REVIEW SUMMARY

HYDROLOGY

Linkages between flow regime, biota, and ecosystem processes: Implications for river restoration

Margaret Palmer*† and Albert Ruhi*

BACKGROUND: Early civilizations developed around seasonal river floodplains, and the natural rhythm of rivers remains critical to humans today. We use streams and rivers to meet drinking water, irrigation, and hydropower needs by storing and moving water in complex ways, at the times and places of our choosing. Consequently, many of Earth's rivers have flow regimes that are "unnatural" in magnitude, frequency, duration, and timing. The rise in river degradation globally has motivated research on the link between hydrologic alteration and declines in valued biota. At the same time, largely fueled by new technologies and methods, research has expanded to understand the patterns in, and drivers of, riverine processes like primary production, in both near-pristine and degraded rivers. A third line of research, stymied by how difficult it has been to restore degraded rivers, has called for process-based restoration, building on knowledge from the other two research thrusts. Today's hydroecological science seeks to understand the mechanisms whereby flow regimes affect biota and ecosystem processes, and the interplay between them, in a three-way interaction we call the flow-biota-ecosystem processes nexus.

ADVANCES: By shifting the focus from static patterns at sites to dynamic processes along river networks, advances are being made to understand the interactions and feedbacks at the nexus. Fueled by increasingly available time-series data and novel modeling, emerging research ranges from studies on regime-based properties such as flow periodicity and its change, to studies on river network structure and associated spatial variation in flow and water chemistry. These studies demonstrate how flow variability influences long-term persistence of riverine assemblages, and they are disentangling the direct effects of flow on communities and ecosystem processes from its indirect effects (e.g., via species interactions, light-blocking turbidity). Changes in temporal patterns in flow magnitudes can increase risk of community collapse and alter key ecosystem processes such as primary production. Growing research shows that storm flows not only enhance inputs and downstream export of terrestrially derived carbon to rivers but, when associated with sustained hydrologic connectivity with soils, exert particular influence on water chemistry and biogeochemical processes that can influence food webs. Increased availability of environmental sensors has stimulated research, showing that extreme flows may impart disproportionate impacts on stream metabolism, but the relationship can depend on the predictability of those flows. Research combining changes in flow patterns with stable isotope analyses is revealing how temporal fluctuations in habitat, and in the quality and quantity of basal resources, influence trophic pathways and resulting food-web structure. Evidence suggests that restoring particular facets of a flow regime can produce desirable conservation outcomes, but context is paramount. Restoration actions going beyond discrete flow events and enhancing groundwater-influenced river habitat or redirecting subsurface flow paths may be critical in future climates.

OUTLOOK: Our understanding of the flow-biota-ecosystem processes nexus is still incomplete and is a frontier research topic. Challenges include connecting organismal and ecosystem-level processes, and understanding the role of microbial communities as intermediaries. Capturing the effects of watershed-level physical and biogeochemical heterogeneity, and parsing out direct, indirect, or cascading effects of flow alteration on biota and processes would also reduce uncertainty in restoration outcomes, particularly in novel, nonstationary environments. Understanding how much flow restoration alone can achieve in urban watersheds is an urgent need, as is translating findings from hydroecology to design green infrastructure and flow release programs from reservoirs. These management tools may offer growing opportunities to experiment with flow regimes, which will assist in refining process-based river restoration. Both solid science and effective translation into practice will be needed to curb the fast pace of global river ecosystem degradation. ■

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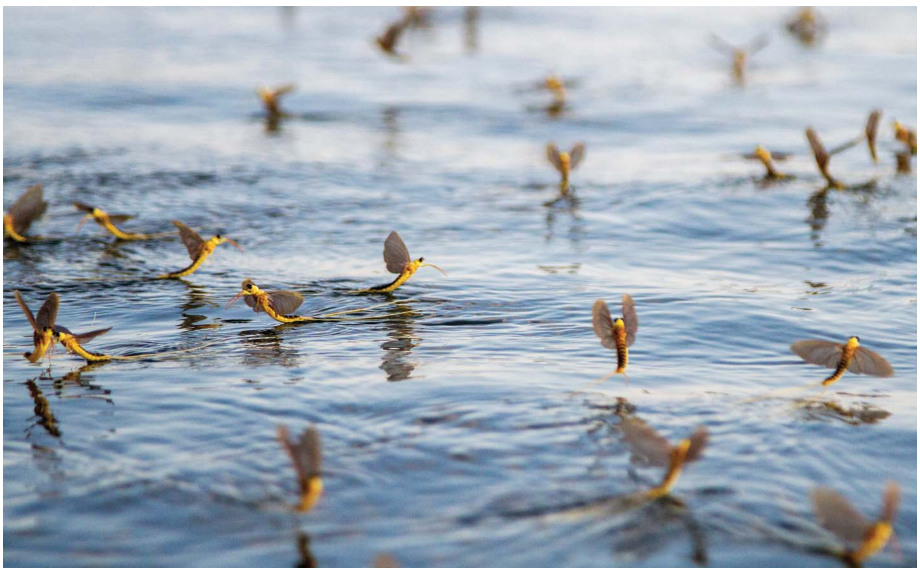

River flow regimes have shaped the life history strategies of plants and animals over evolutionary time scales. River regulation and associated alteration of flow and thermal regimes alter organismal development, often shifting important events such as insect emergence, depicted here by *Palingenia* mayflies entering their winged, flying stage to mate.

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REVIEW

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Linkages between flow regime, biota, and ecosystem processes: Implications for river restoration

Margaret Palmer[1]*† and Albert Ruhi[2]*

River ecosystems are highly biodiverse, influence global biogeochemical cycles, and provide valued services. However, humans are increasingly degrading fluvial ecosystems by altering their streamflows. Effective river restoration requires advancing our mechanistic understanding of how flow regimes affect biota and ecosystem processes. Here, we review emerging advances in hydroecology relevant to this goal. Spatiotemporal variation in flow exerts direct and indirect control on the composition, structure, and dynamics of communities at local to regional scales. Streamflows also influence ecosystem processes, such as nutrient uptake and transformation, organic matter processing, and ecosystem metabolism. We are deepening our understanding of how biological processes, not just static patterns, affect and are affected by stream ecosystem processes. However, research on this nexus of flow-biota-ecosystem processes is at an early stage. We illustrate this frontier with evidence from highly altered regulated rivers and urban streams. We also identify research challenges that should be prioritized to advance process-based river restoration.

Rivers have been critical to human existence since antiquity and are a central part of the biosphere. Flowing waters sustain riverine, terrestrial, and marine biodiversity, and make important contributions to global biogeochemical cycles. However, river ecosystems are increasingly degraded by dam building, diversion or abstraction of water, clearing of land, and climate change. Some rivers that once were healthy and diverse, now only support drought- or pollution-tolerant species; others shunt eutrophic water toward coastal regions or offer new habitat to non-native species. These degraded rivers all have one characteristic in common: some or all aspects of their flows have been altered (Fig. 1).

Flow regime, or the characteristic pattern of flow variation, has long been known to be a key driver of a river's structure and functioning (*1*). The characteristic magnitude, frequency, duration, timing, and rate of change in river flows have shaped a wide range of species adaptations—from life history strategies to behaviors and morphologies of both aquatic and riparian organisms (*2*). A river's flow regime also influences in-stream and flood-plain ecosystem processes, including primary production and nutrient cycling. Because flow dynamism is central to a river's functioning and its ability to provide ecosystem services, flow alteration is rarely inconsequential.

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When flows are altered, a combination of biotic and abiotic pathways are triggered. For instance, flash floods that reduce predators can have cascading biotic effects on primary producers and on associated nutrient dynamics. Flows that increase suspended sediments may inhibit organismal feeding and reproduction or reduce primary production. These are both examples of indirect abiotic effects. Although altered flows are often not the proximate mechanism of ecological degradation, they can exacerbate the impacts of other abiotic stressors (*3*). For example, extreme low flows resulting from excessive withdrawals can increase water temperature and pollutant concentrations to the point that they exceed tolerable levels for organismal survival or reproduction. The mechanisms linking flow regime alteration to ecological degradation can be numerous and complex.

Given the magnitude and global extent of river degradation, it is fitting that the United Nations Decade on Ecosystem Restoration has just been declared (*4*). Science to heal streams and rivers has never been more needed. Most restoration practices have focused on improving channel morphology or habitat, and, unfortunately, recovery of biodiversity or species of interest has proven difficult (*5*, *6*). This has prompted increased calls by scientists to move from morphological to ecosystem-level "process-based" practices (*7*) that focus on restoring flow regimes, as well as other physical and ecological processes that sometimes covary with flow and support aquatic communities. In this Review, we summarize the current understanding of the relationship between river flow regimes, biota, and ecosystem processes and outline how future river restoration can benefit from a better understanding of the three-way interaction that we call the flow-biota-ecosystem processes nexus (Fig. 2). We address the following: How does flow variation control river biota, directly and indirectly? How does it control river ecosystem processes? When flow regimes are altered, are changes in ecosystem processes coupled with changes in biota? Can these bodies of research inform restoration practice, and where could advances in hydroecology be better leveraged? We close by identifying key challenges and opportunities in hydroecological research.

This Review focuses primarily on fundamental research advances; however, regulated rivers (i.e., those with dams) and urban streams help ground findings in real-world problems. These two ecosystem types have experienced some of the largest shifts in their flow regimes and are central to numerous restoration efforts. Building off of advances needed to restore these degraded ecosystems, we highlight research that can inform process-based restoration more generally. We show that, despite calls for improving the link between science and restoration in practice, there remains a great need to advance research on the flow-biota-ecosystem processes nexus. This need opens exciting opportunities for both fundamental and applied interdisciplinary research.

How does flow variation control river biota?

Flow is essential to river life but can also be a source of stress: scouring floods remove organisms, droughts stress organismal physiology, and flow conditions dictate the changing type, quantity, and quality of the physical habitat in which organisms live (*8*). However, flow variation also influences organisms indirectly by keeping predators, competitors, and invaders at bay (*9*, *10*), by controlling the energy sources that enter the food web (*11*), or by affecting movement of organisms and matter across river networks and floodplains (*12*, *13*). At the inception of the natural flow regime concept (*1*), the study of flow-ecology relationships focused on static representations of flow and local-scale research. Over the past 20 years, important progress has been made toward understanding how ecological communities respond to dynamic flow regimes across entire river networks.

Organisms respond to patterns of flow variation

Stream ecologists have long known that low- and high-flow events can temporarily reduce abundance and diversity of invertebrates and fishes, particularly when droughts fragment the riverine habitat or when spates mobilize the streambed. However, it is not only discrete events that are important: long-term patterns of flow variability have historically selected for organismal life histories related to growth, reproduction, dispersal, and the ability to persist under physical and chemical stress. The increasing availability of temporally extensive and/or high-frequency datasets is now spurring the use of spectral methods, which allow the identification of dominant

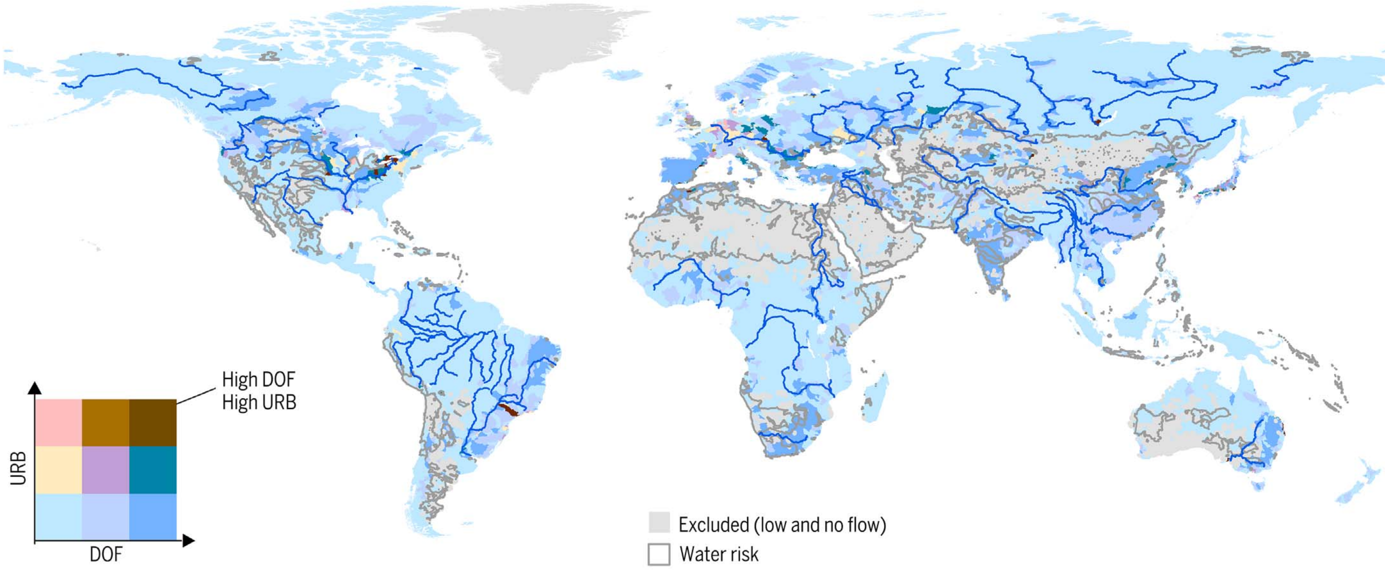

Fig. 1. Impacts of river fragmentation by dams, urban areas, and water risk across the world's watersheds. Degree of fragmentation (DOF) represents the effects of dams on longitudinal habitat connectivity, and urban impacts (URB) capture the degree of infrastructure development in riparian and floodplain areas (measured as nightlight intensity in urban areas) (*153*). We averaged river-reach level data at the watershed scale using streams with long-term average discharge higher than 1 m^3/s, and we then distributed averaged values among the following categories: <5% (low impact), 5 to 20% (medium impact), and >20% (high impact). Colors represent different impact combinations at the watershed level, and flow lines represent the major rivers of the world. Polygons outlined in gray are areas with "high" and "extremely high" exposure to water-related risk; an aggregated measure of water quantity, quality, and regulatory risk proposed by the World Resources Institute (*154*). Around 23% of the world's watersheds are subject to water-related risks, and 19% of the watersheds with flow show substantial impacts (i.e., in >5% of the river network) related to longitudinal habitat fragmentation by dams or urban areas. These dimensions capture the major sources of flow-related river ecosystem degradation.

frequencies, amplitudes, and phases in the environment (*14*). These characteristic patterns of variation, or regimes, can then be connected to organismal dynamics. For example, a wavelet analysis of discharge and abundance of silver carp larvae found a strong association between spawning and peak flows over a particular magnitude (*15*). Using a similar approach, temporal change in stream invertebrate diversity was found to be influenced not only by the seasonality of rainfall but by the reliability of this variability, i.e., its predictability (*16*).

