

Riverine macrosystems ecology: sensitivity, resistance, and resilience of whole river basins with human alterations

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Riverine macrosystems are described here as watershed-scale networks of connected and interacting riverine and upland habitat patches. Such systems are driven by variable responses of nutrients and organisms to a suite of global and regional factors (eg climate, human social systems) interacting with finer-scale variations in geology, topography, and human modifications. We hypothesize that spatial heterogeneity, connectivity, and asynchrony among these patches regulate ecological dynamics of whole networks, altering system sensitivity, resistance, and resilience. Long-distance connections between patches may be particularly important in riverine macrosystems, shaping fundamental system properties. Furthermore, the type, extent, intensity, and spatial configuration of human activities (eg land-use change, dam construction) influence watershed-wide ecological properties through effects on habitat heterogeneity and connectivity at multiple scales. Thus, riverine macrosystems are coupled social–ecological systems with feedbacks that influence system responses to environmental change and the sustainable delivery of ecosystem services.

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Riverine ecosystems are some of the most diverse on Earth and provide important services (Palmer and Richardson 2009; Strayer and Dudgeon 2010). Understanding how they function is critical to sustainable management but challenging given their complex spatial and temporal structure and multi-scale processes. Riverine systems comprise hydrological–ecological networks organized by the flow of water, sediment, nutrients, and organisms downhill

and downstream and the active movement of animals uphill and upstream. Rivers are multidimensional, including longitudinal (upstream–downstream), lateral (upland to channel), vertical (hyporheic, or the zone below the stream bed), and temporal components (Ward 1989; Fausch *et al.* 2002). Despite this multidimensionality, many ecological processes are influenced by the rapid flow of water downhill, providing strong directional connectivity (Wiens 2002). Rivers are also organized hierarchically, with fine-scale structures (eg gravel patches) embedded within channel bed features (eg riffles), which in turn are embedded within reaches, valley segments, basins, and regions (Table 1; Frissell *et al.* 1986; Thorp *et al.* 2008). Uplands are fundamental to riverine organization, with variations in land use, land cover, and soils influencing surface-water and groundwater flow paths, thereby altering water, nutrient, and sediment fluxes to rivers (eg Lewis and Grimm 2007). Rivers are also temporally variable, partially due to hydrology that varies within and across basins and climatic regions (Poff *et al.* 1997). Thus, we define riverine macrosystems as hierarchical dynamic networks, influenced by strong directional connectivity that integrates processes across multiple scales and broad distances through time (Figure 1; see Heffernan *et al.* [2014] for macrosystem definition).

Ecologists have typically studied riverine ecosystems at the scale of bed features or reaches distributed longitudinally along rivers of varying size, in an attempt to understand the strong influences that upstream and watershed processes, including human modifications, can have (Poole 2010). Our conceptualization of rivers and watersheds as “macrosystems” is a logical extension of these approaches (Figure 1). We view riverine macrosystems as repeating, interacting

In a nutshell:

- We define riverine macrosystems as networks of connected and interacting upland, floodplain, and in-channel habitat patches
- Local riverine ecosystems are sensitive to remote environmental change due to strong reciprocal effects between upstream and downstream habitats, but whole macrosystems can be resistant and resilient to change
- The spatial configuration of multiple types of human alterations (eg dams, urbanization) can modify macrosystem dynamics, often leading to rapid and difficult-to-reverse ecological change, influencing the sustainable delivery of ecosystem services

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habitat patches, distributed throughout watersheds and along hydrologic flow paths. Moreover, ecological responses of whole basins reflect cumulative and emergent properties and processes operating across scales, including basin-level variation in climate that interacts with human activities, modifying hydrology, connectivity, and watershed processes (Figure 1). Thus, macrosystems have important “cross-scale interactions” (Soranno *et al.* 2014) and teleconnections (ie “strong links between distant and otherwise disconnected regions” *sensu* Heffernan *et al.* 2014).

Although the study of riverine macrosystems focuses on large ecological networks, consideration of regional context can provide information on local dynamics. For example, by considering differences in runoff amounts across the central US and variations in dispersal distance, Muneeppeerakul *et al.* (2008) were able to predict fish diversity in sub-basins of the Mississippi River. In general, riverine macrosystems ecology may improve riverine management by: (1) considering interactions between patterns and processes across scales that can lead to nonlinear system shifts, such as how regional climate interacts with localized human alterations (eg urbanization); or (2) explicitly focusing on interactive effects of multiple spatially structured human alterations (eg dams, agriculture) on basin-wide conditions (Figure 1).

Riverine networks can contribute to a broader under-

standing of macrosystems in general. Owing to their directional connectivity, rivers are more likely to be affected by macroscale phenomena than many other ecosystems. However, this connectivity makes such systems tractable to macroscale study because we know where to look for teleconnections.

The framework we present for understanding riverine macrosystems builds on a history of river science that recognizes the interconnected and variable nature of rivers and incorporates several well-developed research themes (Townsend 1989; Fausch *et al.* 2002; Ward *et al.* 2002; Wiens 2002; Benda *et al.* 2004; Thorp *et al.* 2008; Poole 2010). Here, we discuss: (1) advances in theory and techniques for studying whole watersheds, (2) emergent properties of riverine macrosystems, (3) measurement of changes in macrosystem condition, (4) potential effects of multiple human alterations on entire river systems, including ecological thresholds, and (5) research challenges for riverine macrosystem ecology and management.

