Introduction: Downstream Changes and Dynamics in River Environments

River networks sculpt the Earth’s landscapes. Along river networks, channel and riparian environments change in partially predictable ways that strongly influence river organisms and their interactions. Width, depth, and average flow velocities of rivers change downstream and also vary through time at a single station according to a set of empirical relationships known as hydraulic geometry. As channels widen downstream, they are less shaded and therefore receive more solar radiation, which increases both water temperature and the potential for primary production (growth of aquatic plants and algae). Habitat structure and disturbance regimes in channels also change along the river gradient. Bed sediments become finer downstream as channel gradients decrease. Steep headwaters often have coarse boulder and bedrock substrates, whereas mid-elevation mainstem rivers are likely to have gravel, pebble, and cobble substrates, with boulders and bedrock emerging as habitat islands, and lowland rivers with large floodplains typically have beds of mobile sand and silt. Events that erode or mobilize the river bed are rare at any given site in headwaters and largely result from debris flows that may recur only every 1000–10 000 years. Scouring disturbances can happen several times per year when storm flows mobilize cobble, pebble, or gravel beds in meandering mainstem rivers. In rivers with beds of sand and silt, portions of the substrate (and small organisms attached to them) are in constant motion, except for large debris jams or on floodplains or elevated banks.

In general, ecological gradients in rivers demonstrate the effect of physical environment on food–web interactions. In addition, rivers offer repeated opportunities to study species interactions on varied temporal scales as food webs reassemble after disturbance by drought or flood.

Changes in Communities over Time: Disturbance and Succession

Food webs reassemble after flood or drought disturbances as surviving and colonizing species rebuild their local populations and interact with each other during ecological succession, the period of biotic recovery following disturbance. Disturbances caused by bed movement are rare in headwater streams with gradients steeper than 10%, where channel substrates are bedrock or boulder dominated. Bed mobilization at these sites occurs infrequently (perhaps once or twice in 1000–10 000 years) when debris flows deliver sediments to channels. In lowland floodplain rivers, sand and silt making up the bed sediments are constantly in movement. Here, bed mobilization is not a pulsed event, hence not a disturbance in the ecological sense. Lowland river benthic biota adapt to fine, shifting river sediments by attaching to stable substrate, such as inundated floodplain vegetation or log jams, or by burrowing into channel walls strengthened by clay or roots. Bed mobilization is an important disturbance process at intermediate positions in the drainage network, where gravel, pebble, and cobble bedded rivers offer repeated opportunities to study species interactions as food webs reassemble after flood scour or dewatering.

In Mediterranean climates, which are typical of coastlines, the seasonal timing of flood and drying disturbance is somewhat predictable. Typically, a rainy winter season is followed by a summer drought with little or no rainfall. Variation occurs from year to year, however, in the magnitude and timing of flood and the severity of subsequent drought. In continental (inland) regimes, precipitation heavy enough to cause floods may fall during any month of the year, although where snow melt is important, large spring floods may predictably dominate the annual hydrograph. Under either Mediterranean or continental climate regimes, the timing of disturbance relative to the life histories of organisms will strongly influence the effect of these hydrologic events on abundances of species.

After gravel-dominated river beds are mobilized, rock-bound organisms (attached algae, mosses, or invertebrates with limited mobility) that cannot escape are damaged or removed. Mobile fauna, on the other hand, may escape. Fish can swim above the mobilized bed. When flow velocities become unmanageable, fish can take refuge in the slack water refuges of inundated off-channel habitats, undercut banks, or behind logs, bedrock formations, boulders, or large cobbles. Water-filled pore spaces within coarse bed substrates are critical refuges at high flow for fish and macroinvertebrates. Fish and invertebrates also can seek refuge from drought in groundwater underlying the stream. Fish and invertebrates may reach this
refuge through the burrows of larger organisms (alligators, burrowing catfish). Such refuges from erosion or drying of the riverbed are lost to the community when coarse substrates become embedded with fine sediments. Excessive mobilization of fine sediments is one of the most widespread forms of environmental degradation of river ecosystems; it is caused by land-use practices such as forest clearing, road construction, agriculture, and stock grazing.