Flow regimes differ across river types and climates (*1*) but can also shift temporally at a given place as a consequence of changes in climate, land use, or flow management (Fig. 3). Although changes in dominant frequencies in the environment can have strong impacts on communities, studying the effects of time-varying flow regimes is still rare (*17*). Faster flow cycles may filter out species with longer generation times and a preference for stable environments (*18*), and increased frequencies of extreme events (e.g., recurrent unpredictable droughts) may drive communities to novel stable states (*19*). However, we still do not know which temporal scales of flow variation may entrain organismal phenology and which may simply represent a source of stress. Although most work to understand this question has used correlational approaches, mathematical models based on metabolic theory and biomechanical constraints may help in predicting the effects of changing frequencies of environmental fluctuations and extremes on river organisms, food webs, and ecosystem processes (*20*).

Spatiotemporal variation in flow controls biotic persistence

River network structure and directional streamflow influence the movement of drifting organisms and materials downstream (*21*) and the main ways in which communities disperse and assemble. Experiments suggest that the local environment exerts control of community composition in the more isolated headwaters, whereas dispersal and environmental influences together operate in the well-connected main stem, or primary downstream channel. This is known as the network position hypothesis (*22*). Although findings have sometimes been inconsistent with respect to this idea, a recent study using graph theory and replicate fish metacommunities (i.e., multiple communities linked by dispersal) suggests that support for this hypothesis may depend on network structure and the degree of environmental heterogeneity in headwaters relative to the mainstem (*23*). Incorporating network structure into the study of flow regimes is also important because the dendritic connectivity of streams and rivers constrains organismal movement and associated persistence (*24*). This is particularly relevant to climate change because shifts in both wet-channel network structure and habitat quality across the network are anticipated to occur. In this vein, recent research has demonstrated that in arid climates, downstream sections of rivers may be more suitable for fish spawning, whereas in wetter conditions, the most suitable habitat occurs in the headwaters (*25*).

The spatial coordination of flow regimes across the river network also has key implications for biodiversity persistence. In sets of populations linked by dispersal, or metapopulations, a combination of diverse physical and biological features helps maintain asynchronous dynamics, thus maximizing stability at larger scales (i.e., risk spreading or portfolio effect). Only recently have the simultaneous effects of spatial and temporal variation in flows been incorporated into stream ecology. For example, widespread flood events may cause synchronous mortality of early life stages of salmonids [e.g., (*26*)], thus weakening the portfolio effect. On the flip side, river branches can provide diversity in flow and habitat conditions, ensuring that populations are maintained across the network. Using an agent-based model, validated with long-term fish time series, research has shown that population asynchrony tends to be higher across branches than within branches; thus, branching network complexity is key to preserving metapopulation stability (*27*). Given that dams and climate change are making flow regimes more similar, synchrony in flow-dependent ecological processes could be increasing as well. The phenomenon of environmentally forced synchrony has long been studied in terrestrial

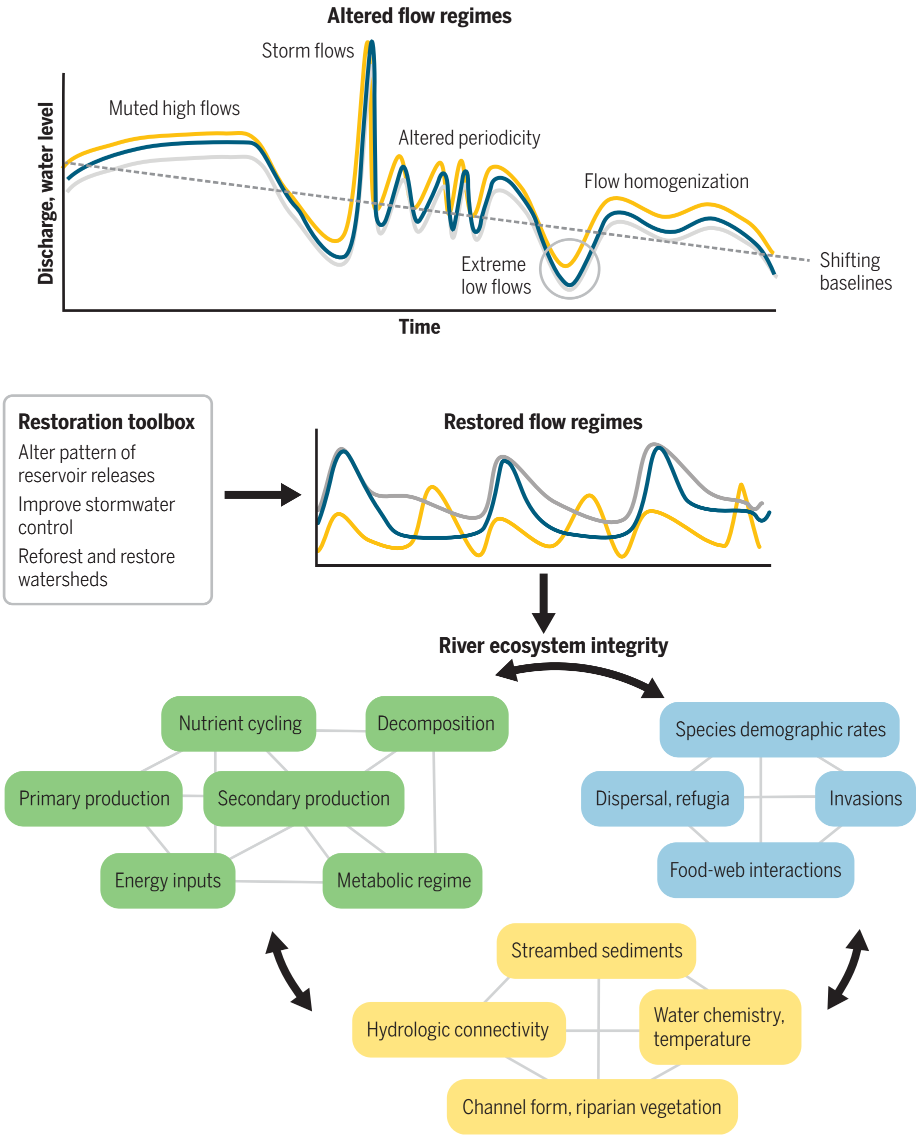

Fig. 2. Process-based restoration posits that actions must target processes, not patterns, that have been degraded. River ecosystems are sustained by a host of environmental conditions, or ecosystem structure (gold rectangles), which in turn influence ecosystem processes (green rectangles) and biotic processes (blue rectangles). These processes, as well as ecosystem structure, are all controlled by the flow regime. Thus, correcting facets of flow regime alteration may enhance river ecosystem integrity in both direct and indirect ways.

population ecology [Moran theorem (*28*)], and could represent an underappreciated, emerging risk in fresh waters.

Abiotic and biotic influences of flow

Stream ecologists traditionally interpreted the dynamics of communities as a deterministic result of biotic interactions, or as a stochastic consequence of the environment (*29*). However, research has shown that these fluctuate in relative importance over space and time and may even influence each other. For instance, biotic interactions may occur only under particular environmental conditions (*30*). Inferences gathered from long-term data, combined with time-series methods imported from econometrics, can help elucidate when and where abiotic influences have primacy. For example, multivariate autoregressive state-space models applied to long-term flow and fish community data showed that interannual variation in flow anomalies were the ultimate driver of the dynamics of a desert stream fish community (*31*). Although non-native and native fishes interacted, such effects were small compared with the direct effects of flows on the native component. Biotic interactions that emerge from known species-specific relationships between components of the flow regime such as flood timing and population dynamics can also be predicted from model simulations of community trajectory (*30*). A recent application of these interaction-neutral models found that flows departing from the natural regime simplified interaction networks among plant guilds in desert rivers (*32*).

A fundamental challenge for community ecology for decades has been quantifying the relative influence of abiotic (flow-driven) and biotic (flow-mediated) effects. This is important for the accurate design and prediction of restoration outcomes, including, for example, anticipating when flow alteration facilitates species invasions by creating new niches (*33*), by enhancing propagule pressure or eroding native enemies (*34*), or by a combination of these mechanisms. Distinguishing these could help managers compare the benefits of eradicating non-natives relative to restoring ecologically important facets of the flow regime.

Flow alteration filters species and traits

Trait-based approaches are becoming increasingly popular in hydroecology because they enhance comparison of flow-ecology relationships across climates (*35*), they lead to predictions about how community change may affect ecosystem functioning (*36*), and they identify the mechanisms that filter or promote particular taxa under stressful conditions, such as drought (*37*). In the case of flow intermittency, traits can be used to identify community tipping points by connecting local environmental conditions to organisms with traits that allow them to persist in isolated pools or wet sediment; or connecting network-level water conditions to the ability of highly resilient organisms to drift or actively recolonize from perennial refugia (*38*). Traits can also be used to assess restoration trajectories—for instance, by assessing fluctuations in the share of strategies that represent different life-history trade-offs [e.g., species limited by reproductive capacity or by resources (*39*)].

By studying a community's taxonomic characteristics (e.g., species composition) and functional characteristics (e.g., dispersal modes, feeding strategies), ecologists can determine to what extent trait redundancy across species may ensure against loss of functional diversity. For example, in a study on Alpine stream communities subject to climate change and flow regulation, functional diversity increased while functional redundancy decreased (*40*). This finding indicates that ongoing hydroclimatic change can reduce the ability of a community to withstand further alteration, even if trait diversity is high, because the persistence of individual traits may be linked to the fate of a few sensitive species. In an experimental study, communities affected by drought presented comparable taxonomic and functional decays, implying that these communities were both taxonomically and functionally vulnerable (*41*). The risk of community collapse in response to flow alteration also depends on the way in which "winning" and "losing" traits co-occur in a given species, and across species in a community, as a result of a particular stress. Thus, community-wide responses to a particular alteration may be stronger if species are maladaptive to that change, for instance, by being large-bodied, longer-lived, and collector-feeding (filtering particulate organic matter) in a scenario of increased flow variability (*18*). Understanding how flow alteration impairs species with

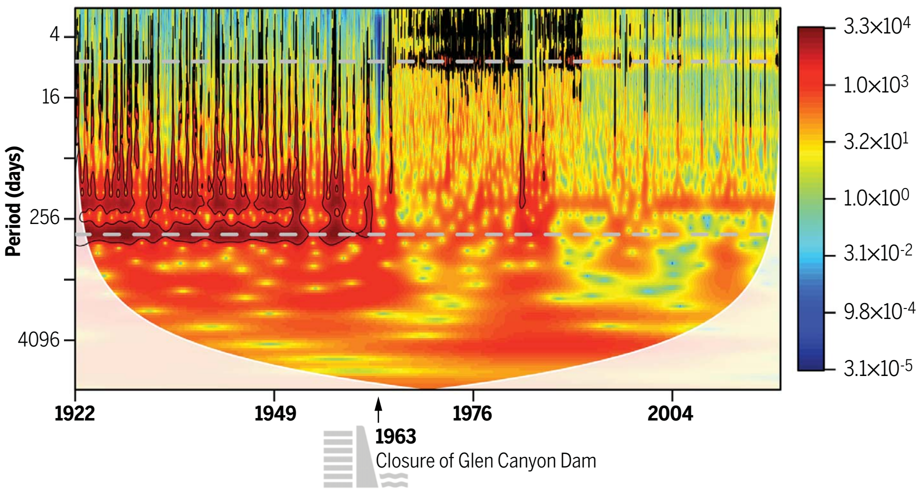

Fig. 3. Flow regime shifts in the Colorado River at Lees Ferry, Arizona, over the past 97 years (1922–2018). The flow regime changed drastically around 1963 with the closure of Glen Canyon Dam. Natural seasonality was dampened, and artificial weekly and subweekly scales emerged. Gray dashed lines indicate 7-day flow cycles resulting from flow management for hydropower, and yearly flow cycles resulting from extended base flows and spring snowmelt floods. Colors represent wavelet power; and confidence level contours identify statistically significant power. A very wet period in the mid-1980s, and the experimental releases that took place after 1996, restored flow events but not the regime. Across dammed rivers of the American Southwest, muted flow seasonality has opened niches for non-natives, particularly organisms adapted to living in stable, resource-limited environments at the expense of many native fishes adapted to highly variable (periodic or stochastic) flow conditions that characterized free-flowing hydrographs (*155*). Plot created with the biwavelet R package (*156*) using mean daily discharge data from United States Geological Survey station 09380000. [Dam logo: U.S. National Park Service]

traits that have effects on ecosystems (e.g., by particular feeding strategies) will help anticipate the risks of losing major ecosystem functions, such as detrital decomposition (*36*).