■ Advances in theory and techniques for studying whole watersheds

In keeping with previous research (see Poole [2010] for review), we view large river systems as a series of con-

Table 1. Examples of questions, hypotheses, and study approaches appropriate for each spatial scale; patterns and processes interact across scales and can lead to ecological thresholds or tipping points

Scale	Questions	Hypotheses	Study approaches	Patch grain sizes
Micro- (Microhabitat 100 m^2 – reach 10^4 m^2)	(1) What are the mechanistic drivers of individual components of ecological condition at a site? (2) What are the mechanistic drivers of species behavior, interactions, and demographics at a site?	(1) Weather events (2) Variation in biophysical filters	(1) Manipulative experiments (2) Gradient analysis (3) Simple quantitative models	Microhabitat 10^0 m^2 – pool/riffle 10^1 m^2
Meso- (Reach 10^4 m^2 – basin 10^9 m^2)	(1) What determines ecological condition within a region? (2) How do species of conservation concern respond to environmental change within particular management areas?	(1) Weather patterns (2) Connectivity and dispersal (3) Average effects of biophysical filters (4) Spatiotemporal variation	(1) Gradient analysis (2) Correlative niche models (3) Theory-based quantitative models	Reach 10^4 m^2 – valley segment 10^5 m^2
Macro- (Basin 10^9 m^2 – global 10^{14} m^2)	(1) What are the determinants of patterns of diversity, productivity, or trait distributions across regions with dissimilar species? (2) How do species of conservation concern respond to environmental change across their entire range? (3) Where and how do nutrients and gasses emerge from a landscape?	(1) Climate and biogeography (2) Connectivity and dispersal (3) Aggregated effects of local biophysical filters (4) Spatial structure	(1) Observational tests of simple theory (2) Correlative models (3) Multi-factor theory-based quantitative models	Reach 10^4 m^2 – basin 10^9 m^2

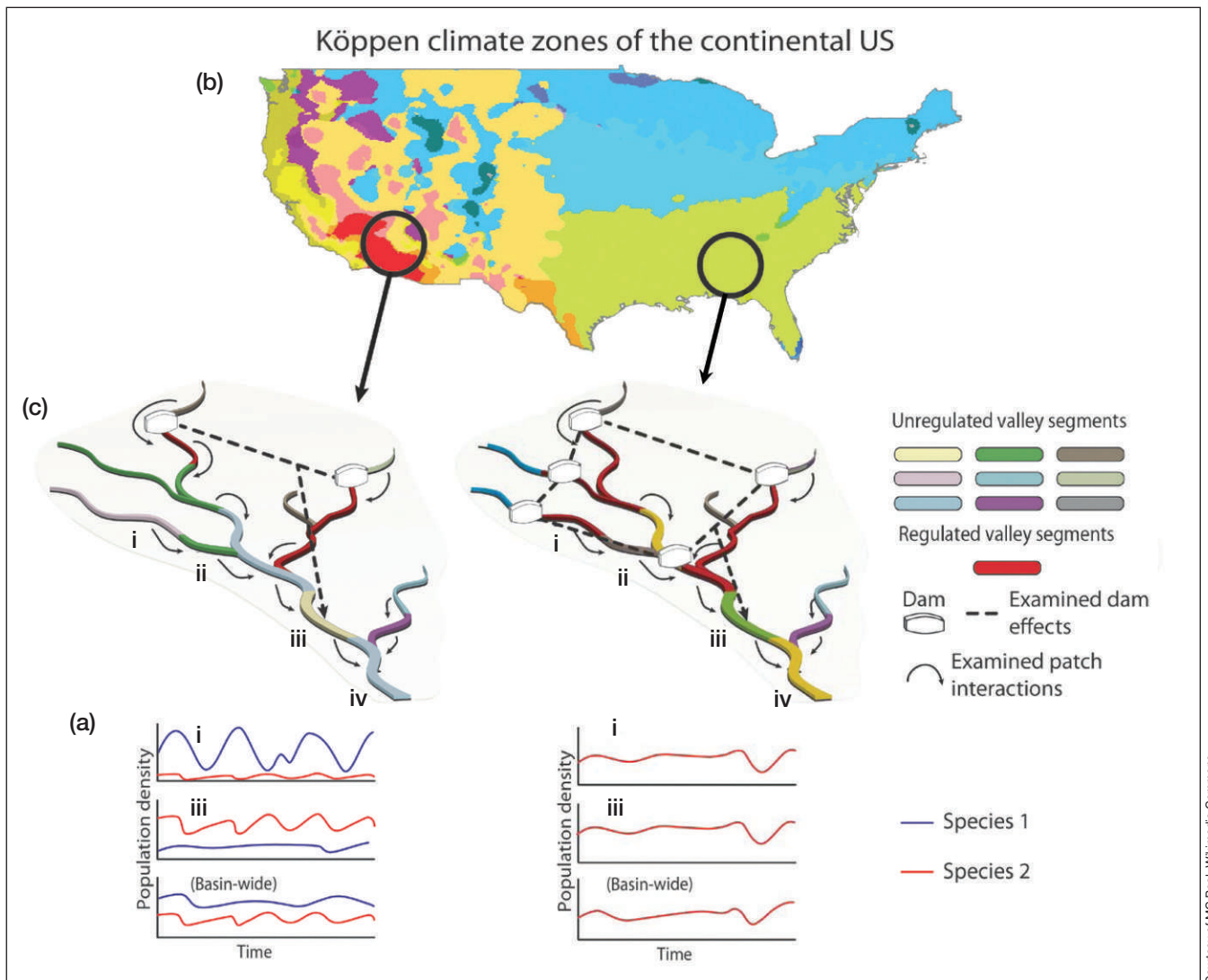


Figure 1. The multi-scale factors influencing riverine macrosystems. Fluctuations in population density (a) are influenced by regional context (eg climate, social systems) (b), habitat patch and human alteration spatial structure (c), and gradients associated with network position (sites i–iv in [c]). Social, physical, and biological factors interact across scales and great distances, influencing population asynchrony among habitat patches and recovery following disturbance, generating thresholds in macrosystem condition (see text and WebFigure 2 for further explanation).

nected and interacting habitat patches that are influenced by regional conditions, with spatially and temporally variable hydrology, geomorphology, and biogeochemistry that affects the ecology of entire basins. In theory, habitat patches can be defined at any scale, but we propose that for macrosystem studies, sizes from reach to basin are most appropriate (Table 1; Thorp *et al.* 2008). Hydrogeomorphic variation is crucial to understanding riverine macrosystems, so patch sizes need to be of suffi-

cient magnitude to capture this variation. We therefore focus on valley-segment-sized riverine patches for examples and discussion (cf functional process zone, ie “hydrogeomorphic patch[es] intermediate in scale between valleys and reaches”; Thorp *et al.* 2008). Patches can be identified by geographic information system (GIS) data and remote sensing (Panel 1) and should contain characteristic and unique spatial and temporal distributions of microhabitat (WebFigure 1). For instance, valley seg-

Panel 1. How can habitat units be defined?