Animals that survive drought or flood in refuges, as well as attached algae, mosses, and microbes that are not completely removed from rock surfaces become the seeds for recovery during ecological succession, the process that re-establishes river biota after disturbance. Surviving organisms are joined by colonists that immigrate from other habitats into recently disturbed, sparsely populated areas. For example, aquatic insects rebuild their populations from the ‘air force reserve’ of winged adult aquatic insects.

Organisms at different trophic positions in river food webs have different mobilities and vulnerabilities to disturbance. Because predators are often more mobile than rooted, drifting, or attached prey, they often survive disturbances that exterminate much of the biota at lower trophic levels. As food webs recover from disturbance during succession, the first prey species to recover or colonize tend to have traits that favor high dispersal and high growth rates, rather than defensive traits such as toxins, armor, or protective attached shells that require organisms to allocate energy and nutrients away from growth. During early stages of succession, food webs tend to have surviving predators that encounter relatively edible, vulnerable prey. Therefore, disturbances in rivers often cause food webs to have food chains that link predators to consumers of plants (herbivores). Energy from primary producers (plants) flows efficiently up these food chains to predators.

The Eel River of Northern California has a Mediterranean hydrologic regime; rainy winters precede the biologically active low flow season of summer. Each spring, the green macroalga *Cladophora*...
glomerata, which dominates primary producer biomass of summer, initiates growth vegetatively from basal cells that survived winter flood scour on stable boulder and bedrock substrates (Figure 1). Cladophora and other algae are grazed by invertebrates that vary markedly in their vulnerability to local predators. Mobile, unarmored taxa such as mayflies and chironomids are vulnerable to predatory invertebrates and fish. In contrast, heavily armored taxa (e.g., stone cased caddisflies) and sessile grazers (immobile grazers: some chironomids, caddisflies, and aquatic moth larvae) are less vulnerable. Summer biomass of Cladophora is affected by predatory juvenile steelhead trout if flood scour occurred during the preceding winter. During flood years, fish suppress either herbivores or small predators that affect herbivores, thus exerting indirect effects on algae. During drought years without winter flood scour, large armored caddisflies that are invulnerable to fish abound during the subsequent summer, and Cladophora grows only when these caddisflies are experimentally removed. Thus, drought years produce shorter food chains in which fish fail to enhance algal biomass because of predator resistant grazers. Flood disturbance, by suppressing these resistant grazers, sets the stage for fish-mediated enhancement of algal growth in this river food web (Figure 2).

In a small Montana stream, J. McAuliffe found that interactions among sessile grazers also were influenced by frequency of disturbance. On shallow cobble substrates (15–24 cm deep) that were infrequently disturbed, a sessile and highly territorial caddisfly, Leucotrichia, dominated, and excluded other mobile and sessile grazers, whose densities and diversity increased when Leucotrichia was experimentally removed. The competitive dominance of Leucotrichia also was disrupted when the stream bed dried. After these disturbances removed Leucotrichia, short-lived subordinate competitors including the midge Eukiefferiella colonized the newly inundated habitats. Thus, changes in river discharge through time determine the interactions of organisms that make up the river food web.

Changes in Interactions across Space: Depth Zonation

In gravel-bed streams of central Panama, armored catfish (Loricariidae) are the dominant grazers of algae. These grazers can outgrow smaller swimming predators in streams. Armored catfish do not, however, graze in shallow water where they are vulnerable to birds and other large predators. Herons, egrets, and kingfishers fish most frequently and effectively in water <20 cm deep, where there is insufficient warning between the bird’s surface splash and its strike for fish to escape. In streams of central Panama, high algal biomass rims the river margin. Rock and wood

Figure 2  The food chains that control Cladophora biomass are longer following winters with scouring floods that remove predator resistant grazers, and shorter following drought winters, when invulnerable grazers like the caddisfly Discomoecus persist. (Photo credits: mayfly and Dicosmoecus: Will Swalling, high flow tributary of Eel River: Bill Trush.)
substrates that have green carpets of attached algae in shallow areas become abruptly barren when deeper than 20 cm, indicating a spatial threshold. Above this threshold, in shallow water, birds protect algae from grazing fish; below the threshold, in deeper water, unimpeded grazers prevent accumulation of algal biomass. Similar patterns occur in pools along prairie-margin streams of Oklahoma (Figure 3).

