

From meta-system theory to the sustainable management of rivers in the Anthropocene

Núria Cid^{1*}, Tibor Erős², Jani Heino³, Gabriel Singer⁴, Sonja C Jähnig^{5,6}, Miguel Cañedo-Argüelles^{7,8}, Núria Bonada^{7,9}, Romain Sarremejane¹, Heikki Mykrä³, Leonard Sandin¹⁰, Riikka Paloniemi¹¹, Liisa Varumo¹¹, and Thibault Datry¹

Regional-scale ecological processes, such as the spatial flows of material, energy, and organisms, are fundamental for maintaining biodiversity and ecosystem functioning in river networks. Yet these processes remain largely overlooked in most river management practices and underlying policies. Here, we propose adoption of a meta-system approach, where regional processes acting at different levels of ecological organization – populations, communities, and ecosystems – are integrated into conventional river conservation, restoration, and biomonitoring. We also describe a series of measurements and indicators that could be assimilated into the implementation of relevant biodiversity and environmental policies. Finally, we highlight the need for alternative management strategies that can guide practitioners toward applying recent advances in ecology to preserve and restore river ecosystems and the ecosystem services they provide, in the context of increasing alteration of river network connectivity worldwide.

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River ecosystems sustain disproportionate levels of biodiversity at landscape, regional, and continental scales (Reid *et al.* 2019). They contribute substantially to global biogeochemical

cycles through release of carbon dioxide to the atmosphere and transport of carbon and nutrients from continents to oceans (Raymond *et al.* 2013). Rivers also provide key ecosystem services, including provision of drinking water, food production, and climate and water regulation, which are critical to sustaining human wellbeing (Reid *et al.* 2019). However, in the current Anthropocene era (Panel 1), rivers worldwide are increasingly impaired by human activities, and are now among the most threatened ecosystems on Earth (Dudgeon 2019). This global trend necessitates the development of more effective management strategies and policies to ensure maintenance of the biodiversity and functional integrity of river ecosystems in the future.

Most river management practices, independently of the spatial scale at which they are implemented, are based on local assessments, as a legacy of the niche paradigm that has prevailed in ecology for decades (Panel 1; Heino 2013). In contrast, scientific understanding of how biodiversity, ecosystem functions, and ecosystem services are organized across river networks has progressed considerably with the emergence of meta-system theory (Gounand *et al.* 2018). This framework acknowledges that both local (ie niche selection and biotic interactions within a river reach) and regional (ie dispersal of organisms and spatial flows of material and energy across the river network) mechanisms interact to shape the spatial and temporal organization of populations and communities, and drive ecosystem processes and services. The meta-system framework is particularly relevant for river networks due to their dendritic topology (Panel 1) and the predominantly unidirectional flow of water, which constrain the exchange of matter and organisms at larger spatial scales (Tonkin *et al.* 2018). Current river management practices and underlying policies often fail to incorporate important regional processes, hindering efficient conservation and

In a nutshell:

- Rivers are hotspots of biodiversity and provide essential ecosystem functions and services, but face numerous threats globally
- Understanding of how rivers are organized across spatial scales has progressed considerably over the past several decades, proving that regional-scale processes are vital for preserving population, community, and ecosystem dynamics
- However, most existing river conservation, restoration, and biomonitoring practices focus on local-scale strategies and measures
- To improve the management of river networks in the Anthropocene, we suggest additional metrics and assessment approaches that incorporate regional processes more effectively

¹INRAE, UR RiverLy, Centre de Lyon-Villeurbanne, Villeurbanne Cedex, France (nurcia.cid-puey@inrae.fr; nurcia.cid@irta.cat); ²Balaton Limnological Research Institute, Tihany, Hungary; ³Finnish Environment Institute, Freshwater Centre, Oulu, Finland; ⁴Department of Ecology, University of Innsbruck, Innsbruck, Austria; ⁵Leibniz Institute of Freshwater Ecology and Inland Fisheries, Department of Ecosystem Research, Berlin, Germany; ⁶Geography Department, Faculty of Mathematics and Natural Sciences, Humboldt-Universität zu Berlin, Berlin, Germany; ⁷Freshwater Ecology, Hydrology and Management Research Group, Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona, Barcelona, Spain; ⁸Institut de Recerca de l'Aigua, Universitat de Barcelona, Barcelona, Spain; (continued on last page)

Panel 1. Glossary of terms

Alpha diversity: diversity within a specific ecosystem or area (the local species richness), usually expressed as the number of species present (Whittaker 1972).