How does flow variation control river ecosystem processes?

Rivers produce, transform, and store organic matter (OM) and nutrients. Carbon (C) and nutrient concentrations and fluxes vary longitudinally and laterally, as river networks expand and contract with rain. These variations influence and are influenced by stream ecosystem metabolism, which can be described as net ecosystem production, or the difference between gross primary production (GPP) and ecosystem respiration (ER). The metabolic balance between heterotrophic and autotrophic production that provides resources for consumers can shift seasonally or with changing flows, as can hydrologic connectivity that influences inputs of OM and solutes to rivers (*42*). Increasing availability of sensors and advances in modeling (*43*) have made the study of metabolism, OM processes, and solute dynamics ripe for linking to biotic processes.

Flow variability and ecosystem metabolism

Spatiotemporal variability in ecosystem processes is a fundamental characteristic of rivers, and flow regime is a major driver of this variability (Fig. 4). Recent work shows that many rivers in the United States have strong seasonal patterns in primary production, with spring peaks for larger rivers and summer peaks for smaller rivers; generally, GPP is negatively correlated with high variation in daily discharge (*44*). In regions with little seasonality and/or continual canopy cover, GPP is lower and its patterns are less predictable (*44*). Bernhardt *et al.* (*45*) provide a comprehensive review of stream metabolism, the factors that influence it, and why it is difficult to predict. Flow has the largest effect at the extremes, such that at low flows when the streambed begins to dry, large drops in GPP occur (*46*). Storms also often reduce GPP (*45*). However, patterns may vary as a function of flow predictability. For example, research in a river characterized by predictable peaks during spring snowmelt found over two seasons that GPP rose during spring snowmelt sampling (*47*), whereas high flows during the winter and summer reduced GPP. Within a year, this pattern resulted in a switch from net autotrophic to net heterotrophic production.

The paths that water takes as it moves to and within a stream—a spatial aspect of its flow regime—influences metabolism. By coupling metabolism and chemistry time series with information on hydrologic connectivity and flow paths, ER was shown to increase in an organic-rich watershed during peak flows and remained elevated for weeks (*48*). Sustained hydrologic connectivity with soils likely fueled inputs of dissolved organic carbon (DOC) that promoted bacterial respiration. Such inputs can lead to nonlinear responses in metabolism. For example, increasing flows have led to decreases in GPP up to some threshold flow, beyond which GPP was suppressed by reduced water clarity from flow-elevated humic DOC (*49*). In the same vein, higher riverine GPP has been associated with reduced suspended sediments and high temperatures during low-flow droughts (*50*). When flows cease entirely and sections of riverbeds dry up, carbon dioxide fluxes to the atmosphere can be far higher than those in flowing sections of the channel (*51*), presumably because of spikes in aerobic microbial respiration; however, as is the case with methane in rivers, partitioning fluxes of these gases to changes in metabolism (aerobic or anaerobic) is difficult, particularly under variable flows (*52*).

Hydrologic connectivity drives solute dynamics

Research is growing on how hydrologic connectivity to hillslope soils influences water chemistry (*53*) and how variation in discharge and river stage influence the strength of bidirectional water exchanges that affect nitrogen (N) uptake, retention, and removal (*54*). Periods of hydrologic connectivity may be followed by long periods with limited exchange, which may differ greatly along the stream corridor. This can lead to complex C, N, and phosphorus (P) dynamics that influence or are influenced by microbial and algal productivity. When connectivity with watershed solute sources is extensive, inputs of solutes, such as DOC, may be so high that they exceed the ability of river ecosystem processes, such as microbial uptake, to regulate their fluxes (*55*). Theory posits that large storms pulse terrestrially derived dissolved organic matter (DOM) into streams and it is quickly shunted downstream by high flows where it is processed in larger parts of the network (*56*). However, how far DOM in pulsed water is transported is governed not only by discharge but by the composition of DOM. Understanding the relationship between DOM sources and its composition is being advanced by combining time-series data with isotopic information to evaluate spatial variability in hydrologic flow paths, transit time, and chemistry as water moves from the terrestrial to aquatic realms (*53*, *57*). It is difficult to measure biotic uptake in streams during storms, however, recent work suggests that assuming storm flows transport DOM too quickly for in-stream processing may be a poor assumption if the DOM composition renders it readily utilizable by biota (*58*). Although hydrologic connectivity is not a new concept, it is not typically considered part of the flow regime, yet it can be characterized by its timing, duration, and frequency and then linked to stream processes or patterns. New methods for quantifying connectivity [e.g., (*59*)] are emerging, and the energetic and water quality importance of network connectivity to soils and diverse landscape elements (such as wetlands and ponds) is becoming a major area of research (*42*, *59*).

Hydrology influences decomposition via consumers

Detritus (or decaying OM) plays key roles in stream ecosystems, and most consumers, even

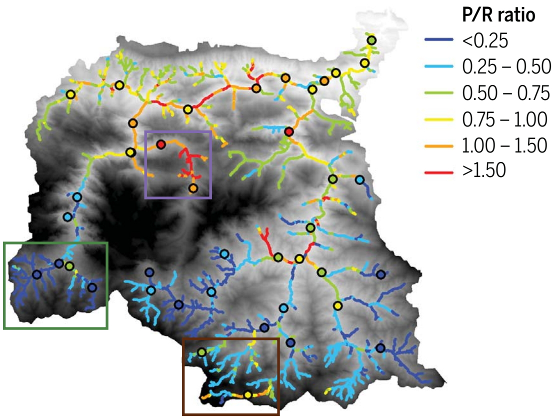

Fig. 4. Ecosystem metabolism patterns across a river network. Spatial patterns in river ecosystem metabolism for the Deva-Cares catchment in northern Spain, as represented by the ratio of gross primary production (P) to ecosystem respiration (R). A P:R > 1 indicates autotrophic processes dominate, so these river sections are accumulating or exporting organic carbon. P:R < 1 indicates dominance by heterotrophic processes in river sections that are receiving organic C input (e.g., from terrestrial sources). The boxes indicate regions of the network impacted by human pressures including deforestation (brown box), waste products from urban sites (green box), and a combination of the two (purple box). Such visualizations are useful to managers in understanding regions of concern that may need the most restoration actions. [Reproduced with permission from (*157*)]

apical predators, are at least partially supported by it (*60*). Macroconsumers break up particulate organic matter (POM) into small pieces, enhancing the overall mineralization rate by bacteria and fungi, and even moderate flows may result in export of OM, particularly fine POM resulting from macroconsumer shredding activities. Overall, however, microbes largely drive C losses through respiration (*61*) and although nutrient availability, temperature, and POM composition (e.g., leaf type) influence this, how flow mediates relationships has been more difficult to pin down. Recent work (*62*) designed to separate the effects that different components of the flow regime have on the mechanisms driving decomposition in perennial streams found that dissolution and microbial processing consistently exceeded the effects of fragmentation, and microbial processing was best explained by daily variability in discharge. When flow regimes become intermittent, the lack of water can impede microbial and consumer colonization of POM, resulting in decreases in decomposition, the extent of which is related to the duration of the drying (*46*, *63*). Consistent water cover is therefore important to decomposition, and thus shifts toward lower flows when litter inputs are high (e.g., in the fall) can have a large impact on consumers and associated food webs (*63*, *64*).

When flows are altered, are changes in biota and ecosystem processes linked?

To help ground this question in the world of restoration practice, we begin with a focus on two of the most common forms of river flow alteration: damming and urbanization. For the former, we emphasize hydropower dams because they are growing in number, they strongly alter flow regimes, and the mitigation of their impacts has spurred the field of environmental flow research. We also focus on urban streams because studies on the impacts of imperviousness have been extensive and these streams have been the target of numerous restoration efforts. We summarize knowledge on the effects of flow on organisms, ecosystem processes, and their interaction in these two types of river systems, and then describe how this can inform river restoration in general.

Urbanization and dams change flow regimes

With few exceptions, flow regimes below hydropower dams and in urban streams are highly altered at one or both ends of the flow spectrum. Regimes in impounded rivers are typically less seasonal than daily rainfall would suggest, particularly below large hydropower dams with high water-storage capacity rather than below smaller, less impactful run-of-the-river facilities (*65*). Hydropower dams can mute peak river flows, but power-generation cycles induce rapidly fluctuating flow patterns (hydropeaking) that often occur on human-relevant scales [i.e., hours to weeks (*18*)], tending to be more pronounced in seasons of high energy demand. Hydropeaking is often accompanied by spikes in temperature (thermopeaking), either cold or warm, depending on season and reservoir operation (*66*). Thus, downstream organisms and ecosystems are generally subject to multiple periodic stresses. In urban streams, baseflows can be higher or lower depending on watershed characteristics and infrastructure; however, peak flows are invariably larger than those prior to urbanization. Understanding the ecological impacts of urban stormflow is complicated by indirect effects on water quality. Increases in flow magnitude, frequency, and rates of change during storms leads to elevated concentrations of pollutants. Despite this, studies separating the causes of biological impairment have reported that the unique effects of altered urban flows can be significant (*67*, *68*). Spikes in stream temperature caused by runoff from hot pavement (*69*) add to stress on the biota.

Hydropeaking and urban stormflows might be expected to reduce primary production by scouring algae (*70*), yet some studies have reported elevated GPP or alternating periods of net autotrophy and heterotrophy (*71*–*73*). Light can override the effects of flow on metabolism by enhancing algal photosynthesis (*74*); however, if hydropeaking increases turbidity, GPP may decline (*73*). In urban streams, elevated GPP is often attributed to open canopies and/or to elevated nutrient concentrations, both of which often co-occur with their altered flow regimes (*72*). As discussed later, such shifts in primary productivity have been linked to changes in trophic structure, e.g., more algal-based food webs (*75*), depending on the relative availability of terrestrial carbon inputs (both DOM and POM) (*76*). Inputs of POM and its quality as a food resource change with landscape context (e.g., vegetative cover) and catchment hydrology (*77*), but POM availability can also be limited by flow variability, which can increase decomposition rates and decrease residence times (*78*, *79*).

As is the case for running-water systems in general, high flows in urban streams bring pulses of solutes, including N, DOM, and various pollutants (*80*). Solute dynamics and biogeochemical processes in regulated rivers have been insufficiently studied, with researchers focusing more on such processes in reservoirs rather than in downstream river ecosystems. We found no studies attempting to link urban or regulated flow regimes and solute fluxes to changes in food webs or stream metabolic balance. However, recent studies show shifts in microbial taxonomic and functional composition in response to pulsed urban flows (*81*), and these may help in exploring a potential link but are complicated by the fact that non-flow stressors affect consumer composition. For example, urban and regulated rivers typically have animal communities that are less diverse and composed of tolerant groups, often non-native. Hydropeaking and urban storm flows can certainly cause direct mortality via displacement and transport to unsuitable habitats, but many of the organismal effects are realized through indirect pathways. For instance, hydropeaking reduces the viability of river-edge egg-laying specialists by limiting their access to suitable spawning habitat, disrupting reproductive success and insect emergence (*82*). Flow regulation can even create ecological traps if organismal phenology shifts with the novel environmental conditions. For example, dam-induced warming triggered summer diapause in a mayfly, resulting in the loss of its last generation (*83*). Dams also isolate populations, harming organisms that require migrations to complete their life cycles, whether these are between riverine and marine habitats, or within the freshwater domain. By analogy, altered flow regimes in urban streams can also lead to isolated pools in streams with lowered baseflows. This can be associated with periods of hypoxia punctuated by extreme flow pulses, in which these streams become "scoured or suffocated" (*74*).

As illustrated using urban streams and regulated rivers, research is moving forward and hints at the three-way nexus but is clearly still inadequate to meet restoration needs. Studies on ecosystem processes below dams are particularly limited, and much of what we know comes from only a few river systems. Further, published work focuses primarily on benthic ecosystem processes immediately below dams rather than riverine planktonic realms, where productivity in large regulated rivers can be important.

Linking flow, biota, and ecosystem processes

Research on flow regimes that bridges organismal and ecosystem ecology has traditionally relied on states instead of rates, i.e., nutrient concentrations rather than uptake or fluxes, standing stocks of algae rather than productivity or metabolism, and abundance of organisms rather than secondary productivity. This work generally shows that flow variability suppresses, and stability increases, algal standing stock and grazer densities, with peaks in invertebrate biomass following those of algae [e.g., (*84*, *85*)]. Over the past decade, research began to focus on how flow regimes alter functional aspects of food webs. For example, biofilms in Mediterranean-climate rivers are thicker and metabolically more active downstream of flow-stabilizing dams (*71*). When flow variability increases below hydropower dams, fluctuations can reduce biofilm development and its quality as a food resource (*86*). Using experimental flumes subjected to hydropeaking, shifts have been found in periphyton fatty acid content, from important highly unsaturated compounds to nonessential saturated ones (*87*).