The studies of *Leucotrichia* in a Montana stream and of loricariid catfish in a Panamanian stream both illustrate the difficulty of inferring from casual observation the processes that determine distributions and abundances of river organisms. Without investigating interactions with other organisms, an observer might reasonably assume that attached algae are more abundant in shallow water because they escape flood scour or experienced higher light exposure in shallow water. Likewise, an observer unaware of the competitive effect of *Leucotrichia* might assume that the midge *Eukiefferiella* prefer or differentially settles on shallow stream substrates. In both cases, the simple explanations are incorrect. Ecology is replete with examples in which the importance of a competitor or a consumer on the distribution and abundance of other organisms can be revealed only by an experimental manipulation or a ‘natural experiment’ in which algal abundance or other food-web characteristics could be compared over space or time in the presence and absence of species that affect them. Because interactions usually are hidden, their role in driving ecological patterns in rivers and streams is easily underestimated.

### Changes in Interactions across Space: Position in the Drainage Network

Stream ecologists have long been interested in the effects of systematic downstream changes in environmental factors affecting the distribution, abundance, diversity, and energy sources of stream organisms or functional groups of organisms. We still know very little, however, about changes in species interactions, food-web composition, and ecosystem functions along river drainage networks.

Ecological regimes are sets of conditions and constraints that produce specific outcomes of ecosystem functions or food-web interactions. Ecological regimes may provide answers to questions such as these: Where or when can grazers in streams suppress algal biomass? Where or when can juvenile fish grow and thrive? Where or when can fishing birds remove or exclude fish, or can bats forage effectively over rivers on emerging aquatic insects? Ecological regimes vary across space and time.

A spatial threshold control of algae by grazers occurs in headwater tributaries of the South Fork...
Eel River. Stable isotope analyses have shown that the dominant headwater grazer, larvae of the caddisfly Glossosoma, grows upon algal rather than terrestrial carbon (McNeely et al., 2008). Experiments revealed that Glossosoma cannot suppress accumulation of algal biomass in very small streams (basins < 2 km²) but, in streams with watersheds > 2 km², Glossosoma does reduce the accumulation of attached algae. Removing Glossosoma from the larger streams visibly increases turfs of diatoms, and also increases the flow of algal carbon to other insects, such as mayflies, which are more vulnerable to fish than Glossosoma is. Understanding how species interactions control algal biomass, and the access of vulnerable grazers to algal carbon that subsequently passes to fish and other predators, shows how the ecosystem might respond to future change. For example, if a parasite eradicated Glossosoma from the Eel River, the landscape (drainage area) thresholds at which steelhead trout and other predators could derive energy from herbivores that eat algae might move upstream.

**Changes in Biomass Distribution and Elemental Fluxes Mediated by Interactions and Movements of River Organisms**

Grazers can track the growth rates of their algal foods. Such tracking has profound effects on the distribution of algal biomass in rivers. Armored catfish in streams of central Panama track algal productivity closely from pool to pool, thus making efficient use of the spatially variable algal productivity, which is affected by heterogeneous shading from forest canopy. The Panamanian studies showed that algae grew up to 16 times faster in sunny than in dark pools, but grazing catfish were 16 times more abundant in sunny than in dark pools (Power, 1984). As a result, algal standing crops (biomass accumulation) were similar in dark, half-shaded, and sunny pools. Pre-reproductive catfish also grew (and survived) at the same rate in sunny, crowded pools and in dark, uncrowded pools. In this Panamanian stream, the grazers suppressed heterogeneity in algal biomass that would otherwise have resulted from pool-to-pool variation in solar radiation reaching individual pools.