Recently, several research groups have simultaneously explored methods of categorizing river segments into distinct hydrogeomorphic habitat patches (Thoms and Parsons 2003; Flores *et al.* 2006; Thorp *et al.* 2008; Soranno *et al.* 2010). These approaches have many similarities. In general, all use geospatial datasets, including digital elevation models and flooding models to calculate various metrics at the basin, valley, and floodplain levels. These metrics are then used to delineate relatively homogeneous habitat patches of various lengths that can be classified for convenience into intuitive categories (eg upland constricted zone for a valley segment patch). The methods used to define the underlying habitat template in models of riverine macrosystems will likely have critical effects on performance.

ments with confined channels (eg canyons) will likely have much narrower distributions of temperature and hydraulic micro-environments than unconfined valley segments with complex channels and wide floodplains. These differences will directly influence species distributions and biogeochemical processes (Ward *et al.* 2002).

River ecologists have largely applied patch concepts at small scales and to river networks and corridors (Townsend 1989; Ward *et al.* 2002; Wiens 2002). A macrosystem perspective needs to include consideration of hydrologically connected upland patches (Figure 2), which may be connected via surface or belowground flow paths. For example, where soils are porous, forest patches may intercept nutrients originating from agricultural areas and travelling via belowground flow paths, thereby reducing inputs to rivers. However, where soils are less porous, shallow agricultural runoff can result in high nutrient inputs (Figure 2; Norton and Fisher 2000). Differences in belowground hydrology can be categorized into landscape units or patches with GIS, similarly to aboveground patches (Wolock *et al.* 2004).

Riverine macrosystems may be modeled as interacting upland and riverine patches, where each patch is a node in the model and transitions between nodes are defined by rules for routing water, nutrients, energy, genes, or organisms (*sensu* Helton *et al.* 2014). Watershed models, such as the GIS-based Regional Hydro-Ecologic Simulation System (RHESSys), use this approach to simulate water and nitrogen (N) fluxes (Tague and Band 2004). Emerging techniques using dynamic simulation of material fluxes through spatially explicit networks of riverine patches in small basins (Helton *et al.* 2014) could potentially be scaled up to model riverine macrosystems (Web-Figure 1). In such models, multiple potential rules for routing materials and organisms can form “systems-level hypotheses” about processes in riverine macrosystems that could be tested using available datasets for hydrology, chemistry, and species abundance, collected as part of government monitoring programs. Thus, despite the inherent difficulties of studying large, complex riverine systems, multiple tools are emerging for characterizing and

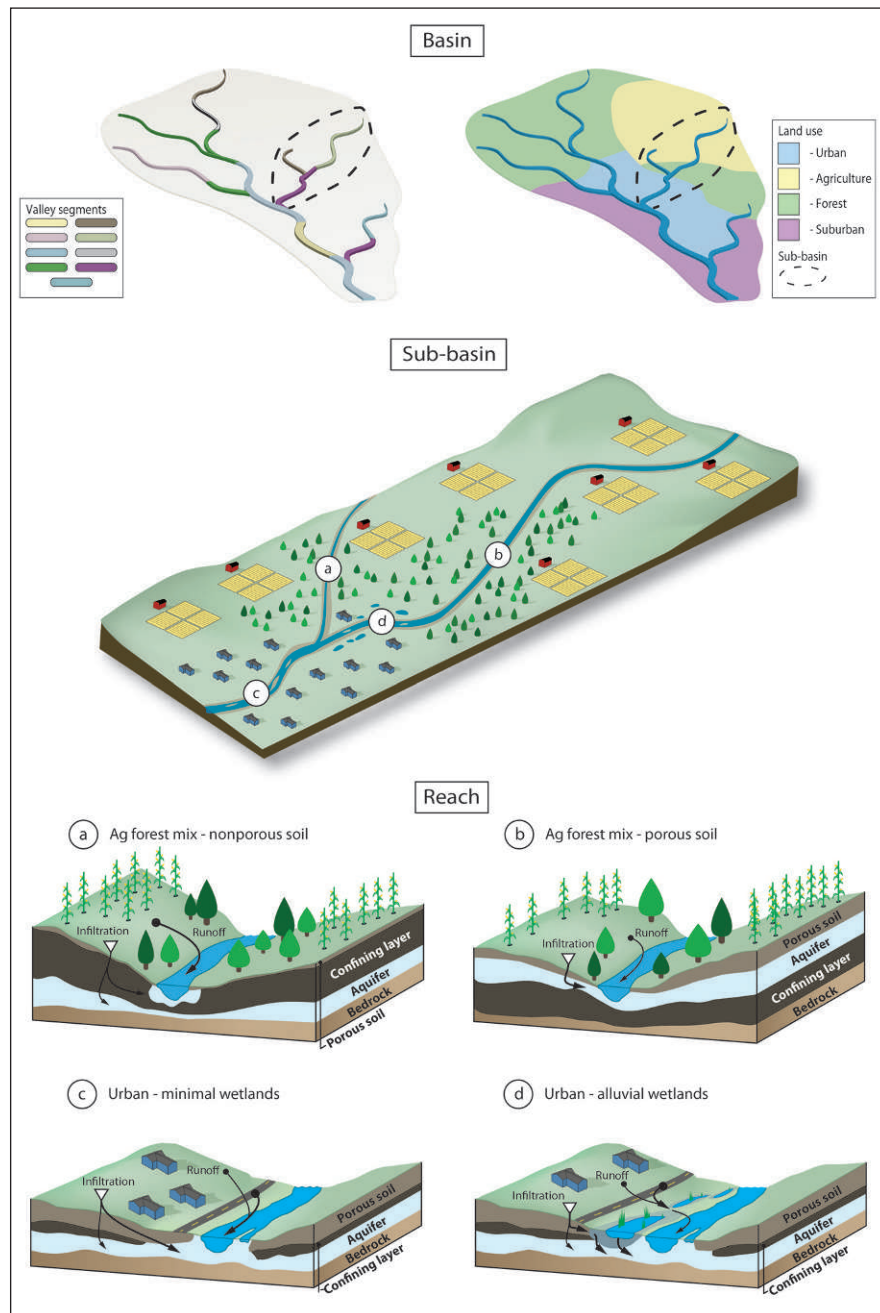


Figure 2. The influence of land-use/land-cover patches at multiple scales on above- and belowground flows in a hypothetical basin. Categorizing upland and riverine patches provides relevant information on sources of water and nutrients, as well as interactive effects on discharge and nutrient fluxes across the river network. Reaches (a) and (c) would likely have higher nutrient inputs than reaches (b) and (d), due to the combination of land-use/land-cover characteristics (eg soil permeability) and the complexity of the riverine landscape. In reaches (a) and (b), “Ag” stands for agriculture and in all reach figures, arrow head sizes represent relative magnitudes of flux.

studying these macrosystems.