Indirect evidence suggests that flow-induced changes in dominant resource type (e.g., algae versus detritus), resource quantity (biomass), or resource quality (nutrient content) can propagate to higher trophic levels via bottom-up effects. For instance, detritivorous invertebrates were found to dominate species richness and invertebrate biomass upstream but not downstream of an irrigation dam (*75*); diets of omnivore insects indicated that flow stabilization shifted a detrital into an algal-fueled food web. Similar evidence comes from Glen Canyon Dam in the Colorado River (*88*). Near the dam, where primary production is high (*73*), food webs are simplified and gut content analyses have suggested algal production supports >50% of invertebrate and >70% of fish production, and the food web can be easily perturbed by flood disturbance. Farther downriver, food webs show increased reliance on detrital resources, have higher trophic efficiency, and are more complex and more resistant to disturbance (*76*). In contrast, recent work on seasonal tropical rivers found algal productivity and zero-flow disturbance did not explain food-web structure. In this case, it seems that highly mobile predators buffered the local effects of drought (*89*). This study, along with earlier ones at the site (*90*), is of particular interest because it links temporal patterns in predatory fish with flow-dependent availability of resources.

Only a few studies have provided evidence of top-down controls on food webs being influenced by flow variation. Fish in a tropical floodplain river were found to exert top-down control on primary producers, but only under certain hydrologic conditions (*91*). Similarly, in a Californian river, winter flood pulses were shown to control insect consumers late in the season, ultimately determining whether fish exerted top-down control on the lower trophic levels (*10*). These illustrate the importance of pulsed hydrology on resource-consumer linkages and show that not just standing stocks, but also the dominant controls structuring food webs, may fluctuate over time in response to flow variation.

An indirect line of evidence supporting the importance of the flow-biota-ecosystem processes nexus comes from theoretically oriented research on food-web structure. Changes in productivity, habitat size, and disturbance underpin the basis of the three main hypotheses of food-chain length, which state that chains should be longer in stable, productive, large ecosystems (*92*). Notably, flow regimes influence these three controls. Because food-chain length determines key aspects of a river ecosystem, such as the risk of trophic cascades or the pollutant accumulation in top predators, understanding how it is affected by flow alteration is important. However, understanding the interplay between the hypotheses of food-chain length and the flow-dependent biological mechanisms that allow food webs to shift in structure (e.g., predator invasions, local extinctions, consumers changing diets) is still a relatively recent endeavor (*93*–*95*). Evidence suggests that zero-flows shorten food chains mainly by keeping streams fishless (*94*, *96*), whereas stabilization of variable flows can lengthen food chains by allowing omnivores to feed on abundant, high trophic level prey (*95*).

New studies are also focusing on interactions between drivers of food-web structure that had been previously only been examined in isolation, such as disturbance regimes and ecosystem size, both influenced by flow regime. Using metabolic theory, predator biomass has been shown to scale with both prey resources and fluctuating stream habitat size, with reductions in predator size leading to declines in predator biomass supported per unit of prey biomass (*97*). Moving forward, the combination of habitat and metabolic constraints on predators may provide a basis to connect flow-induced disturbance, changes in ecosystem processes, and habitat fluctuations to riverine food-web structure. The metabolic theory of ecology (*98*) is a unifying framework that allows scaling responses of organisms to whole ecosystems, and may become particularly useful in situations where flow alteration affects organismal body size or water temperature. In such cases, strong changes in metabolic rates can be expected, affecting resource uptake and organismal growth to ecosystem-level production and respiration.

Finally, an important body of food web–related research that provides strong inferential evidence for the nexus comes from studies on animal-mediated nutrient cycling and ecological stoichiometry. Theory suggests detrital and algal food webs may be linked by cascading effects on nutrient cycling (*99*), and empirical work shows that organismal excretion and migration (which relocates C) may be important to this link (*100*) (Fig. 5). A recent study (*101*) showed that excretion of highly labile dissolved organic C, nitrogen (N), and phosphorus (P) by aquatic insects may be sufficient to support a substantial fraction of microbial energy and nutrient needs. Given that C availability can be too low to meet microbial energy needs [e.g., (*102*, *103*)], and that microbial activity enhances detrital quality to consumers (*104*), a C subsidy from excretory processes could be important, at least during low-flow periods. Additionally, microbial use of excreted dissolved organic nitrogen (DON) and DOP may release algae from potential competition with microbes for inorganic N and P; if this is the case, GPP should increase. Ecological stoichiometry may also be important for understanding constraints on organismal growth rates, as rapid growth disproportionally increases demand of P [as it is used in ribosomal RNA (*105*)]. This could, in turn, limit the ability of organisms to grow fast and exploit temporary habitats. Interestingly, elemental ratios can vary interspecifically in response to temperature or predation pressure (*106*)—factors that increase with low flows and habitat fragmentation. Overall, studies that link biota with biogeochemical processes remain rare (*107*), but analyzing flow regimes as a driver of element turnover rates may provide a way forward.

Can hydroecological advances inform restoration practice?

Shortfalls in the outcomes of river restoration have prompted calls to identify and restore processes that support and sustain biological communities, rather than focusing only on river geomorphology and habitat. In urban streams, scientists have critiqued an overemphasis on structural engineered approaches (*7*, *108*) that do little to restore the full flow regime (*109*). In large regulated rivers, identifying and restoring important features of the flow regime via dam operations is often possible (albeit expensive). However, that does not solve other problems associated with dams, such as habitat fragmentation (*110*), altered sediment and thermal regimes (*111*, *112*), or disrupted biogeochemical processes (*113*). Overall, efforts to alter reservoir releases or improve urban stormwater infrastructure to partially mimic a river's natural flow regime have great potential. Technologies are being evaluated for real-time management of urban flows, and novel ways to design flow releases from dams are being proposed (*114*, *115*); however, research still lags far behind the need for solutions. Importantly, the paucity of studies on the flow-biota-ecosystem processes nexus points to a need for more integrative research connecting hydrologists, population and community ecologists, and ecosystem ecologists in the context of restoration.

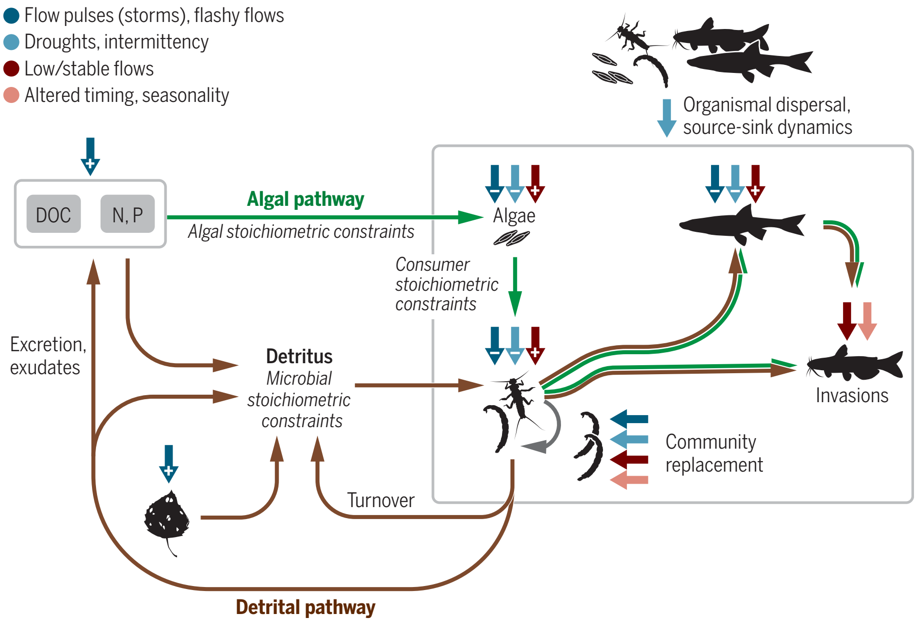

Fig. 5. Flow variation affects biota and ecosystem processes, and food webs integrate both. Hydrologic connectivity along river networks is a first, landscape-level filter constraining dispersal of organisms in river networks. Extreme flow variation (floods and droughts) are a source of disturbance to all organisms (gray box), but particularly to the higher trophic levels given their higher metabolic demands. In turn, flow variation controls inputs of nutrients and terrestrial leaf litter to the stream, which influences microbial activity and the relative contributions of the detrital (brown) and algal (green) pathways in sustaining aquatic consumers. Not just quantity but also food quality (e.g., C:N and C:P ratios) influence dietary choices of consumers and thus trophic transfer efficiency. Finally, alteration of flow regimes may influence all these compartments and may also open niches for new players. If biological invasions occur at the top of the food web, these have the potential to divert energy away from native predators and to alter food-web structure through top-down controls.

Restoring flow regimes rather than events

Scientifically informed flow designs may exist that maintain ecosystem integrity in regulated rivers (*116*, *117*), but these have produced mixed results to date. In the dam-altered Putah Creek in California, mimicking the natural timing of high and low flows enhanced native fish by improving their spawning habitat, reducing water temperatures, maintaining flowing conditions, and reducing the abundance of non-native species (*118*). However, other similar attempts have been less successful. In some cases, non-native fish density also benefitted from flow patterns mimicking an unregulated regime (*119*); in others, non-natives bounced back shortly after the flow release (*120*). These experiences illustrate that even natural flow features may have inadvertent negative effects if only part of the community or ecosystem is considered. Models for the Navajo Dam (San Juan River, New Mexico) show that adequately timed releases could simultaneously enhance native and minimize non-native fish populations (*121*), thus predicted benefits could surpass those of mimicking a natural flow regime, potentially persisting even during dry years. Another study using the "designer" flow paradigm (*114*) attempted to understand how different facets of flow variability control fishery production in the Lower Mekong floodplains. Time-series models combining discharge and fishery catch suggested that enhanced flood pulses and long inter-flood intervals may increase fishery yields.

Although environmental flow practices have mostly focused on re-creating discrete flow events (e.g., flood pulses), these can still serve as valuable experiments. An iconic example of a large-scale flow release is Minute 319, an amendment to the United States–Mexico treaty allowing opening of floodgates in the Lower Colorado River and a one-time rewetting of the parched Colorado River Delta (*122*). Although this pulsed-flow experiment did not promote establishment of native woody riparian seedlings, such trials can inform future restoration practices, for example, by determining whether the provision of bare, moist substrate enhances seed germination (*123*). Hypothesis-driven experimental flow releases combined with deep knowledge of target ecosystems can provide insights into restoration actions [e.g., (*124*)]. Still, an outstanding question is how flow regime restoration could be leveraged to restore other important, altered aspects of the ecosystem, such as sediment and thermal regimes. For example, cold-water releases by existing dams in climate-vulnerable basins could prevent organisms that thrive at low temperatures from becoming replaced by generalist, warm-tolerant taxa (*125*).

Although the concept of environmental flows is generally associated with impounded rivers, its relevance to urban streams is clear (*126*). However, because frequent high storm flows are viewed as the problem, reducing them generally becomes the only restoration goal. This is often attempted by shifting the spatial distribution of velocities within channels through manipulation of channel sinuosity, installation of flow-diverting weirs, or adding other structures. These approaches may reduce local erosion but rarely result in levels of water quality, ecosystem processes, or biodiversity in urban streams that come close to those of unimpacted streams (*127*, *128*). Focusing on the channel rather than the watershed context at large means that key ecosystem processes can remain compromised (*129*). A recent study compared time series of metabolism in two streams—one with stormwater ponds in the watershed, and the other restored by altering channel slope, banks, and in-stream structural complexity (*103*). The study found that peaks in GPP and ER in the "restored" stream were higher, more prone to resets induced by flashy storms, and that recovery time scales were longer compared with the stream in a watershed with stormwater measures (Fig. 6). Ponds are one type of nature-inspired green infrastructure used to restore streamflow to more natural conditions; tree plantings, constructed wetlands, and grass swales can in turn replace gray infrastructure such as concrete tunnels that capture and store water.

Distributing green infrastructure in watersheds helps restore streams because it targets the cause of streamflow alteration, including insufficient infiltration, groundwater recharge, and more generally limited watershed storage capacity (*129*). By tackling the cause rather than the symptoms of flow alteration, these practices can reduce ecological impacts that result from the cascading effects of altered flows, including poor water quality and temperature spikes. Research on the effectiveness of green infrastructure on restoring streams is sparse and limited by lack of data before and after implementation, although studies are beginning to appear. For example, upland green infrastructure in the form of shallow wetland-like pools that capture stormwater and reconnect it to the groundwater has been shown to enhance baseflows while reducing peak flows and pollutant loads more than restoration structures within the mainstem of the receiving stream (*130*). Similar structures built between stormwater outfalls and perennial streams did not modulate the timing, magnitude, or duration of urban storm responses, nor did they improve water quality or biodiversity (*131*), illustrating the need for researchers to understand how exact design and watershed context influence performance.