Anthropocene: a new, human-dominated geological epoch that began somewhere between the years 1610–1964, depending on different lines of evidence (Lewis and Maslin 2015).

Beta diversity: quantification of the number of different communities in a region measured as extent of change (Whittaker 1972).

Dendritic structure (in river networks): rivers and streams follow a geometric pattern of arborescent bifurcation originating from one node and extending out in one direction, forming a hierarchical network of nodes and branches (Heino 2013).

Dispersal: movement of individuals from one locality to another (Leibold *et al.* 2004).

Niche: range of resource availability and physical conditions that a given species can tolerate to survive at a locality (Leibold *et al.* 2004).

Metapopulation: a set of local populations of a single species that are linked by dispersal (Hanski 1998).

Metacommunity: a set of local communities that are linked by dispersal of multiple potentially interacting species (Leibold *et al.* 2004).

Meta-ecosystem: a set of ecosystems connected by spatial flows of energy, material, and organisms across ecosystem boundaries (Gounand *et al.* 2018).

Regional diversity (gamma diversity): total diversity within the entire landscape (ie regional species pool; Whittaker 1972).

Service-providing areas: spatial units that are the sources of ecosystem services in a given landscape (Syrbe and Walz 2012).

Service-connecting areas: spatial units connecting providing areas with benefiting areas in a given landscape (Syrbe and Walz 2012).

Service-benefiting areas: spatial units where the benefits from ecosystem services are required in a given landscape (Syrbe and Walz 2012).

Zeta diversity: number of species shared by multiple communities (Simons *et al.* 2019).

restoration of river biodiversity and ecosystem functions (Erős *et al.* 2018).

Management practices that focus solely on the local scale will increasingly be less effective for achieving desired ecological outcomes. Globally, humans modify catchments through land-use changes; flow regulation by dams, water diversion, and extraction of surface and ground water; and pollution and the introduction of invasive species (Dudgeon 2019). Fragmentation by dams is the major driver of connectivity loss (Grill *et al.* 2019), a process exacerbated by climate-change-related increases in the intensity and frequency of droughts and subsequent drying of river networks (Döll and Schmied 2012). In areas where human population densities are high, the flow regimes of streams and rivers have been altered to such a degree that “novel” ecosystems have been created (Datry *et al.* 2018). Despite having local impacts, most anthropogenic threats at present act at regional or global scales (Dudgeon 2019). Overall, the increasing pressure of multiple threats calls for a better integration of scale-dependent approaches to guide water management and conservation policies in a changing world.

Our primary objective here was to translate meta-system theory into real-world management and policy recommendations for rivers. To do so, we first present the meta-system framework and its relevance for river ecosystems, particularly with respect to decreased connectivity resulting from human-induced fragmentation; we then show why this framework can inform river management to effectively achieve environmental

and conservation targets; and finally, we identify specific policy implications and provide guidance on how a meta-system approach could be implemented.

■ Meta-system theory and its relevance in river networks

Essentially, meta-system theory states that local- and regional-scale processes interact to influence the dynamics of environmental conditions and biota in a given landscape (Figure 1; Gounand *et al.* 2018). Regional-scale processes determine fluxes of individuals, species, and material and energy among local populations, communities, and ecosystems, respectively, whereas local-scale dynamics represent interactions with abiotic conditions and other species (Hanski 1998; Leibold *et al.* 2004; Gounand *et al.* 2018). In turn, sets of local populations, communities, and ecosystems linked by regional fluxes form metapopulations, metacommunities, and meta-ecosystems, respectively (Panel 1; Figure 1). In river networks, dispersal of organisms can be constrained by the dendritic topology, flow regime, physical barriers, and dispersal ability of the organisms, leading to spatial variation among populations and communities (Brown *et al.* 2011). Matter and energy vary spatially, as sources of terrestrial inputs are differentiated across subcatchments (Creed *et al.* 2015) and upstream-to-downstream physical linkage dominates transport with en-route biogeochemical modulation. Such spatial dynamics in the flows of matter and organisms at the regional subcatchment scale can

determine riverine ecosystem functioning at the local reach scale. Meta-system theory upgrades the perspectives of metapopulation and meta-community ecology in river ecosystems focused on spatial flows of organisms by incorporating those of resources, material, and energy (Gounand *et al.* 2018). It offers a framework for gaining a better understanding of the spatial coupling of biodiversity dynamics and ecosystem functioning, eventually contributing to ecosystem services (Gounand *et al.* 2018), and it reinforces previous research on ecological processes across spatial scales in river networks (Fausch *et al.* 2002; Brown *et al.* 2011; McCluney *et al.* 2014). By explicitly distinguishing the different levels of ecological organization, it also provides a robust structure for implementing current biodiversity and environmental policies.