Ziv *et al.* (2012) created a model of migratory fish abundance and extinction risk in the Mekong River Basin that illustrates the practicality of a riverine macrosystems approach (Figure 3). The model examines the combined effects of variable habitat patch carrying capacity (approximated by runoff and surface area) and connectiv-

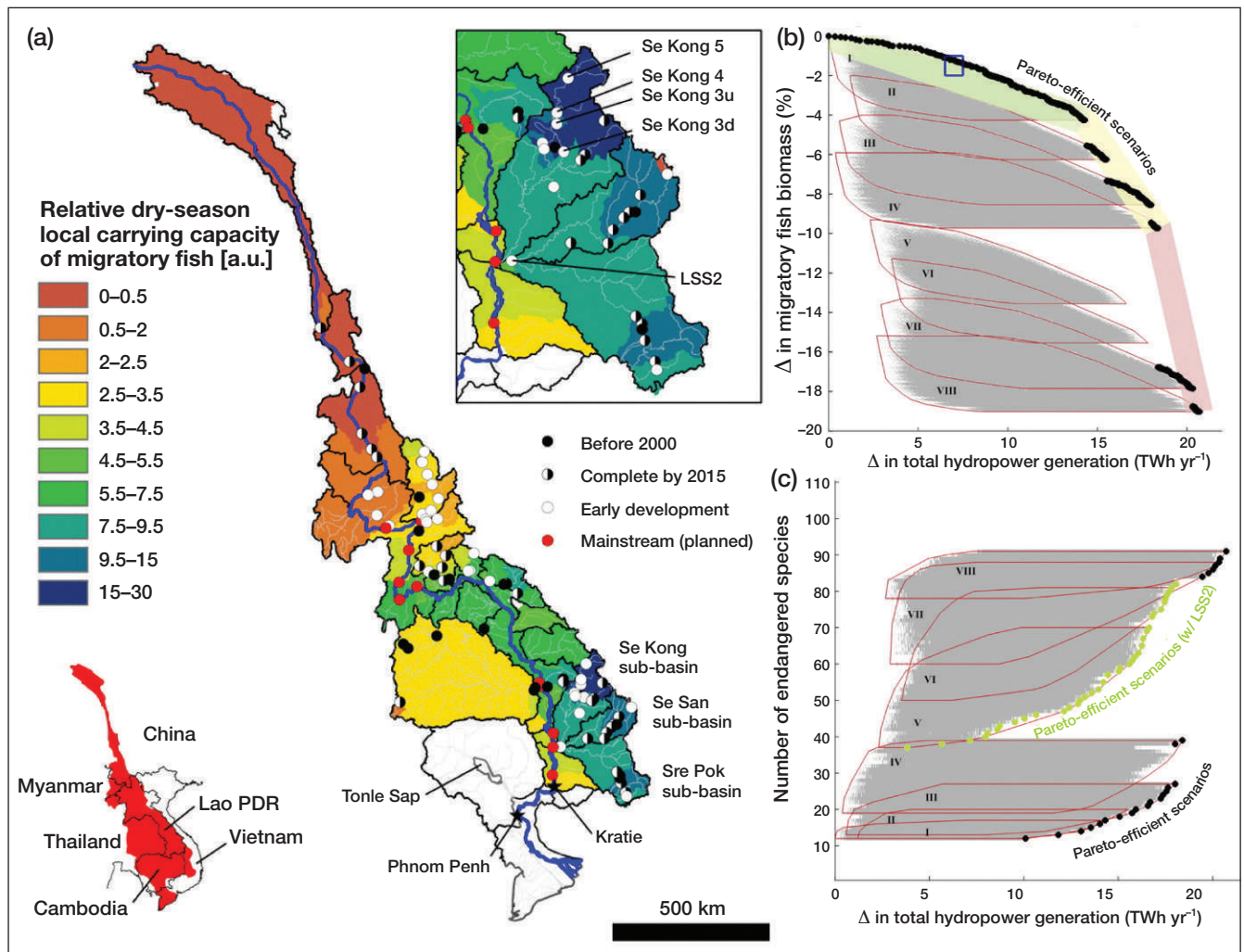


Figure 3. A riverine macrosystem model for the Mekong River Basin (modified from Ziv et al. [2012]) that examines the effects of spatial variation in habitat carrying capacity (approximated by runoff and surface area) and habitat connectivity on migratory fish biomass and extinction risk under scenarios of dam construction. (a) Map of estimated carrying capacity and dams in the Mekong Basin. (b and c) Projected effects of hydropower on changes in migratory fish biomass and extinction risk, respectively, under all possible scenarios of dam creation (approximately 134 million scenarios, gray). These scenarios fall into eight (I–VIII) categories of key changes to parts of the basin (see Ziv et al. [2012] for details). Black or green dots represent scenarios with the “optimal” balance of fish condition and hydropower generation. The wide range of changes in migratory fish biomass and endangerment at any given level of hydropower generation suggests that spatial configuration of dams is an important modifier of dam effects on fish populations. Color-coded backgrounds in (b) represent hydropower generation levels that result in low (green), medium (yellow), or high (red) declines in fish production as a result of small increases in hydropower. a.u.: animal unit; TWh = terawatt hour.

ity between upstream spawning patches and downstream floodplains. The parameterized model was used to evaluate the effects of multiple scenarios of dam development on fish biomass and species persistence within the basin (Figure 3, b and c). Results suggested nonlinear relationships between dam construction and fish biomass and persistence that could not have been easily predictable without this large network approach.

Emergent properties of riverine macrosystems

A broad view of rivers can help to predict watershed-wide ecological responses that emerge from the spatial arrangement of and interactions between upland and riverine

patches. We propose that sensitivity, resistance, and resilience are important properties of riverine macrosystems. We offer the following three definitions:

Sensitivity: changes in one part of a basin influence a distant part of that basin (also referred to as teleconnections; Heffernan et al. 2014).