Spatiotemporal variability and restoration designs

Research showing how local and watershed-scale environmental drivers vary temporally and along river networks in ways that shape biota

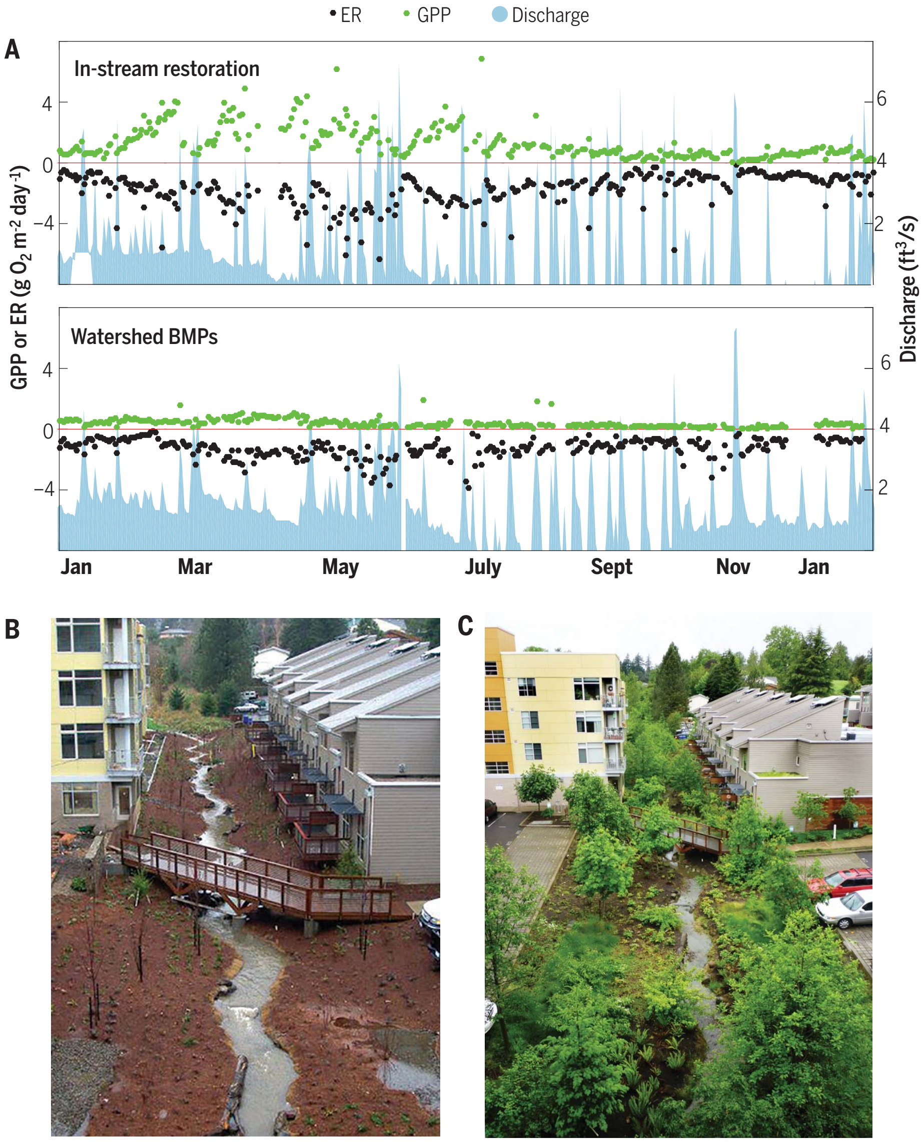

Fig. 6. Green infrastructure as a means to restore stream ecosystems. (**A**) Discharge and ecosystem respiration (ER; more-negative values mean higher respiration) and gross primary production (GPP) for two urban streams in which restoration efforts involved (top) modifications in the stream channel and (bottom) traditional stormwater best management practices (BMPs). [Reproduced with permission from (*103*)]. (**B** and **C**) Example of a comprehensive green infrastructure approach to ecologically restore an urban headwater stream that also supports the lifestyle of resident urban communities. (B) Stream at the onset of restoration and (C) after restoration. [Reproduced with permission from Greenworks, Portland, OR]

and ecosystem processes, can help prioritize selection of sites for restoration. For example, using the concept of river network saturation (*55*) to identify river sections where in-stream removal of nutrients cannot keep up with high source inputs of nutrients suggests that restoration actions targeting those sections may disproportionately improve water quality. Identification of subcatchments that disproportionately influence stream chemistry may also be informed by combining methods from landscape ecology and catchment hydrology focusing on the spatial scale of variance in water chemistry (*132*). Headwaters are often prioritized for restoration because poor water quality in them can have downstream impacts. Research showing that local environmental constraints on river communities are important in headwaters as well as in the larger channels but dispersal constraints are much less important in the former (*133*, *134*) implies that headwaters should be prioritized. However, research quantifying time-varying contributions of local communities to river-wide (network) biodiversity can also inform prioritization by identifying sites that host a disproportionate share of species, or that host unique species—for example, because they shelter sensitive taxa during critical flow bottlenecks. This idea encapsulates the concept of keystone habitats, or local sites that strongly influence metacommunity dynamics (*135*). This has been applied to aquatic invertebrates across intermittent river networks, by tracking time-varying, site-specific contributions to community dissimilarity (or beta diversity) (*136*).

Other approaches to prioritize restoration actions may be based on contributions to system-wide stability rather than numbers of individuals or species. For example, the restoration of fall-run Chinook salmon portfolios may be assessed via the contributions that different periods and locations make to metapopulation-wide stability, owing to spatiotemporal variation in habitat conditions (*137*). Additionally, interventions could promote conditions that are not important now but could be important in the future [i.e., proto-refugia (*138*)]. For example, restoration of groundwater-influenced habitats could mitigate future stress to drought-sensitive taxa under scenarios of increased intermittency. Patches of undisturbed land that protect flow regimes in streams within a larger catchment that is otherwise urbanized can be sources of colonists to restored sites. Priorities that focus on present degradation of river sections may fail to address site contribution to impairment or recovery at broader scales or under different scenarios. These insights indicate a great potential for new methods to prioritize restoration of both urban and regulated streams.

We know little about how altered flow regimes propagate through entire river networks, but work is starting to assess the cumulative effects of dams on flow regimes, as well as dam-level contributions to alteration. Although these approaches have largely focused on dam cascades [e.g., (*139*)], if expanded, they could help identify favorable sections in river networks to develop environmental flow operations. Here, experimentation could again help with testing of new strategies. For instance, large-scale flow experiments could be designed that coordinate releases among dams or between dams and free-flowing tributaries to enhance the restorative effects of natural pulses (*140*).

Hydrologic connectivity influences restoration

Recovering critical flow paths and their connectivity to rivers is important, but it remains a substantial challenge for flow-degraded rivers and streams. Whereas regulated rivers tend to have reduced lateral and longitudinal hydrologic connectivity, urban streams have unnatural levels of connectivity because pipes and overland runoff route water quickly. In both cases, fundamental hydroecological insights into streambed structure, landscape storage capacity, and groundwater connectivity can help to envision novel restoration approaches (*130*, *141*, *142*). More generally, hydrologic connectivity is becoming a framework to identify alternative ways to restore streams via stormwater management (*143*). For example, a recent study suggested that reducing road density and hydrologic connectivity between roads

Table 1. Research challenges and opportunities. Despite the progress that has been made in understanding how flow regimes affect biota and ecosystem processes, major challenges persist that prevent a complete understanding of the flow-biota-ecosystem processes nexus. Making progress on these challenges requires a mix of fundamental and applied research.

Topic	Research challenge	Opportunity
Connecting organismal to ecosystem-level processes	Research on the effects of flow on organisms and ecosystem processes has followed parallel tracks—hindering our mechanistic understanding of the flow-biota-ecosystem processes nexus.	Generate theory that connects concepts and frameworks that are well accepted in river community and ecosystem ecology. For example, the notion of environmental filters that connect regional to local composition via a combination of dispersal and environmental conditions (community ecology), with analogous theory on solute transport versus reactivity (ecosystem ecology).
	Our current understanding of the links between phenology of biota and ecosystem processes is precursory.	Use high-frequency sensors to characterize metabolic regimes at sites with ongoing organismal monitoring. Leverage citizen-science biodiversity data to detect spatiotemporal shifts in animal phenology (e.g., insect emergence, fish spawning). Use remote sensing tools to better understand links between hydrology and aquatic and riparian plant phenology.
	The link between stoichiometry and flow variation remains largely unexplored.	Repurpose data that is already being collected to test flow-stoichiometry relationships, e.g., studies using C and N stable isotopes to describe C:N ratios across flow regime types. Perform field experiments to quantify indirect effects of invertebrate and fish consumption on ecosystem metabolism.
Ecological consequences of hydrologic connectivity	The importance of anaerobic metabolism in carbon processing as flows cease and parts of streambeds dry is a major frontier research area.	Create networks of sites across different geologies and flow regimes that collect time-series data on methane, nitrous oxide, and carbon dioxide fluxes from intermittent streams.
	We ignore how biota in the wet phase is influenced by processes and patterns from the dry phase.	Research the functions of dry riverbeds. Use camera traps and drone technology to investigate the role of dry riverbeds as a dispersal corridor; metabarcoding to quantify "dark biodiversity" in the hyporheic.
	Wetlands and their links to stream networks are poorly delineated globally. Even in the United States and Europe, current wetland inventories do not capture these links, yet understanding how their connectivity to river systems influences network-scale ecosystem processes is needed.	Analyze time series from high-frequency sensors distributed in river networks varying in wetland connectivity. Further development and application of time-series methods used by neuroscientists.
	We need to identify the relationship between varying flows and solute dynamics associated with changes in catchment-scale hydrologic exchanges.	Design collaborative work among catchment hydrologists and stream ecologists combining methods to estimate transit times, residence times, and identify sources across heterogeneous landscapes. Link these properties to land management and water quality aspects.
Scaling and transferring flow-ecology relationships across space and time	We ignore how biodiversity responds to propagation of flow regime alteration across river networks.	Leverage extensive hydrometric networks (e.g., United States Geological Survey National Water Information System) to perform spatially replicated time-series analyses on flow, and use these to generate expectations on how river network position should mediate biodiversity responses to flow alteration.
	Flow-ecology relationships do not account for nonstationarity and abrupt change.	Use process-based models that account for mechanisms and associated uncertainties. When using time-series data and models, select methods that are robust to nonstationarity. Linear flow-ecology relationships should not be assumed.
	Current flow-ecology relationships assume that responses of species do not change over time.	Consider flow regime alteration as a process with ecological and evolutionary consequences. Include intraspecific variation in traits and potential for rapid evolution in models.

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Topic	Research challenge	Opportunity
Cascading implications of hydrologic alteration	We have a poor understanding of the interactions among physical drivers.	Build on large-scale flow experiments to test hypotheses on the combined effects of altered flow, sediment, and thermal regimes. Experiment with multilevel intakes in reservoirs. Promote collection of non-flow variables (e.g., temperature, water quality parameters) at hydrometric stations.
	At low flows, biota are being exposed to high concentrations of new classes of pollutants whose impacts are poorly known, especially if biotic impacts interact with impacts on ecosystem processes.	Design realistic experimental studies to advance knowledge on the ecological effects of multiple stressors. Collect long-term data at sites varying in contaminant inputs and hydrologic regimes. Link microbial to organismal and ecosystem-level responses.
Using hydroecological science to inform river ecosystem restoration	Environmental flow science largely ignores human dimensions.	Use methods that allow identifying causal networks in complex, socioenvironmental systems. Include human needs and thresholds in research on flow-ecology relationships.
	Environmental flows are generally prescribed at the scale of single infrastructures; restoration designs and assessment are generally at reach scales.	Promote coordinated, large-scale flow experiments and restoration designs at the river basin scale. Extend assessment of green infrastructure effectiveness beyond individual structures to infrastructure networks and link both to river outcomes.
	Environmental flows in impounded rivers generally target the conservation of some particular species, rather than outcomes at the food-web or ecosystem level.	Advance fundamental research on microbial–ecosystem process linkages. Expand the notion of designer flows to food-web structure and ecosystem services when possible.
	Environmental flow science has largely ignored surface water–groundwater interactions.	Expand science to understand the link between restoration actions, groundwater recharge, and inputs to streams. Provide science relevant to the implementation of new legislation on groundwater management (e.g., Sustainable Groundwater Management Act in California).
	Uncertainty regarding future hydroclimate and river flows is growing.	Refine regional climate models. Promote research on the interaction between land-use change and evapotranspiration. Incorporate groundwater influence in macroscale hydrology models.

and streams may improve water quality more than other restoration options (*70*). Additionally, research on the age and lability of DOC entering streams has shown how precipitation or land disturbance can change watershed flow paths (*53*), and this could inspire new restoration approaches focused on land use and soil properties. Many studies on hydrologic connectivity and network structure suggest a need for restoration to focus on landscape heterogeneity, especially on the presence of wetlands, lakes, and ponds (*144*). Such features are frequently lost in urbanized catchments, and outcomes could be improved by restoring or increasing connectivity with these ecosystems (*145*). Hydrologic connectivity associated with groundwater inputs or abstractions, land-use management, and return flows from wastewater treatment plants, also need to be considered in these initiatives (*146*).

Restoring hydrologic connectivity is also key to achieving biodiversity outcomes—particularly in dammed systems. Longitudinal connectivity for fish inhabiting dam-altered rivers can be enhanced by the construction of fishways and sophisticated passage facilities. However, monitoring data on the effectiveness of such interventions are still scarce, and available evidence suggests that passage effectivity largely depends on technology used and species-specific fish behavior (*147*, *148*). Although trap-and-transport programs for migratory fishes can help augment threatened populations (*149*), these practices often increase straying and thus the potential for genetic homogenization, as seen from juvenile salmon collected at dams and transported downstream to increase out-migration success (*150*). Overall, a combination of engineering and management solutions may be best to restore functional connectivity in dam-altered rivers. The link between hydrologic connectivity and ecological restoration is also central to considerations on where to build, remove, and reoperate hydrologic infrastructure. Hundreds of dams have been intentionally removed since the 1970s, and removal of large dams such as the Elwha River Dam (Washington, USA) has shown that restoring longitudinal connectivity can have immediate geomorphic effects with complex temporal dynamics (*151*). Infrastructure can also be designed, or reoperated, to manage for restoring lateral connectivity and enhanced floodplain processes. For example, the Yolo Bypass in the Sacramento River, California, has become a prime rearing and migration site for chinook salmon, showing that flood control and habitat for fish and wildlife do not need to be at odds (*152*). All these examples show the importance of integrating hydrologic connectivity in ecological restoration, whether the goal is to minimize the ecological effects of fragmentation, restore free-flowing watercourses, or operate green infrastructure to enhance infiltration, floodplain connectivity, or other ecological processes.