The relevance of the meta-system framework for improving river management can be illustrated through fragmented river networks. Fragmentation, by weirs, dams, or channel drying, not only alters the local environment and biota (eg Datry *et al.* 2014) but also disrupts the fluxes of water, resources, and organisms (Gounand *et al.* 2018; Grill *et al.* 2019). The effects of fragmentation cascade across organizational levels, from populations to ecosystems and eventually to socioecological systems, with detrimental effects on the provision of ecosystem services (Figure 2). Fragmentation can isolate local populations and reduce gene flow within a metapopulation, jeopardizing their long-term persistence due to genetic drift and inbreeding (Fitzpatrick and Reid 2019). Ultimately, this can lead to reductions in species ranges and eventually to local or regional extinctions (Hanski 1998). Responses to the fragmentation of metapopulations cascade to altered meta-community dynamics. Reduced dispersal among isolated local communities can lead to shifts in community composition, biodiversity patterns, and biological interactions at local and regional scales (Jaeger *et al.* 2014), transforming ecosystem functions (Gounand *et al.* 2018). Fragmentation can also have direct effects on fluxes of material (Figure 2). For example, drying resulting from excessive water abstraction, dam construction, or climate change can alter the storage and transport of coarse organic matter and nutrients in the network, as these are retained at sites without flow before subsequent massive releases at flow resumption (Datry *et al.* 2018). Fragmentation may ultimately impact ecosystem service provision at the river basin scale by altering service-providing, service-connecting, and service-benefiting areas (Panel 1; Figure 2; Datry *et al.* 2017). Understanding regional processes occurring at each level of organization (ie metapopulation, metacommunity, and meta-ecosystem) can therefore be crucial for guiding effective river conservation, monitoring, and restoration.

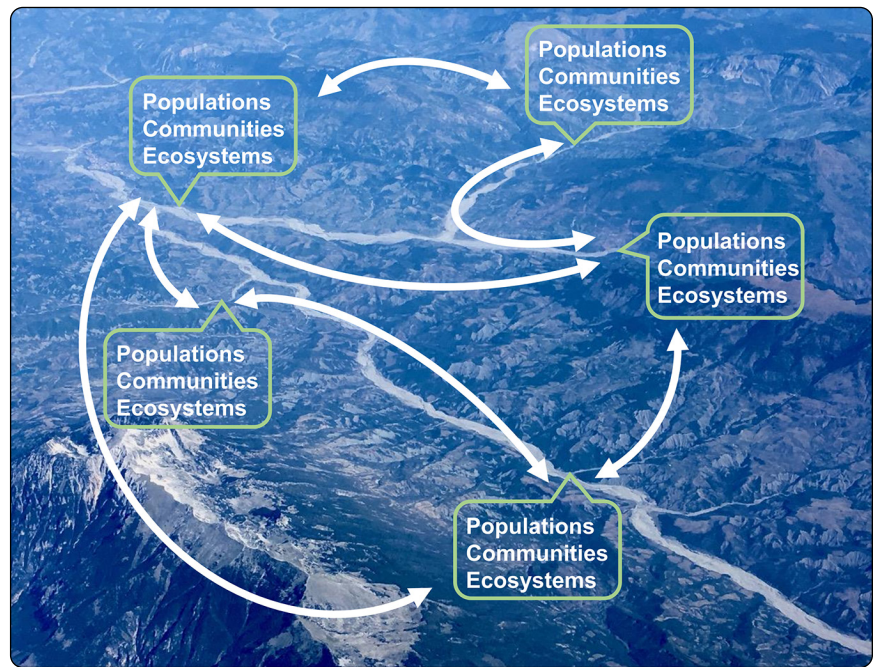


Figure 1. Schematic representation of metapopulations, metacommunities, and meta-ecosystems in a drying river network. Local populations, communities, and ecosystems (green rectangles) are connected by gene flow, dispersal of individuals, and flow of resources (white arrows), respectively, across the landscape.