The opposite pattern occurred in a stream of similar size in south-central Oklahoma, where light was intense and similar from pool to pool. Algivorous minnows (Campostoma) are the dominant grazer in this prairie-margin stream. Campostoma is vulnerable to predatory bass. Schools of Campostoma can denude stream substrates of algae. Barren pools, however, often are adjacent to pools that are filled with filamentous green algae. The green pools lack Campostoma and contain their predators, spotted and largemouth bass. Experimental transfers of bass and Campostoma can change pools from green to barren (by removing bass and adding Campostoma) or barren to green (adding bass to a Campostoma pool) within weeks. Natural floods that rearrange bass and minnows among pools trigger the predicted changes in algal biomass.

If grazers are able to track their resources, they can offset differential algal accumulation despite large spatial heterogeneity in algal growth rates, but when grazers are constrained in their movement by predators, great heterogeneity of algal biomass develops, even when environmental contrasts among habitats in algal growth rates are small. Without experiments, an observer might think that differences in algal biomass distribution among pools in the Oklahoma stream arise because of differential algal resources (e.g., nutrients). Similarly, the uniformity of algal biomass in the Panamanian stream might be interpreted as meaning light is not limiting to algae in this habitat; in fact such an inference that has been made in other rivers without recourse to experiments that could check for the importance of species interactions in controlling algal abundance.

Ecological regimes that determine where algal biomass can or cannot accumulate have important consequences, not only for the animals that feed from or live within algal turfs or mats, but also for fluxes (movements) of nutrients and organic matter through watersheds. Downstream solute fluxes are of societal concern, as nutrients or organic matter not retained high in drainage networks can accumulate downstream, with potentially adverse effects, such as eutrophication of drinking water reservoirs or harmful algal blooms in lowland water bodies or nearshore marine environments.

Stream ecologists have developed models of the spiraling downstream movement of nutrients (e.g., P, N, C), which includes not only downstream movement by water flow, but also periodic interruption of movement caused by nutrient uptake and release, often through uptake by the biota. Flowing water ecosystems that tend to immobilize atoms of nutrients through use and re-use for local biological production are characterized by short spiral lengths. Lateral wetlands greatly increase retention times and spiraling lengths for nutrients in river networks. Less retentive channels, such as those that have been straightened artificially, tend to have longer spiral lengths, less biological production per length of channel, and are less effective at buffering downstream waters from eutrophication. Species interactions influence nutrient spiraling through several paths. Of these, biological backflows caused by salmon...
migration, predation, and scavenging have recently received considerable attention.

One of the earlier studies of biological flows mediated by fish migration was done by Hall (1972) in New Hope Creek, North Carolina. He found that upstream migrations of large fish such as redhorse suckers (*Moxostoma*) played an important role in maintaining phosphorus reserves in New Hope Creek's headwaters. More recently, other scientists have documented large backflows of marine-derived nutrients on Alaskan rivers by migrating salmon, which are then carried upslope out of river channels to riparian vegetation by bear, eagles, mice, and other birds and mammals that prey on or scavenge these salmon. Nutrients may also be carried upslope across river valleys by emerging river insects and their terrestrial predators. The ecological importance of these backflows relative to nutrient cycles in situ is still largely unknown. Clearly, however, upstream and upslope fluxes mediated by large vertebrates were much larger before humans reduced their populations. Humans have also blocked vertebrate migrations through river habitats with dams, levees, channel simplification, and by eliminating beavers and large trees and logs that increased habitat complexity in rivers by forming deep pools, undercut banks and floodplain water bodies and marginal channels.

### Forecasting Ecological Change in River Networks

River networks and their watershed source areas are experiencing accelerating change in climate, land use, and biota (e.g., invasions and extinctions). The pace of global environmental change demands ecological forecasting over time scales of societal importance, e.g., decadal. Insights from local observations and experiments must be expanded in spatial scale (‘upscaled’) to be useful in predicting effects at the watershed scale. Similarly, effects of regional changes in climate, land use, or biota must be ‘downscaled’ to local environments. Ecosystem science can reveal the mechanisms that will either foster or destroy the resiliency of watershed ecosystems, and sustain or damage the vital ecosystem services that watersheds provide: clean water supplies, soil stabilization and fertility, and biota with ecological as well as cultural or commercial value. Ecological scaling requires an understanding of the linkages between climate, landscapes, food webs, and ecosystem functions.