Research challenges and opportunities

Two decades of concerted efforts to research the effects of flow regime alteration have tremendously advanced our understanding of the ways in which streamflow influences biota and ecosystem processes. However, important challenges remain. These are mainly related to the scarcity of science connecting organismal to ecosystem-level processes through, for example, microbial links; the difficulty of studying watershed-level physical and biogeochemical heterogeneity and its influence on riverine processes and biota; the complexity of parsing out the direct effects of flow from flow-mediated effects and co-occurring stressors (particularly in urban streams); and the challenge of predicting outcomes when both the physical and the biological environments are changing.

Achieving a predictive understanding of hydroecological relationships is essential to designing successful, self-sustaining restoration actions in river ecosystems. However, translating basic hydroecological insights into restoration practice requires understanding the complexities of working within a human-dominated water cycle. Although it is rarely possible to restore all facets of a natural flow regime, ecologically informed designs may help mimic key aspects of the natural flow regime (e.g., periodic pulse flows), or create regimes that are not natural but maximize outcomes given socioeconomic constraints. In Table 1, we identify persisting and emerging challenges in hydroecological research. We pair each challenge with an opportunity (related to research design, technology, or implementation). We contend that these challenges should be prioritized to advance process-based river ecosystem restoration.

REFERENCES AND NOTES

1. N. L. Poff *et al.*, The natural flow regime. *Bioscience* **47**, 769–784 (1997). doi: 10.2307/1313099
2. D. A. Lytle, N. L. Poff, Adaptation to natural flow regimes. *Trends Ecol. Evol.* **19**, 94–100 (2004). doi: 10.1016/j.tree.2003.10.002; pmid: 16701235
3. S. Sabater, A. Elosegi, R. Ludwig, in *Multiple Stressors in River Ecosystems* (Elsevier, 2019), pp. 1–22.
4. United Nations, New UN Decade on Ecosystem Restoration offers unparalleled opportunity for job creation, food security and addressing climate change (2019); https://www.unenvironment.org/news-and-stories/press-release/new-un-decade-ecosystem-restoration-offers-unparalleled-opportunity.
5. A. W. Lorenz, P. Haase, K. Januschke, A. Sundermann, D. Hering, Revisiting restored river reaches - Assessing change of aquatic and riparian communities after five years. *Sci. Total Environ.* **613-614**, 1185–1195 (2018). doi: 10.1016/j.scitotenv.2017.09.188; pmid: 28954379
6. M. A. Palmer, K. L. Hondula, B. J. Koch, *Ecological Restoration of Streams and Rivers: Shifting Strategies and Shifting Goals* (2014), vol. 45.
7. T. J. Beechie *et al.*, Process-based principles for restoring river ecosystems. *Bioscience* **60**, 209–222 (2010). doi: 10.1525/bio.2010.60.3.7
8. S. E. Bunn, A. H. Arthington, Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environ. Manage.* **30**, 492–507 (2002). doi: 10.1007/s00267-002-2737-0; pmid: 12481916
9. K. D. Fausch, Y. Taniguchi, S. Nakano, G. D. Grossman, C. R. Townsend, Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. *Ecol. Appl.* **11**, 1438–1455 (2001). doi: 10.1890/1051-0761(2001)011[1438:FDRIRT]2.0.CO;2
10. M. E. Power, M. S. Parker, W. E. Dietrich, Seasonal reassembly of a river food web: Floods, droughts, and impacts of fish. *Ecol. Monogr.* **78**, 263–282 (2008). doi: 10.1890/06-0902.1
11. V. Acuña, A. Giorgi, I. Muñoz, U. R. S. Uehlinger, S. Sabater, Flow extremes and benthic organic matter shape the metabolism of a headwater Mediterranean stream. *Freshwater Biol.* **49**, 960–971 (2004). doi: 10.1111/j.1365-2427.2004.01239.x
12. K. Tockner, F. Malard, J. V. Ward, An extension of the flood pulse concept. *Hydrol. Processes* **14**, 2861–2883 (2000). doi: 10.1002/1099-1085(200011/12)14:16/17<2861::AID-HYP124>3.0.CO;2-F
13. J. S. Perkin *et al.*, Fragmentation and dewatering transform Great Plains stream fish communities. *Ecol. Monogr.* **85**, 73–92 (2015). doi: 10.1890/14-0121.1
14. J. L. Sabo, D. M. Post, Quantifying periodic, stochastic, and catastrophic environmental variation. *Ecol. Monogr.* **78**, 19–40 (2008). doi: 10.1890/06-1340.1
15. F. Shuai *et al.*, Silver carp larva abundance in response to river flow rate revealed by cross-wavelet modelling. *Ecol. Modell.* **383**, 98–105 (2018). doi: 10.1016/j.ecolmodel.2018.05.020
16. J. D. Tonkin, M. T. Bogan, N. Bonada, B. Rios-Touma, D. A. Lytle, Seasonality and predictability shape temporal species diversity. *Ecology* **98**, 1201–1216 (2017). doi: 10.1002/ecy.1761; pmid: 28144975
17. N. L. Poff, Beyond the natural flow regime? Broadening the hydro-ecological foundation to meet environmental flows challenges in a non-stationary world. *Freshwater Biol.* **63**, 1011–1021 (2018). doi: 10.1111/fwb.13038
18. A. Ruhi, X. Dong, C. H. McDaniel, D. P. Batzer, J. L. Sabo, Detrimental effects of a novel flow regime on the functional trajectory of an aquatic invertebrate metacommunity. *Glob. Change Biol.* **24**, 3749–3765 (2018). doi: 10.1111/gcb.14133; pmid: 29665147
19. M. T. Bogan, D. A. Lytle, Severe drought drives novel community trajectories in desert stream pools. *Freshwater Biol.* **56**, 2070–2081 (2011). doi: 10.1111/j.1365-2427.2011.02638.x
20. G. Woodward *et al.*, The effects of climatic fluctuations and extreme events on running water ecosystems. *Philos. Trans. R. Soc. London Ser. B* **371**, 20150274 (2016). pmid: 27114576
21. M. A. Palmer, C. M. Swan, K. Nelson, P. Silver, R. Alvestad, Streambed landscapes: Evidence that stream invertebrates respond to the type and spatial arrangement of patches. *Landsc. Ecol.* **15**, 563–576 (2000). doi: 10.1023/A:1008194130695
22. D. Schmera *et al.*, Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. *Freshwater Biol.* **63**, 74–85 (2018). doi: 10.1111/fwb.12973
23. R. Henriques-Silva *et al.*, A comprehensive examination of the network position hypothesis across multiple river metacommunities. *Ecography* **42**, 284–294 (2019). doi: 10.1111/ecog.03908
24. K. L. Jaeger, J. D. Olden, N. A. Pelland, Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 13894–13899 (2014). doi: 10.1073/pnas.1320890111; pmid: 25136090
25. S. Garbin, E. A. Celegon, P. Fanton, G. Botter, Hydrological controls on river network connectivity. *R. Soc. Open Sci.* **6**, 181428 (2019). doi: 10.1098/rsos.181428; pmid: 30891270
26. F. Cattanéo, B. Hugueny, N. Lamouroux, Synchrony in brown trout, *Salmo trutta*, population dynamics: A 'Moran effect' on early-life stages. *Oikos* **100**, 43–54 (2003). doi: 10.1034/j.1600-0706.2003.11912.x
27. A. Terui *et al.*, Metapopulation stability in branching river networks. *Proc. Natl. Acad. Sci. U.S.A.* **115**, E5963–E5969 (2018). doi: 10.1073/pnas.1800060115; pmid: 29895695
28. P. A. P. Moran, The statistical analysis of the Canadian Lynx cycle. *Aust. J. Zool.* **1**, 291–298 (1953). doi: 10.1071/ZO9530291
29. G. D. Grossman, P. B. Moyle, J. O. Whitaker Jr., Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: A test of community theory. *Am. Nat.* **120**, 423–454 (1982). doi: 10.1086/284004
30. D. A. Lytle, D. M. Merritt, J. D. Tonkin, J. D. Olden, L. V. Reynolds, Linking river flow regimes to riparian plant guilds: A community-wide modeling approach. *Ecol. Appl.* **27**, 1338–1350 (2017). doi: 10.1002/eap.1528; pmid: 28263426
31. A. Ruhí, E. E. Holmes, J. N. Rinne, J. L. Sabo, Anomalous droughts, not invasion, decrease persistence of native fishes in a desert river. *Glob. Change Biol.* **21**, 1482–1496 (2015). doi: 10.1111/gcb.12780; pmid: 25430731
32. J. D. Tonkin, D. M. Merritt, J. D. Olden, L. V. Reynolds, D. A. Lytle, Flow regime alteration degrades ecological networks in riparian ecosystems. *Nat. Ecol. Evol.* **2**, 86–93 (2018). doi: 10.1038/s41559-017-0379-0; pmid: 29180707
33. M. C. Mims, J. D. Olden, Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. *Freshwater Biol.* **58**, 50–62 (2013). doi: 10.1111/fwb.12037
34. P. T. J. Johnson, J. D. Olden, M. J. Vander Zanden, Dam invaders: Impoundments facilitate biological invasions into freshwaters. *Front. Ecol. Environ.* **6**, 357–363 (2008). doi: 10.1890/070156
35. N. Bonada, S. Doledec, B. Statzner, Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: Implications for future climatic scenarios. *Glob. Change Biol.* **13**, 1658–1671 (2007). doi: 10.1111/j.1365-2486.2007.01375.x
36. M. I. Pyne, N. L. Poff, Vulnerability of stream community composition and function to projected thermal warming and hydrologic change across ecoregions in the western United States. *Glob. Change Biol.* **23**, 77–93 (2017). doi: 10.1111/gcb.13437; pmid: 27429092
37. D. B. Herbst, S. D. Cooper, R. B. Medhurst, S. W. Wiseman, C. T. Hunsaker, Drought ecohydrology alters the structure and function of benthic invertebrate communities in mountain streams. *Freshwater Biol.* **64**, 886–902 (2019). doi: 10.1111/fwb.13270
38. M. T. Bogan, E. T. Chester, T. Datry, A. L. Murphy, B. J. Robson, A. Ruhi, R. Stubbington, J. E. Whitney, in *Resistance, Resilience, and Community Recovery in Intermittent Rivers and Ephemeral Streams*, T. Datry, N. Bonada, A. Boulton, Eds. (Academic Press, 2017), pp. 349–376.
39. S. Höckendorff *et al.*, Characterizing fish responses to a river restoration over 21 years based on species' traits. *Conserv. Biol.* **31**, 1098–1108 (2017). doi: 10.1111/cobi.12908; pmid: 28218807
40. D. Bruno *et al.*, Structural and functional responses of invertebrate communities to climate change and flow regulation in alpine catchments. *Glob. Change Biol.* **25**, 1612–1628 (2019). doi: 10.1111/gcb.14581; pmid: 30698905
41. T. W. H. Aspin *et al.*, Extreme drought pushes stream invertebrate communities over functional thresholds. *Glob. Change Biol.* **25**, 230–244 (2019). doi: 10.1111/gcb.14495; pmid: 30346098
42. S. E. Tank, J. B. Fellman, E. Hood, E. S. Kritzberg, Beyond respiration: Controls on lateral carbon fluxes across the terrestrial-aquatic interface. *Limnol. Oceanogr. Lett.* **3**, 76–88 (2018). doi: 10.1002/lol2.10065
43. A. P. Appling *et al.*, The metabolic regimes of 356 rivers in the United States. *Sci. Data* **5**, 180292 (2018). doi: 10.1038/sdata.2018.292; pmid: 30532078
44. P. Savoy *et al.*, Metabolic rhythms in flowing waters: An approach for classifying river productivity regimes. *Limnol. Oceanogr.* (2019). doi: 10.1002/lno.11154
45. E. S. Bernhardt *et al.*, The metabolic regimes of flowing waters. *Limnol. Oceanogr.* **63**, S99–S118 (2018). doi: 10.1002/lno.10726
46. M. Colls, X. Timoner, S. Sabater, V. Acuña, Effects of duration and frequency of the non-flow period on stream metabolism. *Ecosystems* 10.1007/s10021-019-00345-1 (2019). doi: 10.1007/s10021-019-00345-1
47. A. J. Ulseth, E. Bertuzzo, G. A. Singer, J. Schelker, T. J. Battin, Climate-induced changes in spring snowmelt impact ecosystem metabolism and carbon fluxes in an Alpine stream network. *Ecosystems* **21**, 373–390 (2018). doi: 10.1007/s10021-017-0155-7
48. B. O. L. Demars, Hydrological pulses and burning of dissolved organic carbon by stream respiration. *Limnol. Oceanogr.* **64**, 406–421 (2019). doi: 10.1002/lno.11048
49. R. T. Hensley, L. Kirk, M. Spangler, M. N. Gooseff, M. J. Cohen, Flow extremes as spatiotemporal control points on river solute fluxes and metabolism. *J. Geophys. Res. Biogeosci.* **124**, 537–555 (2019). doi: 10.1029/2018JG004738
50. J. D. Hosen *et al.*, Enhancement of primary production during drought in a temperate watershed is greater in larger rivers than headwater streams. *Limnol. Oceanogr.* **64**, 1458–1472 (2019). doi: 10.1002/lno.11127
51. L. Gómez-Gener *et al.*, When water vanishes: Magnitude and regulation of carbon dioxide emissions from dry temporary streams. *Ecosystems* **19**, 710–723 (2016). doi: 10.1007/s10021-016-9963-4
52. E. H. Stanley *et al.*, The ecology of methane in streams and rivers: Patterns, controls, and global significance. *Ecol. Monogr.* **86**, 146–171 (2016). doi: 10.1890/15-1027
53. R. T. Barnes, D. E. Butman, H. F. Wilson, P. A. Raymond, Riverine export of aged carbon driven by flow path depth and residence time. *Environ. Sci. Technol.* **52**, 1028–1035 (2018). doi: 10.1021/acs.est.7b04717; pmid: 29313674
54. G. Pinay *et al.*, Riparian corridors: A new conceptual framework for assessing nitrogen buffering across biomes. *Front. Environ. Sci.* **6**, 47 (2018). doi: 10.3389/fenvs.2018.00047
55. W. M. Wollheim *et al.*, River network saturation concept: Factors influencing the balance of biogeochemical supply and

demand of river networks. *Biogeochemistry* **141**, 503–521 (2018). doi: 10.1007/s10533-018-0488-0