■ Integrating regional-scale processes in river conservation, restoration, and monitoring

Meta-system theory can also help managers to better predict how populations respond to anthropogenic stressors at the regional scale, and consequently to design conservation plans accordingly (Schiesari *et al.* 2019). When a population follows source–sink dynamics, the regional persistence of the species primarily depends on key “source” populations that contribute via dispersal to “sink” populations (Hanski 1998). Identifying where these key populations and their main dispersal routes are located is crucial to ensure adequate species conservation. For instance, studies on salmonid fishes show that fragmentation by large reservoir dams, hatchery introductions, and deterioration of habitat quality can substantially alter metapopulation structure, and that optimal management strategies should be based on maintaining habitat quality and connectivity of key source populations (Fullerton *et al.* 2016). In very fragmented metapopulations, local populations decline, and the risk of extinction is higher than in large and connected metapopulations (Fitzpatrick and Reid 2019). For example, historically connected metapopulations of the endangered Iberian cyprinid fish *Iberochondrostoma almacai* now experience fragmentation as a result of river drying and are subjected to strong genetic drift (Sousa *et al.* 2010). Protecting local habitats alone would not be effective to sustain the species, and conservation strategies should target increasing gene flow (Sousa *et al.* 2010). On the contrary, historically isolated populations

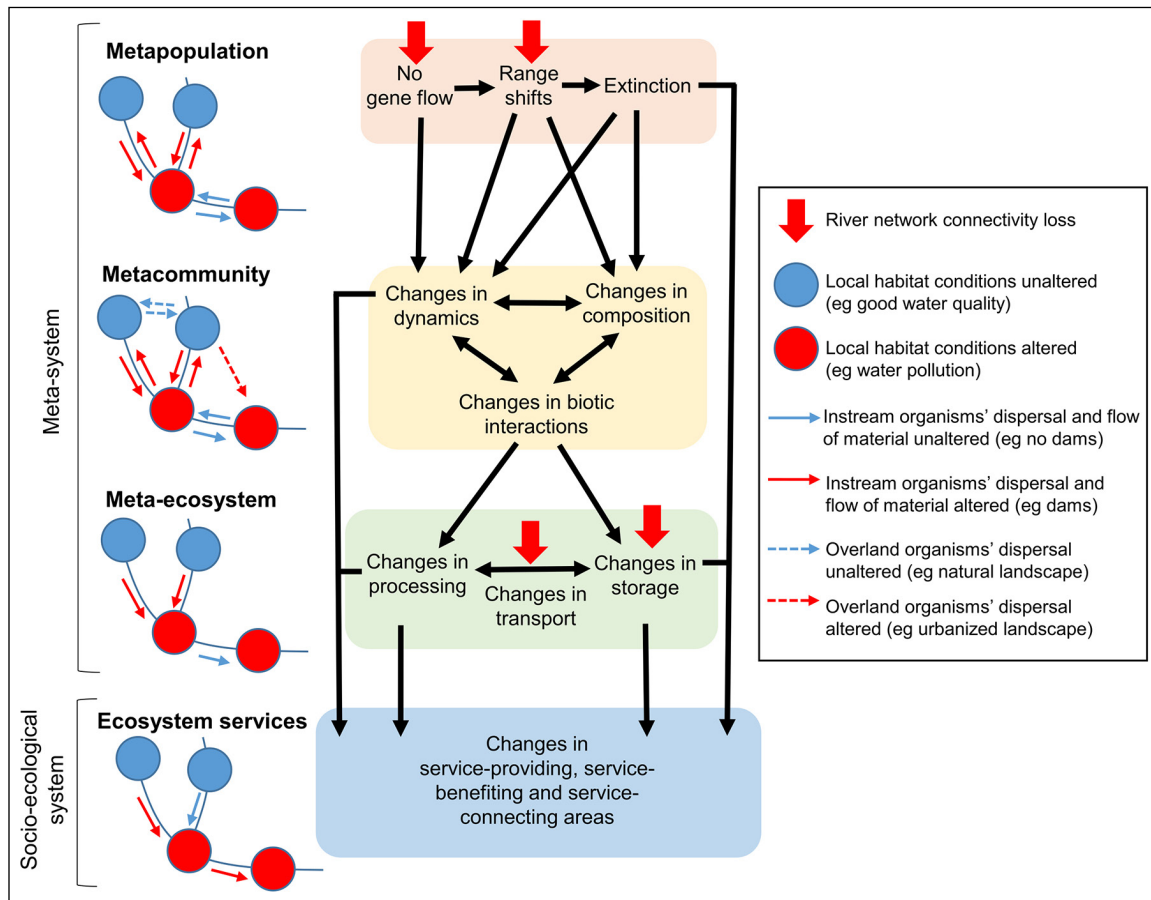


Figure 2. Conceptual diagram of the cascading effects of the alteration of river network connectivity across different levels of the meta-system (ie metapopulation, metacommunity, and meta-ecosystem) and the socioecological system (ie ecosystem services). Note that for ecosystem services, blue and red arrows represent the flow between service-providing and service-benefiting areas (Panel 1).

require careful management to maintain isolation-driven evolutionary processes at the landscape scale (Rahel and McLaughlin 2018). Information about population sizes, dispersal abilities, and physical distance among populations is necessary to distinguish among different metapopulation structures in landscapes, which require varying management strategies and priorities (Fullerton *et al.* 2016).

Regional-scale thinking is also critical for understanding the spread of invasive species (Strecker and Brittain 2017). In river networks, however, their management is still poorly developed and can be controversial (Chen and Olden 2017). For example, artificial barriers alter natural metapopulation dynamics but also can limit the spread of invasive fish (Rahel and McLaughlin 2018). In contrast, altering naturally intermittent flow regimes of river networks by artificially producing perennial flows can promote new invasions of alien species (Ruhí *et al.* 2019). Identifying the respective role of local and regional processes in the dynamics of invasive species relative to native ones is fundamental if undesired conservation and management effects are to be avoided (Rahel and McLaughlin 2018).