Ecological forecasting remains challenging because of three factors: (1) the spatial heterogeneity and temporal fluctuation of environments, (2) the diversity and idiosyncrasies of the biota interacting with these environments, and (3) species–environment interactions that are mediated indirectly through webs of interactions with other species and physicochemical factors. Recent advances in mapping, sensing, and tracing technologies have greatly improved documentation of ecological interactions. Remote sensing technologies (e.g., airborne laser altimetry, multispectral imaging from satellites) can resolve land cover and provide topographic data that allow us to map whole watersheds or even larger regions. Concomitantly, automated wireless sensing networks hold out the promise of monitoring environmental conditions at scales that for the first time have the necessary resolution to capture variation meaningful to individual organisms. Finally, over the past several decades, ecologists have made increasing use of tracer technologies, particularly involving stable isotopes, to study movements of organisms and fluxes of biologically relevant materials. These technological advances will enhance the scope and resolution with which key ecological patterns and processes can be analyzed, and will improve ecological upscaling, downscaling, and forecasting.

A very old and unresolved question in ecology is whether distributions and abundances of organisms are controlled primarily by the physiological constraints and requirements of individual species or by interactions such as competition and predation. The question resurfaces in light of attempts to predict ecological responses to global climate change. Will climate envelopes (specific ranges of climate conditions) based on the physiological requirements and tolerances of individual species suffice to predict their fate under greenhouse warming, or must species interactions also be considered? Indirect feedbacks mediated by species interactions are important in forecasting effects of climate change in several terrestrial systems (e.g., boreal wolf-moose-spruce ecosystems, or California grassland). In rivers, the direct adverse effects of scouring floods on algae can be reversed within a year by the indirect effects of flood scour on the biota that grazes algae, and the direct effect of light environment on algal accumulation can be completely obscured by food-web interactions of algal grazers and their predators. Advanced technologies, combined with careful natural history observations and field experiments (Figure 4), can allow us to compare more quantitatively the relative importance of ecophysiological constraints on individual species versus higher-level limitations imposed by ecological interactions. River networks, with their dynamic, heterogeneous, but partially predictable physical environments, and their crucial roles in maintaining health of ecosystems and societies, must remain foremost as an arena for this exploration.
**Glossary**

**Autotrophs** – Organisms that use light or chemical energy to convert inorganic carbon to organic matter, thus producing their own biomass.

**Climate envelopes** – Ranges of climatic conditions (temperature, moisture, radiation intensity, etc.) within which a species can persist, through adequate survival, growth, and reproduction.

**Disturbance** – A pulsed event that kills or removes organisms, freeing space and resources.

**Functional groups** – Groups of species or life stages of species that function in similar ways, for example, consuming similar types of resources, or exerting similar effects in biogeochemical cycles. Functional groupings are flexible; they are defined according to the particular process under investigation (e.g., processing of organic matter).

**Hydraulic geometry** – A set of empirical relationships that predict changes in the depth, width, or velocity of rivers from their discharge, either at a station over changing discharges, or downstream at a discharge of a given recurrence interval.

**Hydrograph** – A record over time of the stage (water level) or discharge (flow) of water in a river past a specific cross section.

**Primary productivity** – Rate of conversion inorganic carbon to organic matter by autotrophs.

**Sessile** – Living in a stationary position. Sessile animals often build and live within protective retreats that they attach to rock, woody debris, or vegetation.

**Spiraling (carbon or nutrient)** – The downstream movement of atoms through rivers, interspersed with periodic uptake and release (cycling) by biota or abiotic substrates.

**Ecological succession** – The sequence of processes that re-establishes biota after disturbance.

*See also:* Algae of River Ecosystems; Benthic Invertebrate Fauna, Small Streams; Hydrology: Streams.

**Further Reading**