56. P. A. Raymond, J. E. Saiers, W. V. Sobczak, Hydrological and biogeochemical controls on watershed dissolved organic matter transport: Pulse-shunt concept. *Ecology* **97**, 5–16 (2016). doi: 10.1890/14-1684.1; pmid: 27008769
57. C. Tunaley, D. Tetzlaff, J. Lessels, C. Soulsby, Linking high-frequency DOC dynamics to the age of connected water sources. *Water Resour. Res.* **52**, 5232–5247 (2016). doi: 10.1002/2015WR018419
58. S. Bernal *et al*., Supply, demand, and in-stream retention of dissolved organic carbon and nitrate during storms in Mediterranean forested headwater streams. *Front. Environ. Sci.* **7**, 60 (2019). doi: 10.3389/fenvs.2019.00060
59. J. Harvey *et al*., How hydrologic connectivity regulates water quality in river corridors. *J. Am. Water Resour. Assoc.* **55**, 369–381 (2019). doi: 10.1111/1752-1688.12691
60. J. C. Moore *et al*., Detritus, trophic dynamics and biodiversity. *Ecol. Lett.* **7**, 584–600 (2004). doi: 10.1111/j.1461-0248.2004.00606.x
61. A. D. Rosemond *et al*., Freshwater ecology. Experimental nutrient additions accelerate terrestrial carbon loss from stream ecosystems. *Science* **347**, 1142–1145 (2015). doi: 10.1126/science.aaa1958; pmid: 25745171
62. A. C. Y. Yeung, J. L. Musetta-Lambert, D. P. Kreutzweiser, P. K. Sibley, J. S. Richardson, Relations of interannual differences in stream litter breakdown with discharge: Bioassessment implications. *Ecosphere* **9**, e02423 (2018). doi: 10.1002/ecs2.2423
63. R. M. Northington, J. R. Webster, Experimental reductions in stream flow alter litter processing and consumer subsidies in headwater streams. *Freshwater Biol.* **62**, 737–750 (2017). doi: 10.1111/fwb.12898
64. E. Mas-Martí, I. Sanpera-Calbet, I. Muñoz, Bottom-up effects of streambed drying on consumer performance through changes in resource quality. *Aquat. Sci.* **79**, 719–731 (2017). doi: 10.1007/s00027-017-0531-6
65. B. D. Richter, G. A. Thomas, Restoring environmental flows by modifying dam operations. *Ecol. Soc.* **12**, 12 (2007). doi: 10.5751/ES-02014-120112
66. G. Zolezzi, A. Siviglia, M. Toffolon, B. Maiolini, Thermopeaking in Alpine streams: Event characterization and time scales. *Ecohydrology* **4**, 564–576 (2011). doi: 10.1002/eco.132
67. T. Meißner, B. Sures, C. K. Feld, Multiple stressors and the role of hydrology on benthic invertebrates in mountainous streams. *Sci. Total Environ.* **663**, 841–851 (2019). doi: 10.1016/j.scitotenv.2019.01.288; pmid: 30738264
68. I. R. Waite *et al*., Effects of urban multi-stressors on three stream biotic assemblages. *Sci. Total Environ.* **660**, 1472–1485 (2019). doi: 10.1016/j.scitotenv.2018.12.240; pmid: 30743940
69. K. C. Nelson, M. A. Palmer, Stream temperature surges under urbanization and climate change: Data, models, and responses. *J. Am. Water Resour. Assoc.* **43**, 440–452 (2007). doi: 10.1111/j.1752-1688.2007.00034.x
70. J. R. Blaszczak, J. M. Delesantro, Y. Zhong, D. L. Urban, E. S. Bernhardt, Watershed urban development controls on urban streamwater chemistry variability. *Biogeochemistry* **144**, 61–84 (2019). doi: 10.1007/s10533-019-00572-7
71. L. Ponsatí *et al*., Biofilm responses to flow regulation by dams in Mediterranean rivers. *River Res. Appl.* **31**, 1003–1016 (2015). doi: 10.1002/rra.2807
72. J. M. Alberts, J. J. Beaulieu, I. Buffam, Watershed land use and seasonal variation constrain the influence of riparian canopy cover on stream ecosystem metabolism. *Ecosystems* **20**, 553–567 (2017). doi: 10.1007/s10021-016-0040-9; pmid: 30416371
73. R. O. Hall Jr *et al*., Turbidity, light, temperature, and hydropeaking control primary productivity in the Colorado River, Grand Canyon. *Limnol. Oceanogr.* **60**, 512–526 (2015). doi: 10.1002/lno.10031
74. J. R. Blaszczak, J. M. Delesantro, D. L. Urban, M. W. Doyle, E. S. Bernhardt, Scoured or suffocated: Urban stream ecosystems oscillate between hydrologic and dissolved oxygen extremes. *Limnol. Oceanogr.* **64**, 877–894 (2019). doi: 10.1002/lno.11081
75. J.-R. Mor *et al*., Dam regulation and riverine food-web structure in a Mediterranean river. *Sci. Total Environ.* **625**, 301–310 (2018). doi: 10.1016/j.scitotenv.2017.12.296; pmid: 29289778
76. H. A. Wellard Kelly *et al*., Macroinvertebrate diets reflect tributary inputs and turbidity-driven changes in food availability in the Colorado River downstream of Glen Canyon Dam. *Freshw. Sci.* **32**, 397–410 (2013). doi: 10.1899/12-088.1
77. S. J. Imberger, R. M. Thompson, M. R. Grace, Urban catchment hydrology overwhelms reach scale effects of riparian vegetation on organic matter dynamics. *Freshwater Biol.* **56**, 1370–1389 (2011). doi: 10.1111/j.1365-2427.2011.02575.x
78. R. T. Martins, A. S. Melo, J. F. Gonçalves Jr., N. Hamada, Leaf-litter breakdown in urban streams of Central Amazonia: Direct and indirect effects of physical, chemical, and biological factors. *Freshw. Sci.* **34**, 716–726 (2015). doi: 10.1086/681086
79. C. M. Yule, J. Y. Gan, T. Jinggut, K. V. Lee, Urbanization affects food webs and leaf-litter decomposition in a tropical stream in Malaysia. *Freshw. Sci.* **34**, 702–715 (2015). doi: 10.1086/681252
80. T. A. Newcomer *et al*., Influence of natural and novel organic carbon sources on denitrification in forest, degraded urban, and restored streams. *Ecol. Monogr.* **82**, 449–466 (2012). doi: 10.1890/12-0458.1
81. A. Chaudhary, I. Kauser, A. Ray, R. Poretsky, Taxon-driven functional shifts associated with storm flow in an urban stream microbial community. *MSphere* **3**, e00194-18 (2018). doi: 10.1128/mSphere.00194-18; pmid: 29976643
82. T. A. Kennedy *et al*., Flow management for hydropower extirpates aquatic insects, undermining river food webs. *Bioscience* **66**, 561–575 (2016). doi: 10.1093/biosci/biw059
83. A. Glazaczow, D. Orwin, M. Bogdziewicz, Increased temperature delays the late-season phenology of multivoltine insect. *Sci. Rep.* **6**, 38022 (2016). doi: 10.1038/srep38022; pmid: 27905493
84. S. G. Fisher, L. J. Gray, N. B. Grimm, D. E. Busch, Temporal succession in a desert stream ecosystem following flash flooding. *Ecol. Monogr.* **52**, 93–110 (1982). doi: 10.2307/2937346
85. G. J. Scrimgeour, M. J. Winterbourn, Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia* **171**, 33–44 (1989). doi: 10.1007/BF00005722
86. E. Bondar-Kunze, S. Maier, D. Schönauer, N. Bahl, T. Hein, Antagonistic and synergistic effects on a stream periphyton community under the influence of pulsed flow velocity increase and nutrient enrichment. *Sci. Total Environ.* **573**, 594–602 (2016). doi: 10.1016/j.scitotenv.2016.08.158; pmid: 27585428
87. M. J. Cashman, G. L. Harvey, G. Wharton, M. C. Bruno, Wood mitigates the effect of hydropeaking scour on periphyton biomass and nutritional quality in semi-natural flume simulations. *Aquat. Sci.* **79**, 459–471 (2017). doi: 10.1007/s00027-016-0510-3
88. W. F. Cross *et al*., Food-web dynamics in a large river discontinuum. *Ecol. Monogr.* **83**, 311–337 (2013). doi: 10.1890/12-1727.1
89. D. M. Warfe *et al*., Productivity, disturbance and ecosystem size have no influence on food chain length in seasonally connected rivers. *PLOS ONE* **8**, e66240 (2013). doi: 10.1371/journal.pone.0066240
90. T. D. Jardine *et al*., Consumer-resource coupling in wet-dry tropical rivers. *J. Anim. Ecol.* **81**, 310–322 (2012). doi: 10.1111/j.1365-2656.2011.01925.x; pmid: 22103689
91. K. O. Winemiller *et al*., Pulsing hydrology determines top-down control of basal resources in a tropical river–floodplain ecosystem. *Ecol. Monogr.* **84**, 621–635 (2014). doi: 10.1890/13-1822.1
92. D. M. Post, The long and short of food-chain length. *Trends Ecol. Evol.* **17**, 269–277 (2002). doi: 10.1016/S0169-5347(02)02455-2
93. D. M. Post, G. Takimoto, Proximate structural mechanisms for variation in food-chain length. *Oikos* **116**, 775–782 (2007). doi: 10.1111/j.0030-1299.2007.15552.x
94. P. A. McHugh, A. R. McIntosh, P. G. Jellyman, Dual influences of ecosystem size and disturbance on food chain length in streams. *Ecol. Lett.* **13**, 881–890 (2010). doi: 10.1111/j.1461-0248.2010.01484.x; pmid: 20482579
95. A. Ruhí *et al*., Flow regulation increases food-chain length through omnivory mechanisms in a Mediterranean river network. *Freshwater Biol.* **61**, 1536–1549 (2016). doi: 10.1111/fwb.12794
96. J. L. Sabo, J. C. Finlay, T. Kennedy, D. M. Post, The role of discharge variation in scaling of drainage area and food chain length in rivers. *Science* **330**, 965–967 (2010). doi: 10.1126/science.1196005; pmid: 20947729
97. A. R. McIntosh *et al*., Capacity to support predators scales with habitat size. *Sci. Adv.* **4**, eaap7523 (2018). doi: 10.1126/sciadv.aap7523; pmid: 29978038
98. J. H. Brown, J. F. Gillooly, A. P. Allen, V. M. Savage, G. B. West, Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789 (2004). doi: 10.1890/03-9000
99. K. Zou, E. Thébault, G. Lacroix, S. Barot, Interactions between the green and brown food web determine ecosystem functioning. *Funct. Ecol.* **30**, 1454–1465 (2016). doi: 10.1111/1365-2435.12626
100. M. J. Vanni, P. B. McIntyre, Predicting nutrient excretion of aquatic animals with metabolic ecology and ecological stoichiometry: A global synthesis. *Ecology* **97**, 3460–3471 (2016). doi: 10.1002/ecy.1582; pmid: 27912023
101. T. B. Parr, K. A. Capps, S. P. Inamdar, K. A. Metcalf, Animal-mediated organic matter transformation: Aquatic insects as a source of microbially bioavailable organic nutrients and energy. *Funct. Ecol.* **33**, 524–535 (2019). doi: 10.1111/1365-2435.13242
102. C. P. Arango *et al*., Urban infrastructure influences dissolved organic matter quality and bacterial metabolism in an urban stream network. *Freshwater Biol.* **62**, 1917–1928 (2017).
103. L. G. Larsen, J. W. Harvey, Disrupted carbon cycling in restored and unrestored urban streams: Critical timescales and controls. *Limnol. Oceanogr.* **62**, S160–S182 (2017). doi: 10.1002/lno.10613
104. H. M. Halvorson, G. White, J. T. Scott, M. A. Evans-White, Dietary and taxonomic controls on incorporation of microbial carbon and phosphorus by detritivorous caddisflies. *Oecologia* **180**, 567–579 (2016). doi: 10.1007/s00442-015-3464-6; pmid: 26497125
105. J. J. Elser *et al*., Biological stoichiometry from genes to ecosystems. *Ecol. Lett.* **3**, 540–550 (2000). doi: 10.1046/j.1461-0248.2000.00185.x
106. E. K. Moody *et al*., Consumption explains intraspecific variation in nutrient recycling stoichiometry in a desert fish. *Ecology* **99**, 1552–1561 (2018). doi: 10.1002/ecy.2372; pmid: 29882955
107. N. Welti *et al*., Bridging food webs, ecosystem metabolism, and biogeochemistry using ecological stoichiometry theory. *Front. Microbiol.* **8**, 1298 (2017). doi: 10.3389/fmicb.2017.01298; pmid: 28747904
108. M. A. Palmer, S. Filoso, R. M. Fanelli, From ecosystems to ecosystem services: Stream restoration as ecological engineering. *Ecol. Eng.* **65**, 62–70 (2014). doi: 10.1016/j.ecoleng.2013.07.059
109. M. J. Burns, T. D. Fletcher, C. J. Walsh, A. R. Ladson, B. E. Hatt, Hydrologic shortcomings of conventional urban stormwater management and opportunities for reform. *Landsc. Urban Plan.* **105**, 230–240 (2012). doi: 10.1016/j.landurbplan.2011.12.012
110. C. R. Liermann, C. Nilsson, J. Robertson, R. Y. Ng, Implications of dam obstruction for global freshwater fish diversity. *Bioscience* **62**, 539–548 (2012). doi: 10.1525/bio.2012.62.6.5
111. J. D. Olden, R. J. Naiman, Incorporating thermal regimes into environmental flows assessments: Modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biol.* **55**, 86–107 (2010). doi: 10.1111/j.1365-2427.2009.02179.x
112. D. B. Osmundson, R. J. Ryel, V. L. Lamarra, J. Pitlick, Flow–sediment–biota relations: Implications for river regulation effects on native fish abundance. *Ecol. Appl.* **12**, 1719–1739 (2002).
113. D. von Schiller *et al*., Regulation causes nitrogen cycling discontinuities in Mediterranean rivers. *Sci. Total Environ.* **540**, 168–177 (2016). doi: 10.1016/j.scitotenv.2015.07.017; pmid: 26233271
114. J. L. Sabo *et al*., Designing river flows to improve food security futures in the Lower Mekong Basin. *Science* **358**, eaao1053 (2017). doi: 10.1126/science.aao1053; pmid: 29217541
115. W. Xu *et al*., Improving the multi-objective performance of rainwater harvesting systems using real-time control technology. *Water* **10**, 147 (2018). doi: 10.3390/w10020147
116. M. Acreman *et al*., Environmental flows for natural, hybrid, and novel riverine ecosystems in a changing world. *Front. Ecol. Environ.* **12**, 466–473 (2014). doi: 10.1890/130134
117. N. L. Poff *et al*., Sustainable water management under future uncertainty with eco-engineering decision scaling. *Nat. Clim. Chang.* **6**, 25–34 (2016). doi: 10.1038/nclimate2765
118. J. D. Kiernan, P. B. Moyle, P. K. Crain, Restoring native fish assemblages to a regulated California stream using the