Considering metapopulation structure can improve predictions of species range shifts in response to climate change, as dispersal ability can determine whether species will be able to shift to

new suitable regions and habitats (Markovic *et al.* 2014). However, most assessments based on species distribution modeling only consider the potential effects of climate change on local conditions (ie niche-based modeling). If the primary goal is to develop more resilient large-scale conservation strategies, then evaluation of species' vulnerability and extinction risk must incorporate dispersal-related processes, as well as the effects of projected river network fragmentation on biota (Markovic *et al.* 2017).

At the community level, information on metacommunity structure can be useful for guiding effective restoration and biomonitoring practices. Currently, most restoration projects may fail to achieve biodiversity and/or ecological quality targets because they are typically limited to the local scale (Tonkin *et al.* 2014). For example, a reduced regional pool of colonizers could hamper achieving expected restoration targets in highly degraded catchments, where unimpacted sites (ie natural recolonization sources) are isolated due to fragmentation (Tonkin *et al.* 2014; Swan and Brown 2017). Similarly, biomonitoring methods to evaluate river health or ecological status may fail to detect anthropogenic impacts, mainly as a result of dispersal limitation (Heino 2013). Most biomonitoring methods assume that local communities respond to local environmental conditions identically, and that all species can eventually

reach all sites (Cid *et al.* 2020). However, fragmentation can prevent species from reaching their optimal habitats, and isolated sites may present lower richness and bioassessment scores despite the presence of high-quality habitat (Heino 2013). In naturally intermittent river networks, although drying can generate habitat heterogeneity in terms of wet and dry habitats and thereby promote species richness, it can also increase fragmentation and prevent some species from colonizing a site, reducing local species richness (Datry *et al.* 2014). Applying the basic tenets of metacommunity ecology in bio-monitoring and restoration practices can be helpful for determining the relative influence of local and regional processes on local community composition (Cid *et al.* 2020).

Metacommunity ecology uses a range of scale-sensitive biodiversity measures that are typically omitted from local biodiversity assessments based on alpha diversity (Panel 1). For example, beta diversity (Panel 1) and its components can be useful for identifying and preserving sites that contribute the most to maintaining regional diversity (Panel 1; Ruhí *et al.* 2017). Expanding the metrics used in routine assessments can provide essential data for evaluating metacommunity structure and function, and improve their conservation (Simons *et al.* 2019).

