creek versus the total water surface area of this section. Riffles = solid line; runs = dashed line; pools = dotted line. The slopes of the regression lines illustrate the change in total section length as a function of size change of each particular reach type. For example, the total surface area of pools within the 12-km section changes little despite the large size changes occurring in the entire stream section, as indicated by the near-vertical regression line. By contrast, as the total surface area of riffles changes, so too does the surface area of the entire 12-km section. Differences in these regression lines indicate that riffles undergo considerable size change and that these changes are responsible for much of the size change of the larger stream section. Conversely, pool size remains fairly constant while these larger-scale size changes are occurring. Runs change less in size than riffles but more than pools.

Figure 5. Patterns of water loss in constrained and unconstrained sections of Sycamore Creek during May, June, and September 1989. For each date, the outer solid lines represent edges of the valley floor, and the central line shows the extent of surface water. During this five-month period, the total channel length declined from 12 to 4 km. The different patch types showed differential susceptibility to drying (i.e., the unconstrained section UC-2 dried before the flanking constrained sections C-1 and C-2). In addition, each patch type showed a different pattern of drying (i.e., the unconstrained section contained long stretches of dry channel, whereas the constrained sections contained short lengths of dry channel interspersed with wetted areas).

time, even during the wettest of years. The absence of water from large sections of the stream significantly reduces habitat availability and ecosystem productivity, and it divides and isolates previously contiguous populations, often for several months at a time. The ecological and evolutionary implications of such population segregation in intermittent streams remain to be studied.
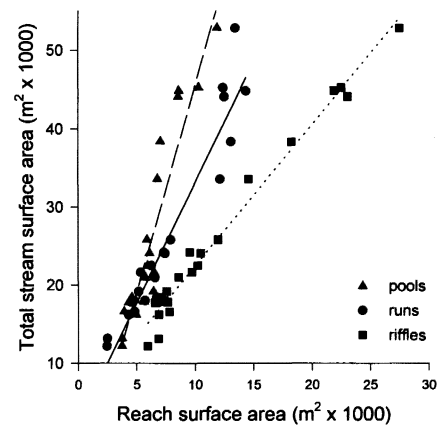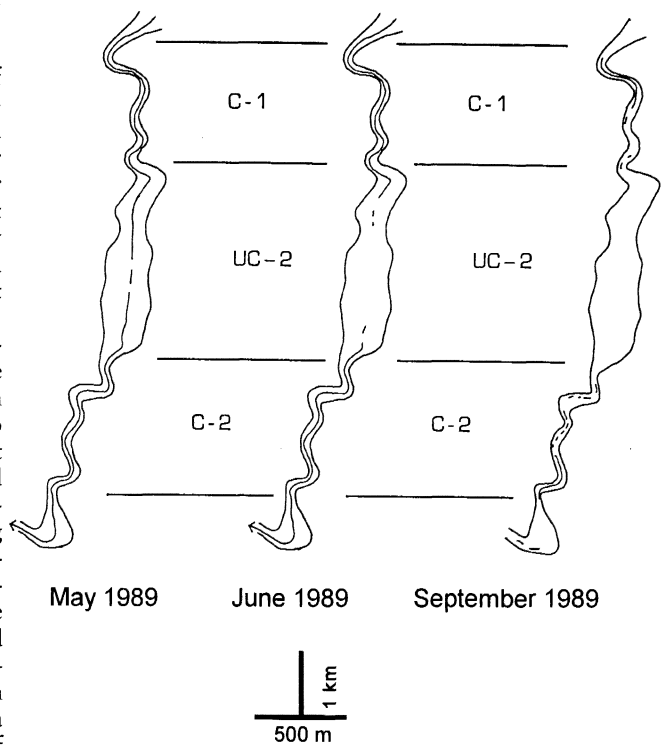
Scales 3 and 4: phases and drainage. A series of maps shows surface water distribution during a period of hydrologic extremes for both phase and basin scales of Sycamore Creek (Figure 6). During the driest month of our study (November 1991), sur-

Figure 6. Surface water distribution in the Sycamore Creek drainage in November 1991, March 1992, and June 1992. Differential susceptibility to drying among patches at the scales of both phase and drainage are apparent, as are pronounced patterns of stream expansion, contraction, and fragmentation throughout the basin.