Resistance: ability of a basin-wide ecological metric to withstand change in the face of temporal environmental variation.

Resilience: ability of a basin-wide ecological metric to return to similar levels after a perturbation.

Riverine ecosystems are particularly sensitive to environmental change occurring within the basin because of the high degree of longitudinal connectivity; for instance, a large dam can alter thermal, sediment, and flow regimes far downstream (Richter *et al.* 1998; Graf 2006). Headwater disturbances (eg surface mining) can modify water quality and ecological conditions for many kilometers (Lindberg *et al.* 2011). River basins are also sensitive to historical changes to the watershed. For example, the geomorphology and sediment dynamics of many mid-Atlantic coastal US streams are still heavily affected by widespread logging and mill dam efforts that occurred more than a century ago (Walter and Merritts 2008). Although river systems may be at one end of the spectrum in terms of effects of teleconnections and macrosystem sensitivity, other systems may experience similar dynamics. Ocean currents create highly directional connectivity between widely separated areas, resulting in high nutrient levels in upwelling zones (eg Galapagos Islands) or influencing local species persistence through variation in inputs of propagules (Possingham and Roughgarden 1990).

Despite the sensitivity of local habitats to distant changes, many basin-wide ecological processes and conditions exhibit high macrosystem resistance because of temporal asynchrony among connected, heterogeneous habitat patches (Ward *et al.* 2002; Palmer *et al.* 2009). For instance, Labbe and Fausch (2000) documented increased persistence of the Arkansas darter (*Etheostoma cragini*) in a heterogeneous river system with cool perennial and warm intermittent pools. Darter growth and reproduction were higher in the warmer pools during wet years; however, during dry years, mortality rose when some of these pools dried up, while populations persisted in the perennial pools. Thus, the overall combined population was more stable over time because of this habitat heterogeneity and asynchrony.

In general, asynchrony among subpopulations or ecological processes in connected habitat patches should lead to decreases in temporal fluctuations in the size of the entire population or in a combined ecological metric across time (Figures 1 and 4; WebFigure 2; Hanski 1999). This principle is often called the “portfolio effect” because asynchronous dynamics across patches reduces broad-scale ecological variability in the same way that a diverse investment portfolio mitigates financial volatility (Schindler *et al.* 2010). Multiple factors can produce asynchronous ecological dynamics across habitats, including heterogeneity of physical conditions, species interactions, age classes, behavior, or genetics (Oliver *et al.* 2010; Schindler *et al.* 2010; Carlson *et al.* 2011). Portfolio effects have been shown to reduce temporal fluctuations in sockeye salmon (*Oncorhynchus nerka*) production in a large Alaskan watershed (Figure 4; Schindler *et al.* 2010). In general, portfolio effects manifest as a decrease in variability with increasing scale. This cross-scale resistance is an important emergent property of riverine macrosystems.

Movement of individuals and materials between dynamically asynchronous patches should enhance macrosystem resilience. Classic metapopulation and metacommunity theories propose that recolonization of patches by extirpated species promotes system-wide species persistence and high diversity (Hanski 1999). Application of metacommunity theory to rivers has explained spatial patterns of species diversity within river networks (Patrick and Swan 2011) and at multi-basin scales (Muneepeerakul *et al.* 2008).

Although portfolio effects and metacommunity dynamics are important in riverine macrosystems, species traits and regional differences in climate or geology may alter the spatial and temporal scales of these phenomena and their relative strength. For instance, one would expect aquatic macroinvertebrates or riparian arthropods with weak adult dispersal mechanisms to exhibit portfolio effects and metacommunity dynamics at small scales (eg a subwatershed), while at the other extreme, migratory fish or birds would be expected to experience portfolio and metacommunity dynamics within or across major watersheds. In support of this idea, Albanese *et al.* (2009) found that relative fish mobility was one of the more accurate predictors of differential recovery of populations following experimental extirpation. Additionally, though not a riverine example, Oliver *et al.* (2010) noted that the population stability of highly mobile butterfly species resulted from habitat heterogeneity at larger spatial scales than less mobile species.

Regional differences may also be important. Areas with broad, simultaneous, catastrophic disturbances (eg floods, fires) may show synchronized ecological dynamics in patches across the basin, thereby decreasing portfolio effects (eg fire in the western US; Kitzberger *et al.* 2007). Any factor that promotes broad-scale synchrony between habitats or across species should decrease the influence of portfolio effects and metacommunity dynamics (see below).

■ Macrosystem effects of human alterations

Certain types of human modifications to river networks or watersheds can compromise macrosystem resistance and resilience and lead to the crossing of ecological thresholds (Palmer *et al.* 2009; Dodds *et al.* 2010). Although the strong directional connectivity of riverine systems could theoretically make rivers less prone to feedback loops at small scales, the cumulative effects of human alterations across a basin can produce nonlinear changes in ecological systems (Dodds *et al.* 2010). Specifically, the spatial configuration of alterations likely influences thresholds and shifts in macrosystem condition. Additionally, as discussed below, human social systems or the presence of migratory species could promote broad upstream–downstream feedbacks that could stabilize or destabilize ecosystem states. The details of these processes are important in predicting nonlinear, difficult