Species in a metacommunity interact at local and regional scales (Hagen *et al.* 2012), and biotic interactions can be altered by changes in hydrologic connectivity across a river network. For instance, fragmentation by dams can isolate freshwater mussel metapopulations from their host fish, on which they depend for completing their life cycles and dispersing across the network (Ferreira-Rodríguez *et al.* 2019), whereas fragmentation by drying can simplify food webs after the loss of top predators, having direct effects on ecosystem processes (Hagen *et al.* 2012). Identifying key biotic interactions across the meta-system will help attain biodiversity targets closely linked with ecosystem functioning (Hagen *et al.* 2012).

By modifying the flow of water, sediments, and organisms, fragmentation affects the fluxes of matter (minerals, carbon, nutrients) across river networks. For instance, current dam removal efforts benefit sediment transportation, counteract coastal erosion, and restore upstream movement of migratory fish, allowing transport of marine nutrients to isolated headwaters (Bellmore *et al.* 2019). Fragmentation can also lead to sub-optimal ecosystem processes both locally and regionally if resources accumulate but organisms processing those are lacking, and vice-versa (Gounand *et al.* 2018). This might occur when natural drying of stream channels in intermittent rivers stops the transport of organic matter from upstream and subsequently limits ecosystem functioning downstream (Datry *et al.* 2018). Identifying when and where various kinds of matter (and energy) are processed and transported is essential for maintaining ecosystem functioning and services (Datry *et al.* 2017).

■ Policy implications and management opportunities

Biodiversity and environmental conservation are governed through several interlinked goals and agreements at the

international and national levels. Global objectives, such as those stated in the Convention on Biological Diversity's Aichi Biodiversity Targets and the UN Sustainable Development Goals aiming for a more sustainable world, are reflected in international and national strategies and policies (Figure 3; Table 1). These policies are articulated and enforced through guidance documents, which include common implementation methodologies describing how to obtain indicator metrics for tracking progress toward environmental and conservation targets (Table 1). Below, we present several options for integrating regional-scale processes into the current local-scale management of river networks, focusing on biodiversity conservation, bio-monitoring, and restoration. We also propose a series of alternative metrics and indicators (Table 1) that could complement such methodologies and sharpen strategies to guide efforts in reversing current trends of freshwater biodiversity loss and ecosystem degradation due to river fragmentation.

Biodiversity conservation

To determine the conservation status of species, conservation policies (such as the EU Habitats Directive or the US Endangered Species Act) rely in part on information obtained from population estimates, most of which only account for species population size and habitat quality (Table 1). Under a meta-system approach, methods and indicators capable of assessing metapopulation structure should be incorporated. This includes molecular tools and techniques for obtaining genetic diversity metrics to infer connectivity within a delimited spatial area (eg catchment or subcatchment) and/or direct measures of dispersal (Table 1) using mark-recapture or genetic methods (Fullerton *et al.* 2016). However, because empirical data on metapopulations are not always available to managers, monitoring efforts and sharing data should be encouraged. Such information could be integrated into individual-based models and thereby contribute to the identification of critical thresholds (Dudley 2018).

Responses for mitigating the effects of altered river network connectivity on biodiversity can be varied (Fuller *et al.* 2015). In general, when freshwater metapopulations experience a lack of gene flow, conservation actions should promote connectivity, for example through the removal of artificial barriers, installation of fish passages, or implementation of environmental flows (Poff *et al.* 2010). Despite efforts to shift environmental flow management from local to regional scales (eg Stewardson and Guarino 2018), most dam management practices remain focused on restoring flow regimes to river segments immediately downstream. Coordinated dam management across the river network would instead provide opportunities to increase connectivity and maintain meta-system dynamics (McCluney *et al.* 2014; Chen and Olden 2017). In a meta-system context, environmental flow management should target the conservation and restoration of variation in regional ecological features (eg through use of the metrics listed in Table 1). If increasing connectivity is not feasible via restoration, or if populations are too isolated to