natural flow regime concept. *Ecol. Appl.* **22**, 1472–1482 (2012). doi: 10.1890/11-0480.1; pmid: 22908707
119. D. L. Propst, K. B. Gido, Responses of native and nonnative fishes to natural flow regime mimicry in the San Juan River. *Trans. Am. Fish. Soc.* **133**, 922–931 (2004). doi: 10.1577/T03-057.1
120. T. K. Pool, J. D. Olden, Assessing long-term fish responses and short-term solutions to flow regulation in a dryland river basin. *Ecol. Freshwat. Fish* **24**, 56–66 (2015). doi: 10.1111/eff.12125
121. W. Chen, J. D. Olden, Designing flows to resolve human and environmental water needs in a dam-regulated river. *Nat. Commun.* **8**, 2158 (2017). doi: 10.1038/s41467-017-02226-4; pmid: 29255194
122. S. M. Nelson *et al*., A history of the 2014 Minute 319 environmental pulse flow as documented by field measurements and satellite imagery. *Ecol. Eng.* **106**, 733–748 (2017). doi: 10.1016/j.ecoleng.2016.10.040
123. P. B. Shafroth *et al*., A large-scale environmental flow experiment for riparian restoration in the Colorado River Delta. *Ecol. Eng.* **106**, 645–660 (2017). doi: 10.1016/j.ecoleng.2017.02.016
124. E. P. Glenn, P. L. Nagler, P. B. Shafroth, C. J. Jarchow, Effectiveness of environmental flows for riparian restoration in arid regions: A tale of four rivers. *Ecol. Eng.* **106**, 695–703 (2017). doi: 10.1016/j.ecoleng.2017.01.009
125. S. Hotaling, D. S. Finn, J. Joseph Giersch, D. W. Weisrock, D. Jacobsen, Climate change and alpine stream biology: Progress, challenges, and opportunities for the future. *Biol. Rev. Camb. Philos. Soc.* **92**, 2024–2045 (2017). doi: 10.1111/brv.12319; pmid: 28105701
126. C. J. Walsh, T. D. Fletcher, M. J. Burns, Urban stormwater runoff: A new class of environmental flow problem. *PLOS ONE* **7**, e45814 (2012). doi: 10.1371/journal.pone.0045814; pmid: 23029257
127. A. Selvakumar, T. P. O'Connor, S. D. Struck, Role of stream restoration on improving benthic macroinvertebrates and in-stream water quality in an urban watershed: Case study. *J. Environ. Eng.* **136**, 127–139 (2010). doi: 10.1061/(ASCE)EE.1943-7870.0000116
128. R. W. Lammers, B. P. Bledsoe, What role does stream restoration play in nutrient management? *Crit. Rev. Environ. Sci. Technol.* **47**, 335–371 (2017). doi: 10.1080/10643389.2017.1318618
129. H. E. Golden, N. Hoghooghi, Green infrastructure and its catchment-scale effects: An emerging science. *WIREs Water* **5**, e1254 (2018). doi: 10.1002/wat2.1254; pmid: 29682288
130. M. R. Williams, G. Bhatt, S. Filoso, G. Yactayo, Stream restoration performance and its contribution to the Chesapeake Bay TMDL: Challenges posed by climate change in urban areas. *Estuaries Coasts* **40**, 1227–1246 (2017). doi: 10.1007/s12237-017-0226-1
131. R. M. Fanelli, K. Prestegaard, M. A. Palmer, *Freshw. Sci.*, 10.1086/706072 (2019).
132. B. W. Abbott *et al*., Unexpected spatial stability of water chemistry in headwater stream networks. *Ecol. Lett.* **21**, 296–308 (2018). doi: 10.1111/ele.12897; pmid: 29282860
133. B. L. Brown, C. M. Swan, Dendritic network structure constrains metacommunity properties in riverine ecosystems. *J. Anim. Ecol.* **79**, 571–580 (2010). doi: 10.1111/j.1365-2656.2010.01668.x; pmid: 20180874
134. C. M. Swan, B. L. Brown, Metacommunity theory meets restoration: Isolation may mediate how ecological communities respond to stream restoration. *Ecol. Appl.* **27**, 2209–2219 (2017). doi: 10.1002/eap.1602; pmid: 28718193
135. N. Mouquet, D. Gravel, F. Massol, V. Calcagno, Extending the concept of keystone species to communities and ecosystems. *Ecol. Lett.* **16**, 1–8 (2013). doi: 10.1111/ele.12014; pmid: 23062191
136. A. Ruhí, T. Datry, J. L. Sabo, Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. *Conserv. Biol.* **31**, 1459–1468 (2017). doi: 10.1111/cobi.12906; pmid: 28188969
137. L. Yamane, L. W. Botsford, D. P. Kilduff, Tracking restoration of population diversity via the portfolio effect. *J. Appl. Ecol.* **55**, 472–481 (2018). doi: 10.1111/1365-2664.12978
138. D. W. Braidwood, M. A. Taggart, M. Smith, R. Andersen, Translocations, conservation, and climate change: Use of restoration sites as protorefuges and protorefugia. *Restor. Ecol.* **26**, 20–28 (2018). doi: 10.1111/rec.12642
139. Y. Wang, D. Wang, Q. W. Lewis, J. Wu, F. Huang, A framework to assess the cumulative impacts of dams on hydrological regime: A case study of the Yangtze River. *Hydrol. Processes* **31**, 3045–3055 (2017). doi: 10.1002/hyp.11239
140. J. L. Sabo *et al*., Pulsed flows, tributary inputs and food-web structure in a highly regulated river. *J. Appl. Ecol.* **55**, 1884–1895 (2018). doi: 10.1111/1365-2664.13109
141. C. Magliozzi, G. Coro, R. C. Grabowski, A. I. Packman, S. Krause, A multiscale statistical method to identify potential areas of hyporheic exchange for river restoration planning. *Environ. Model. Softw.* **111**, 311–323 (2019). doi: 10.1016/j.envsoft.2018.09.006
142. S. S. Schwartz, B. Smith, Restoring hydrologic function in urban landscapes with suburban subsoiling. *J. Hydrol.* **543**, 770–781 (2016). doi: 10.1016/j.jhydrol.2016.10.051
143. C. J. Walsh, T. D. Fletcher, A. R. Ladson, Stream restoration in urban catchments through redesigning stormwater systems: Looking to the catchment to save the stream. *J. N. Am. Benthol. Soc.* **24**, 690–705 (2005). doi: 10.1899/04-020.1
144. N. M. Schmadel *et al*., Thresholds of lake and reservoir connectivity in river networks control nitrogen removal. *Nat. Commun.* **9**, 2779 (2018). doi: 10.1038/s41467-018-05156-x; pmid: 30018449
145. C. D. Sayer, Conservation of aquatic landscapes: Ponds, lakes, and rivers as integrated systems. *WIREs Water* **1**, 573–585 (2014). doi: 10.1002/wat2.1045
146. R. G. Luthy, D. L. Sedlak, M. H. Plumlee, D. Austin, V. H. Resh, Wastewater-effluent-dominated streams as ecosystem-management tools in a drier climate. *Front. Ecol. Environ.* **13**, 477–485 (2015). doi: 10.1890/150038
147. D. W. Roscoe, S. G. Hinch, Effectiveness monitoring of fish passage facilities: Historical trends, geographic patterns and future directions. *Fish Fish.* **11**, 12–33 (2010). doi: 10.1111/j.1467-2979.2009.00333.x
148. C. M. Bunt, T. Castro-Santos, A. Haro, Performance of fish passage structures at upstream barriers to migration. *River Res. Appl.* **28**, 457–478 (2012). doi: 10.1002/rra.1565
149. D. Weigel *et al*., Evaluation of a trap-and-transport program for a threatened population of steelhead (*Oncorhynchus mykiss*). *Conserv. Genet.* **20**, 1195–1199 (2019). doi: 10.1007/s10592-019-01200-5
150. M. H. Bond *et al*., Combined effects of barge transportation, river environment, and rearing location on straying and migration of adult Snake River fall-run Chinook Salmon. *Trans. Am. Fish. Soc.* **146**, 60–73 (2017). doi: 10.1080/00028487.2016.1235614
151. A. C. Ritchie *et al*., Morphodynamic evolution following sediment release from the world's largest dam removal. *Sci. Rep.* **8**, 13279 (2018). doi: 10.1038/s41598-018-30817-8; pmid: 30185796
152. T. Sommer *et al*., California's Yolo Bypass: Evidence that flood control can be compatible with fisheries, wetlands, wildlife, and agriculture. *Fisheries* **26**, 6–16 (2001). doi: 10.1577/1548-8446(2001)026<0006:CYB>2.0.CO;2
153. G. Grill *et al*., Mapping the world's free-flowing rivers. *Nature* **569**, 215–221 (2019). doi: 10.1038/s41586-019-1111-9; pmid: 31068722
154. G. Gassert, M. Luck, M. Landis, P. Reig, T. Shiao, "Aqueduct global maps 2.1: Constructing decision-relevant global water risk indicators," Working paper, World Resources Institute (2015); www.wri.org/publication/aqueduct-global-maps-21-indicators.
155. A. Ruhí, J. D. Olden, J. L. Sabo, Declining streamflow induces collapse and replacement of native fishes in the American Southwest. *Front. Ecol. Environ.* **14**, 465–472 (2016). doi: 10.1002/fee.1424
156. T. C. Gouhier, A. Grinsted, V. Simko, R package Biwavelet: conduct univariate and bivariate wavelet analyses (2018).
157. T. Rodríguez-Castillo, E. Estévez, A. M. González-Ferreras, J. Barquín, Estimating ecosystem metabolism to entire river networks. *Ecosystems* (2018). doi: 10.1007/s10021-018-0311-8

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Linkages between flow regime, biota, and ecosystem processes: Implications for river restoration

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River restoration guided by research
Human activities have altered the flow regimes of many of Earth's rivers, with negative impacts on biodiversity, water quality, and ecological processes. In a Review, Palmer and Ruhi explain how restoration designs now attempt to mimic ecologically important aspects of natural flow regimes, guided by insights into how variations in flow affect biota and ecosystem processes. To be successful, such efforts must go beyond accounting for flood pulses to restore natural flow variability and achieve hydrological connectivity between a river and its surroundings.

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