November 1991   March 1992   June 1992

10 km
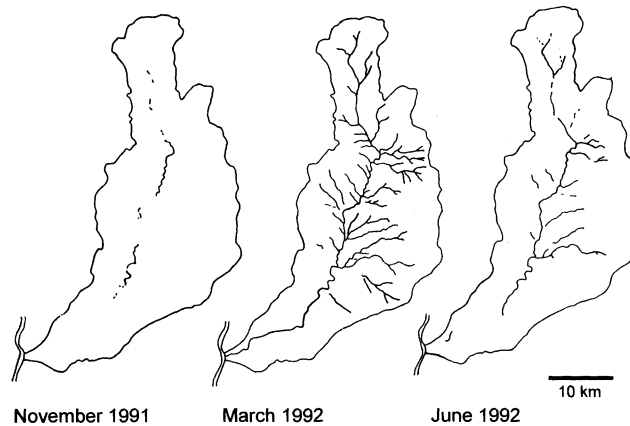
face water was restricted to the canyon, transitional, and, to a lesser extent, boulder–bedrock phases, whereas the lower alluvial phase was completely dry. The persistence of water in canyon regions undoubtedly makes them critical refuges during prolonged drought; indeed, native fishes congregate in canyons to avoid declining water quality and desiccation in desert streams (Meffe and Minckley 1987).

Following the wet winter of 1991–1992, stream size increased dramatically in Sycamore Creek, and in March 1992, surface flow was present in all phases as well as throughout many of the tributaries. Consequently, previously isolated habitats were reconnected. During the transition from March to June, surface flow decreased and became fragmented across the basin. Phases showed differential susceptibility to drying, with water losses occurring in the lower alluvial and boulder–bedrock phases.

At the scale of the entire basin, overall size changes resulted largely from water loss from tributaries. These smaller sub-basins were alternately dry, large, and connected to the mainstem of the creek, and fragmented and isolated from the mainstem (Figure 6). Estimates of habitat size (i.e., total length of channel with water present) show that the stream underwent an eightfold size change (Table 2), underscoring the extreme spatial dynamics across the entire basin.

As long as water is present, channels will support primary and secondary production. Flooding and drying in desert streams favor insects and some fishes with well-developed dispersal abilities (Gray and Fisher 1981, Meffe and Minckley 1987), and tributary channels are colonized relatively quickly following rewetting. In fact, spawning by the native fish *Agosia chrysogaster* (longfin dace) and growth of filamentous green algae occurred earlier in many tributary locations than in the main channel of Sycamore Creek (Stanley 1993). A variety of salmonids has been reported to move into intermittent and ephemeral tributaries early in the year for spawning before these temporary habitats dry because they may provide areas of reduced competition or refuge from disturbance (Brown and Hartman 1988, Erman and Hawthorne 1976).

Although hydrologic extremes have apparently favored recoloniza-

tion traits, these adaptations are not without cost because colonists in tributaries are particularly vulnerable to exposure and desiccation. Nevertheless, our basinwide examination highlights an unexpected feature of flooding, namely that floods can enhance ecosystem productivity. At the scale of an individual reach, floods typically remove more than 90% of algal and invertebrate biomass (Fisher et al. 1982); however, these floods obviously cause no such destruction in biologically inactive, dry channels. If floods rewet dry reaches and expand overall stream size (i.e., habitat availability), then they effectively increase productivity across the basin. Because of their magnitude and duration, winter floods are likely to elicit significant increases in habitat, and, therefore, in productivity. By contrast, summer floods have only a short-term effect on stream size because floodwaters recede within hours (Grimm and Fisher 1992). Floods that do not significantly increase habitat size but do remove biomass are particularly devastating. Mobile insectivores, such as flycatchers and bats, that forage over extended lengths of the stream channel are especially sensitive to these large-scale fluctuations in secondary production. Effects of flooding on large-scale productivity depend on the balance between decreases in biomass and increases in stream size. Drying, however, always decreases stream size and, therefore, productivity.

A general model of drying

The specific hierarchical description of Sycamore Creek (Figure 1) can be presented in a generic form to highlight key features of drying (Figure 7). Each scale is composed of different patches, and each patch has a distinct pattern of water loss and susceptibility to drying. Identifying patch types that are most likely to shrink or dry can serve as the basis for predicting future ecological conditions. If the properties of a particular patch type are known, then it is possible to predict the ecological changes that will occur when that patch type declines or disappears. For example, one might predict that

Table 2. Extent and distribution of surface water in the Sycamore Creek drainage on selected dates in 1991 and 1992.