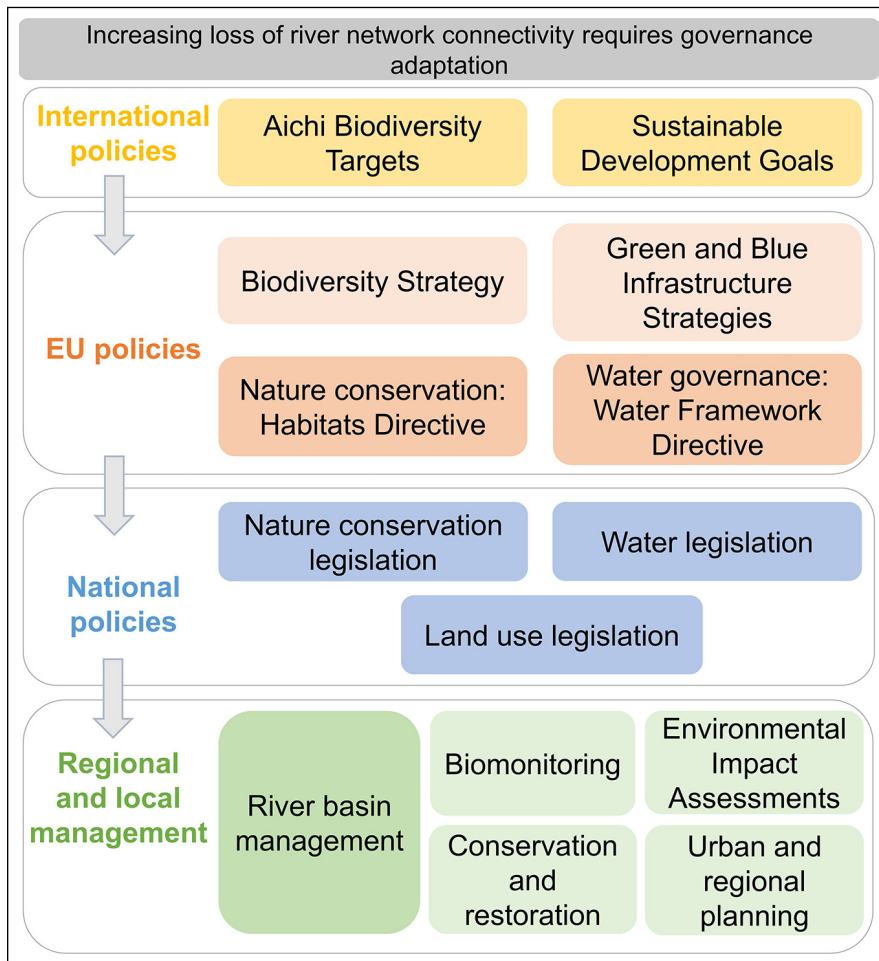


Figure 3. The current loss of river network connectivity worldwide will be exacerbated by climate change and affect the associated socioecological system. Legislation and regulations at all levels should adapt to these changes, including international agreements and related regional policies (here, examples from Europe), which form the basis of national-level regulations for water, nature conservation, and spatial planning.

allow dispersal of individuals after improving connectivity, conservation measures could be directed toward local habitat protection and assisted colonization (Lawler and Olden 2011).

Although vital to current conservation policies, protected areas rarely capture the complex spatial structure of river networks, rendering conservation of riverine biodiversity challenging (Carrizo *et al.* 2017; Acreman *et al.* 2020). Under a meta-system approach, protected areas within a catchment should be designed to ensure conservation of key sites across the network that promote metapopulation and metacommunity persistence. This could be achieved using prioritization methods in conservation planning that include the analysis of connectivity and spatial congruence of multiple species (Albert *et al.* 2017). For example, in river networks experiencing fragmentation through drying, selection of pivotal refugia that act as sources for dispersal is essential for ensuring protection of network-wide biodiversity (Hermoso *et al.* 2013). Sites to be protected and/or restored across the network can be selected using information on the genetic diversity of a population and on the beta diversity components

of a community (Table 1; Ruhí *et al.* 2017; Paz-Viñas *et al.* 2018).

Biomonitoring and restoration

Most legislation protecting surface waters relies on local reach-scale evaluations of ecological status (Heino 2013). In the EU and the US, for instance, despite the management units of the EU Water Framework Directive and the US Clean Water Act defined as the river basin, these policies prescribe evaluation of different river reaches individually, based on the structural and/or functional properties of ecological assemblages; neither policy, however, explicitly encourages biological assessments at multiple spatial scales.