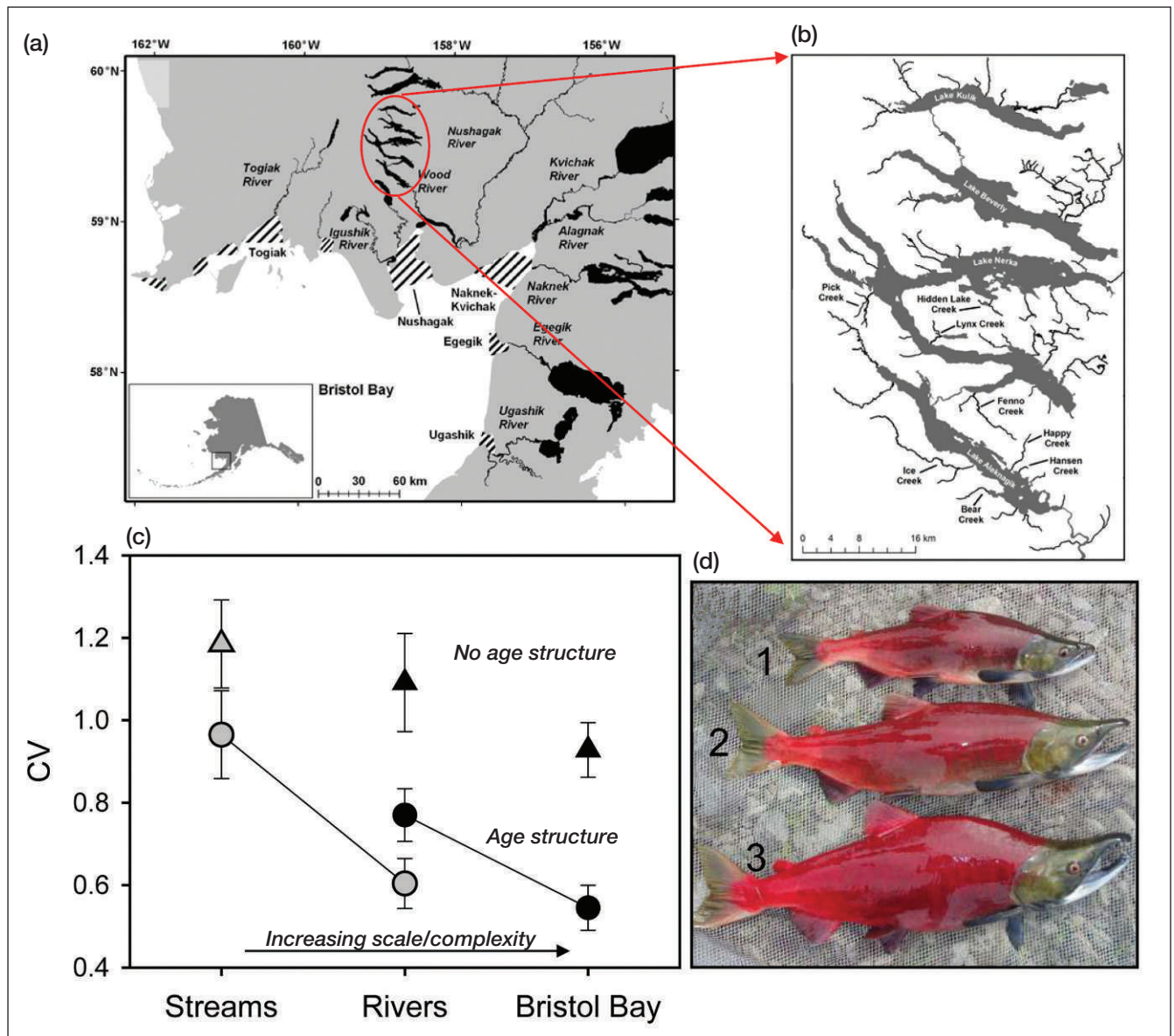


Figure 4. The portfolio effect in sockeye salmon (*Oncorhynchus nerka*) in Alaska. (a) Waters of Bristol Bay, Alaska, associated with sockeye are in black; fishing areas are indicated by striped areas. (b) The Wood River system (WRS). (c) Coefficient of variation (CV) of temporal trends of sockeye salmon stocks across scales. Temporal variability of sockeye abundance in the WRS (gray) is lower for the entire river than for constituent streams and is lower for sockeye across Bristol Bay than for rivers that enter Bristol Bay. This is particularly true when all age classes are included in the analysis (circles) rather than just the dominant age class (triangles). (d) The three age classes represented in the analysis. (Reprinted with permission from Macmillan Publishers Ltd: Nature [Schindler et al. 2010], © 2010.)

to reverse regime shifts in riverine macrosystems and in preserving ecosystem services in the face of climate change.

Measuring macrosystem change

The sensitivity, resistance, and resilience of entire river basins to human alteration can best be represented by metrics of: (1) spatiotemporal heterogeneity of biophysical habitat conditions, (2) connectivity among patches, and (3) temporal fluctuations of ecological variables (eg nutrient retention, population abundances, diversity).

Portfolio effects require spatially heterogeneous habitats that either experience environmental variation (eg drought, floods, thermal extremes) asynchronously or respond differentially to similar environmental variation (ie resulting from variation in population structure, species interactions, or other ecological conditions or processes). Thus, decreases in spatiotemporal habitat heterogeneity should decrease macrosystem resistance. The combined effects of multiple alterations may homogenize spatiotemporal habitat variation across broad scales (Poff et al. 2007) and synchronize ecological dynamics across patches (Moore et al. 2010).

Because habitat connectivity influences the movements of organisms and materials, transmission of disturbances, and refuge availability, macrosystem responses to changes in connectivity are not straightforward. Highly connected patches may homogenize species across a system (Hanski 1999) or may hinder the formation of refugia by conveying disturbances across the network. For example, when pipes connect urban runoff to streams, high energy flows move rapidly through stream networks, homogenizing habitats and synchronizing dynamics (Roy and Shuster 2009). Intermediate connectivity is less likely to synchronize a system, allowing individuals from undisturbed locations to recolonize disturbed areas, thereby promoting resilience (Labbe and Fausch 2000). Patches disconnected by barriers (eg dams, levees) provide little opportunity for recolonization, which reduces the resilience of the system (Fausch *et al.* 2002). Measures of connectivity will vary depending on the ecological response of interest. We advocate creating several complementary measures of hydrologic and landscape connectivity derived from analysis of land use/land cover, river-network structure, and water infrastructure data (eg Cote *et al.* 2009; Ziv *et al.* 2012).

We hypothesize that variation in habitat heterogeneity and connectivity will combine to influence basin-wide temporal variation (eg coefficient of variation) in an ecological metric of interest, such as salmonid population size (Schindler *et al.* 2010). Specifically, a decrease in habitat heterogeneity within a basin will tend to homogenize and synchronize ecological processes and dynamics across patches within the basin, amplifying basin-wide temporal ecological variation. Habitat metrics can focus on a range of biophysical variables (eg flow, sediment, temperature, nutrients) and macrosystem condition can be assessed with multiple ecological variables (eg diversity, abundance, species traits or functional groups, genes). Which metrics are selected will depend on stakeholder needs, scientific interest, and data availability. Comparison of macrosystem metrics to local measures (eg ratios of basin to patch temporal fluctuations in species abundance) and comparisons across multiple basins should enable us to better understand the variations between metrics, to gauge the relative degree of each type of change, and set management priorities.