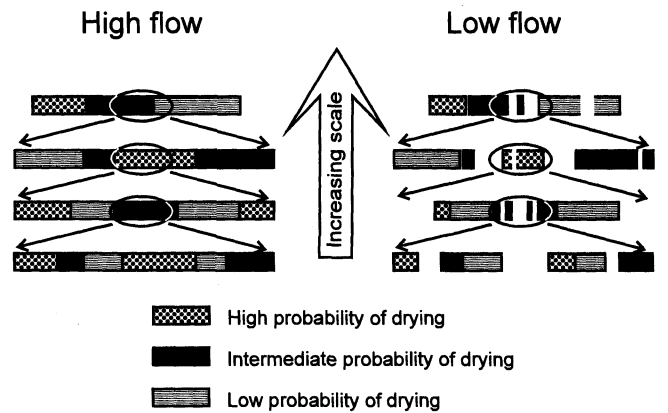| Hydrologic characteristic	13 November 1991	30 March 1992	8 June 1992
Total wetted channel length	23 km	175 km	83 km
Mainstem wetted channel length (percentage of total)	23 km (100%)	60 km (34%)	45 km (54%)
Tributary wetted channel length (percentage of total)	0 km (0%)	115 km (67%)	38 km (46%)
Total change from previous date	—	+152 km	−92 km
Mainstem change from previous date	—	+37 km	−15 km
Tributary change from previous date	—	+115 km	−7 km

populations of pyralid moths at Sycamore Creek would be severely depressed if there were several consecutive drought years, because these insects inhabit drying-susceptible riffles. This sort of approach has been used to evaluate long-term effects of beaver pond creation and collapse on methane emission from drainages in northern Minnesota (Naiman et al. 1991).

As individual patches shrink and expand, not only are functional subunits removed or added, but also the whole stream fluctuates between periods during which ecosystem size is alternately smaller and larger (Figure 7). This model illustrates that streams should be viewed as expanding, contracting, and often fragmenting ecosystems rather than as spatially invariant environments. This spatial dynamic is as fundamental to lotic ecosystems as is discharge.

Changing stream size: when and where is it important?

Size change is clearly pronounced in Sycamore Creek and is likely to be equally pronounced in other dryland streams and rivers. Arid and semiarid lands make up an estimated 67.9% of the world's terrestrial environment (Thomas 1989) and are drained by channels that do not sustain year-round flow (Davies et al. 1994). In these climatic settings, stream shrinkage and fragmentation are likely to take their greatest ecological toll. However, ecosystem expansion and contraction are not unique to xeric regions. Intermittent streams occur in many different environments (Williams 1987), and even under perennial flow regimes streams can undergo significant size change (Sedell et al. 1990), although for many streams, these size changes may not be apparent from an examination of single sites or reaches. In the Sycamore Creek drainage, the magnitude of size change varied from threefold at the section (10^3–10^4 m) and phase (10^5 m) scales to eightfold at the scale of the entire basin (10^6 m). This trend—that is, habitat expansion and contraction becoming more obvious with increasing spatial scale—is likely to hold in all settings.

Although an individual riffle or pool in a temperate zone stream may undergo only subtle size changes during the course of the year, the channels that contain them are likely to experience pronounced expansion and contraction. Small headwater channels are the most abundant type of channel in any drainage (Horton's law of stream number; Horton 1945) and are most susceptible to size change (DeVries 1995). For example, Blythe and Rodda (1973) measured total wetted channel length in a 1856-ha basin in southern England and found that change in channel length (i.e., size change) was related directly to stream order, with small, first-order channels undergoing the greatest size change, followed by second- and then third-order channels. Larger, fourth-order channels remained a constant length throughout the study. Weekly documentation of surface water in this drainage produced results remarkably similar to our patterns for Sycamore Creek: Channel length fluctuated from a maximum of 50 km of stream to a minimum of 10.2 km during the course of a year, different patch types (different stream orders) exhibited differential susceptibility to drying, and "detachment" (fragmentation) of certain stream segments occurred during dry months (Blythe and Rodda 1973).

Climate change always involves concomitant hydrologic modifications. Future global warming is likely to alter hydrologic regimes, the frequency of extreme events (floods and droughts), hydrologic variance, and seasonality (Arnell et al. 1996). Human responses to changing climate and hydrology—new water projects such as dams, canals, interbasin transfers, and accelerated groundwater mining (Carpenter et al. 1992)—will exacerbate these changes. It is not possible to predict the direction of hydrologic change in the American Southwest, where Sycamore Creek is located—the region may become wetter or drier. However, the great year-to-year variation in hydrology already experienced by river systems is likely to intensify (Grimm et al. in press). Although one possibility is that the severity of droughts will increase with global warming, a more likely possibility is that the frequency of droughts will escalate throughout the world (Grimm and Fisher 1992). Models that incorporate the effects of expansion and contraction, connection and isolation, and temporal legacies of these size changes will be able to simulate ecological conditions generated by a changing climate. More static models that do not account for known temporal and spatial ecosystem dynamics, such as those described here, will predict future ecosystem dynamics poorly.