Macrosystem impacts of human modifications

In dynamic networks of directionally connected habitat patches, the extent, degree, and spatial arrangement of human modifications, embedded within regional climate and social systems, should greatly alter macrosystem dynamics. However, insufficient research has focused explicitly on the spatial arrangement of human alterations to watersheds (but see Ziv *et al.* 2012; Grantham *et al.* 2013) or how these alterations influence complex, cross-scale interactions in macrosystems. Individual modifications (eg dams, levees, land-use changes) can vary in

extent or degree, and collections of modifications can vary in density, juxtaposition, heterogeneity, positioning within the network, dispersion, connectivity, and redundancy (WebFigure 3; WebTable 1). Modifications may build on each other, amplifying or even nullifying basin-wide effects. For instance, extensive mining activity adjacent to headwaters can magnify changes in water quality (Lindberg *et al.* 2011) while drainage systems can increase N loading or stream temperatures when they connect urban areas directly to rivers (Craig *et al.* 2008). Alternatively, built landscapes may be interspersed with restoration projects, reducing nutrient inputs to rivers (Craig *et al.* 2008), and hydropower dams that cause large, regular daily peaks in flow can be interspersed with re-regulating dams that convert these cyclic flow peaks to a more natural flow regime (Richter and Thomas 2007). All of these alterations may interact across a single basin and are themselves influenced by regional climate and social systems.

To illustrate the ways in which the spatial arrangement of human modifications may influence macrosystem condition, we qualitatively project changes resulting from varying density, dispersion, and position of dams in a hypothetical basin (Figure 5). We suggest that low densities of dams may cause relatively little macrosystem change, but localized effects will vary with dam size, dispersion, and network position (Figure 5, a–d). Individual dams on small headwater streams may have strong local effects that diminish downstream as a result of hydrologic inputs from unregulated tributaries (Ward and Stanford 1983). Single, large downstream dams also have strong localized effects without modifying the hydrology of tributaries (Figure 5c). However, downstream dams can disconnect upstream habitats from habitats in other basins, lakes, or oceans, thereby preventing migratory fish species from reproducing in headwaters (Hitt *et al.* 2012). Some migratory species (eg salmon) transport large amounts of energy and nutrients into river basins, altering nutrient cycling and ecosystem dynamics in headwater streams and riparian zones (Gende *et al.* 2002). Thus, downstream dams can reduce feedbacks between downstream and upstream sections of rivers, leading to system-wide shifts in ecosystem conditions. The importance of long-distance dispersal and the mode of dispersal for different species (eg in-stream or overland) should influence how a downstream dam affects basin ecosystem dynamics. Cultural differences in the perceived value of affected ecosystem services may also influence the effect of social systems on construction or removal of dams (eg Gowan *et al.* 2006).

High dam densities can lead to local and basin-wide hydrogeomorphic and ecological change (Graf 2006; Poff *et al.* 2007). Large numbers of dams in a particular upstream region may have strong localized effects at the sub-basin scale but comparatively little effect on basin-wide flow homogenization or on basin-wide ecological conditions over time (Figure 5f). When uniformly distrib-