Conclusion

The diverse ecological effects of decreased stream size include the concentration of solutes, materials, and

Figure 7. Conceptual model of hierarchical patch structure and differential patch loss associated with drying in streams. The stream can be viewed as a composite of different patch types; a single patch at one scale is composed of discrete smaller-scale patches. Circled areas are expanded to show the composition of a given patch at the next smaller spatial scale. The different patch types that make up each level have different susceptibility to drying. Streams vary between periods of abundant water, high flow, and large system size to times of low flow and small, fragmented size. Overall stream shrinkage is caused by the contraction of individual patches with high susceptibilities to drying.

High flow

Low flow

Increasing scale

High probability of drying

Intermediate probability of drying

Low probability of drying

organisms; the separation of populations; the reductions in habitat availability; and the alteration of ecosystem processes, such as primary production and nutrient cycling. Despite the widespread occurrence of summertime low flows and system shrinkage, we are unaware of any ecological studies that have adjusted measurements, such as density or productivity, to compensate for the concentration of individuals into a progressively smaller stream. Habitat fragmentation, shrinkage, and subsequent expansion, although generally ignored by stream ecologists (but see Sedell et al. 1990), appeal to conservation biologists (Lord and Norton 1990) and population geneticists because expansion and contraction subject indigenous populations to frequent bottlenecks and dispersal cycles (e.g., Chapman and Kramer 1991, Vrijenhoek 1989). Indeed, intermittent streams are ideal model systems for research in these fields.

Fragmentation of streams counters conventional perceptions of these systems, as exemplified by the river continuum (Vannote et al. 1980) and nutrient spiraling (Newbold et al. 1981) concepts, which emphasize longitudinal trends and upstream–downstream linkages in community structure, food web dynamics, and biogeochemical cycling. Hierarchical models of streams highlighting patch structure, rather than gradual transitions from one zone to another, emphasize the importance of spatial patterns of expansion and contraction in lotic ecosystems. Our intention is not to trivialize the importance of upstream–downstream linkages in streams but rather to point out that our appreciation of this aspect of stream ecology is far more advanced than our understanding of how patch structure, size change, and fragmentation influence the ecological status of streams and rivers.

Patterns of differential patch loss, particularly at larger spatial scales, have implications for research site selection. Study sites are chosen for a variety of reasons, not the least of which is convenience. Unless a study specifically focuses on water loss, researchers tend to avoid areas in the basin that are prone to intermittent flow. This neglect may have contributed to the failure to include low-flow dynamics in current stream paradigms. Avoidance of intermittent channels perpetuates the limited view of streams as perennial systems with temporally, but not spatially, dynamic hydrologic regimes. Enough research has been conducted on intermittent streams to know that these habitats support a diversity of aquatic organisms and are often ecologically distinct from their perennial counterparts (Boulton and Suter 1986, Williams 1987). Although drainages are composed of different patch types with different ecological properties, stream ecologists tend to focus almost exclusively on the most biologically stable and hydrologically invariant among them.

To date, spatial hydrologic data have been the purview of research dealing with floodplain rivers and intermittent streams, in which spatial aspects of changing hydrology are too pronounced to overlook. Assessing hydrologic variation by examining discharge measured at a single point in a stream affords substantial insight into community dynamics (Poff and Ward 1989) but nevertheless provides an incomplete picture of ecosystem structure and function. The perception of the physical template of the stream derived from point-specific hydrologic measurements may be strongly influenced by the site chosen to measure discharge, which is usually the wettest site in the drainage. A consistent relationship between discharge and stream size is likely, but this correlation alone is insufficient to describe spatial variation. To truly understand this spatial component of hydrologic variation, explicit information is needed on pattern, timing, and extent of water loss. Because size change is a defining feature of stream systems, it has the potential to be a key ecological determinant of structure and function and, therefore, should be incorporated into our understanding of stream ecology. Acknowledging that streams are ecosystems that vary in both space and time and fluctuate dramatically in size will facilitate the development of conceptual linkages to the ideas and models of terrestrial landscape ecology, a field in which these dynamics have already been incorporated, to the benefit of both disciplines.

Acknowledgments

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