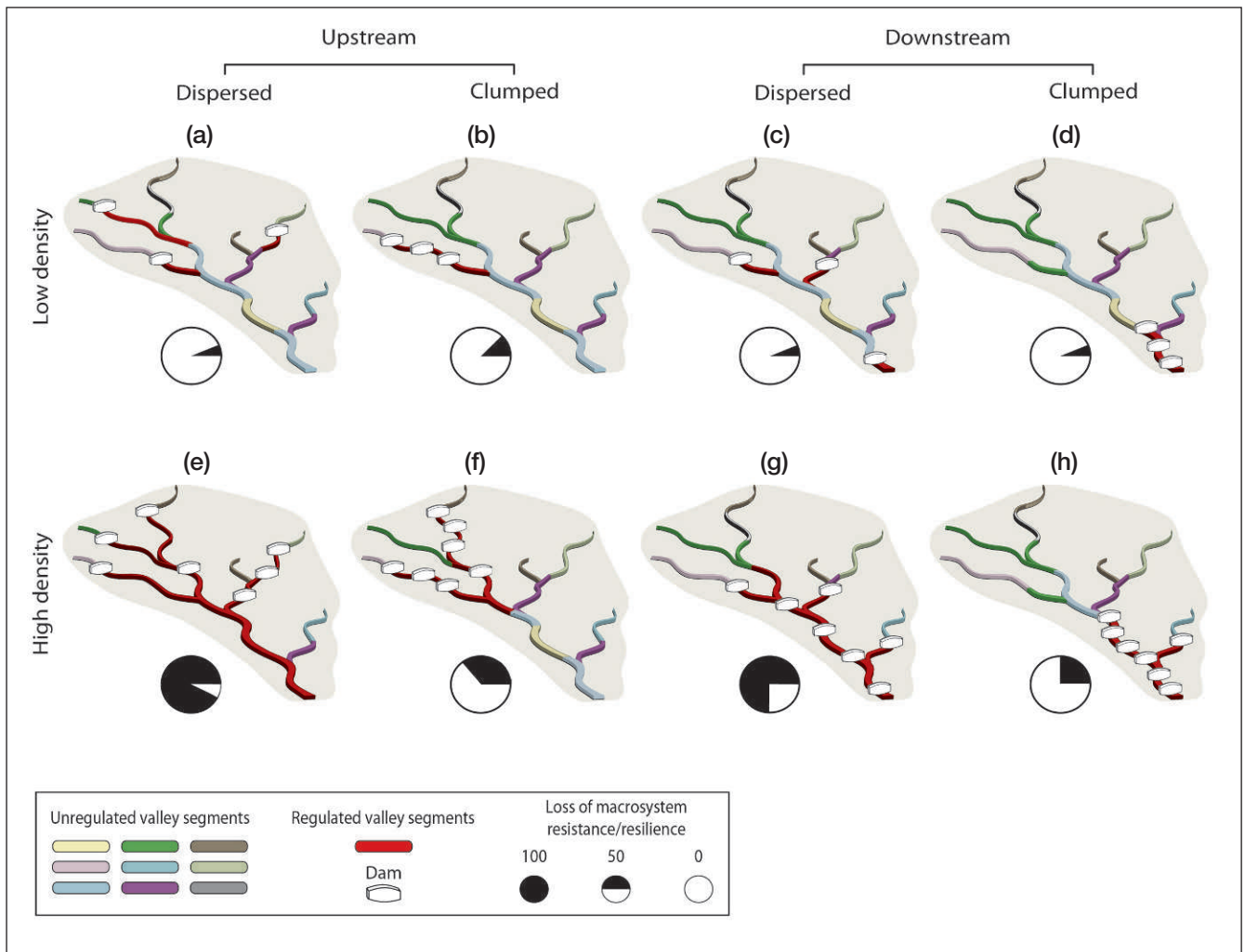


Figure 5. The interactive effects of dam density, dispersion, and positioning (see horizontal and vertical labels) on the macrosystem resistance/resilience of the basin. Panels (a)–(h) represent possible scenarios of dam arrangement varying in each aspect of spatial structure. See text for full explanation. Note: small tributaries are not shown, but they lead to diminishing effects of dams downstream.

uted in upstream positions, dams may create strong basin flow homogenization (synchrony across habitats), substantial declines in habitat connectivity, and major, basin-wide variations in ecological conditions (Figure 5e). Some data support this view. For example, Ziv *et al.* (2012) found that construction of multiple, widely distributed, upstream dams in the Mekong River Basin would likely lead to larger declines in migratory fish biomass and greater increases in extinction risk than would the construction of all the mainstem dams currently under consideration.

Channel shape, density, and other aspects of channel spatial structure will influence riverine responses to human modifications (Benda *et al.* 2004). For instance, the density of dams could be different in two basins of the same size and with an equal number of dams, but with a different density of channels (dam density = number of dams/total channel length). Because unregulated tributaries diminish dam effects and because tributary junctions are important modifiers of channel geomorphology, the position and density of dams relative to tributary posi-

tion and density may also affect the magnitude of local and macrosystem change (Benda *et al.* 2004).

Although we have focused on dams, similar predictions can be made for the ecological effects of the spatial configurations of other modifications, such as land-use/land-cover change (eg deforestation, urbanization, conversion to agriculture). For instance, connectivity of impervious surfaces in urbanized watersheds influences riverine ecosystem condition (Roy and Shuster 2009). Impervious patches directly connected to streams by stormwater infrastructure have a disproportionate impact on stream ecosystems (eg large floods, poor water quality, high water temperature). On the other hand, catchments where water is directed from impervious patches into vegetated patches with permeable soil types can buffer stream N levels (eg Lewis and Grimm 2007). Thus, the spatial configuration of land patch types and hydrologic connectivity to stream channels can form the basis for many best management practices in urban watersheds (Craig *et al.* 2008).

In a macrosystem context, patches could conceivably consist of entire basins, with their land use/land cover

and connectivity influencing regional resistance and resilience. For instance, organisms in a forested watershed could recolonize well-connected urbanized watersheds, contributing to multi-basin resilience. A macrosystem approach is therefore well-suited to various scales, from connected reaches in a watershed to watersheds within a large region (Table 1).

■ Crossing ecological thresholds

Interactions between climate, social systems, geomorphology, and human alterations may promote ecological thresholds in macrosystems by modifying portfolio effects and metacommunity dynamics. We believe that four conditions are associated with nonlinear thresholds: (1) when productive “source” habitats can no longer sustain populations outside these habitats (eg when pollution in headwaters leads to extirpations far downstream); (2) when “source” habitats begin to sustain populations outside sources (eg lentic tolerant species emigrating from reservoirs); (3) when connectivity declines to the point where species can no longer migrate between important habitats or recolonize disturbed or restored habitats; and (4) when human values or perceptions of environmental change interact with systems of governance to cause shifts in policies concerning watershed alterations. These conditions are the result of modifications to river basins that influence habitat heterogeneity, asynchrony, and connectivity, and may interact with one another across scales. For instance, Gido *et al.* (2010) found that in the US Great Plains, groundwater pumping, dams, fish stocking in reservoirs, and agricultural sediments appeared to act in combination to influence nonlinear and threshold-like shifts in the occurrence and abundance of several fish species.

Feedbacks between ecological and social systems may increase or decrease macrosystem resistance and resilience; for instance, increases in the perceived non-market value of salmon in northwestern North America have resulted in dam removals (Gowan *et al.* 2006). Thus, differences in socioecological conditions between basins lead to variation in the type and strength of feedback loops, altering macrosystem resistance and resilience and the expectation of crossing ecological thresholds. Socioecological comparisons across basins could help inform future management efforts.

Finally, by our definitions highly altered river basins can be resistant and resilient to change (including restorations) as a result of legacy effects from human activities and ongoing pressure from human alterations (Dodds *et al.* 2010). This sort of resistance and resilience will likely provide low levels of endemic diversity and ecosystem service delivery because these highly altered basins will not contain suitable habitat for endemic species and will lack spatiotemporal habitat heterogeneity. Thus, macrosystem resistance and resilience may be a necessary but insufficient goal of sustainable manage-

ment, which must also take into account the overall delivery of ecosystem services and their value.

■ Research challenges in the study of riverine macrosystems

Future studies of riverine macrosystem ecology will need to determine: (1) habitat patch sizes that adequately capture the biologically relevant heterogeneity of entire basins; (2) the effects of upland heterogeneity on river function (eg the sensitivity of in-stream processes to land-use/land-cover variation); (3) the level of connectivity required to maintain macrosystem resilience; (4) how landscape features interact spatially to influence basin-wide ecological variability and change; and (5) how cross-scale and socioecological linkages vary across basins and how these feedbacks alter system resistance and resilience. These are not only important fundamental questions in riverine ecology but are directly related to riverine management at basin scales, as managers must balance multiple, often conflicting demands for services. Riverine macrosystems ecology should aid in the management of rivers by helping to determine the appropriate scale, spatial configuration, and extent of management actions in complex, interactive, and dynamic riverine landscapes.

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