River biomonitoring methods typically compare the biotic community of a focal site with a reference value obtained from non-impacted or least-impacted sites (Cid *et al.* 2020). Based on the local environmental conditions observed at those latter sites, the expected biotic community at the focal site (that is, the community that would have most likely existed at that location, in the absence of impacts) can then be predicted (Heino 2013; Cid *et al.* 2020). To consider regional processes in metacommunity dynamics, water managers could integrate proxies for dispersal based on spatial connectivity (eg fragmentation caused by dams, drying, or topographical barriers) and dispersal-related species traits into biomonitoring methods (Cid *et al.* 2020).

Improved consideration of the current and predicted levels of fragmentation may require the redesign of monitoring sites within a river network. For instance, whereas large dams are usually considered when selecting monitoring sites, fragmentation due to small barriers and potential drying events has often been overlooked (Erős *et al.* 2018). Assessing fragmentation within a river network and its potential interactive or additive effects with other stressors will improve predictions of ecological integrity using bioindicators.

Under a meta-system approach, restoration practices should include information on the regional species pool and the ability of species to locate restored habitats. Key sites acting as sources of colonizers should be identified, and their connectivity with restored river reaches should be evaluated (Heino *et al.* 2017). This is especially relevant when fragmentation is due to drying, as source sites within the regional species pool are typically located in dry season refugia (Datry *et al.* 2014). To assess whether improvements in local diversity have positive effects on regional biodiversity, managers could incorporate indices such as taxonomic and functional beta, zeta, and gamma diversity (Panel 1; Table 1; Simons *et al.* 2019).

Table 1. Current metrics and indicators used in core environmental and biodiversity policies, and additional ones that could be implemented in a meta-system approach

Management action and organizational level of application	Policy examples	Current metrics/indicators	Additional metrics/indicators
Conservation/restoration, (meta)population	European Biodiversity Strategy and Habitats Directive; US Endangered Species Act; Australia Environment Protection and Biodiversity Conservation Act	Species range* (km); species occupancy area* (km ²); species population size* (grid, individuals); species age structure; species habitat area and quality	Genetic diversity; gene flow; inbreeding; hybridization; species effective dispersal; number and location of metapopulation key habitats (eg refugia, dispersal routes); area and quality of metapopulation key habitats; connectivity between key habitats (eg dendritic connectivity index)
Biomonitoring/restoration, (meta)community	European Water Framework Directive; US Clean Water Act; Australia Water Act	Local (alpha) taxonomic richness and diversity of different taxonomic groups (ie macroinvertebrates, fish, diatoms, macrophytes, riparian plants)**; species environmental tolerance**; number and richness of alien species**; riparian vegetation cover**; riverbed and riverbank morphology**	Gamma species diversity; beta and zeta species diversity; species dispersal capability (eg using organisms' traits as a proxy for dispersal); species effective dispersal; metacommunity key habitats area and quality (ie refugia, dispersal routes); connectivity between key habitats (eg dendritic connectivity index)
Ecosystem-based management/restoration, (meta)ecosystem and ecosystem services	European Biodiversity Strategy***	Nutrient load and retention; sediment transport and retention; carbon storage, processing, and transport; fish production (catch by fishermen); wood produced by riparian forest; number and quality of swimming areas; fishing reserves; most of the indicators listed above fall within other categories (eg riparian vegetation cover)	Leaf litter decomposition; ecosystem metabolism; food-web structure; riparian stocks (eg using remote sensing); number and location of hotspots of functioning (eg organic matter and nutrient processing); number and location of service-providing, service-connecting, and service-benefiting areas

Notes: *these metrics are reported at the national level, and usually for protected areas; conservation status is assessed using reference values. **These measurements form the basis of the development of biological and hydromorphological quality metrics under the major water policies (eg the EU Water Framework Directive); they are developed at the national level. ***One primary target is the mapping and assessment of ecosystem services, which uses indicators from several sources.

Toward a more holistic ecosystem-based management in rivers

At the ecosystem level, there is a growing need for spatially explicit examinations of biogeochemical, hydromorphological, and ecological patterns and processes (Gounand *et al.* 2018; McCluney *et al.* 2014). Several prioritization tools are currently available for integrating spatial dynamics into conservation planning (eg Hermoso *et al.* 2013, 2018), and most policies and related guidance documents promote adaptive management that incorporates cross-ecosystem processes and scale-dependency. However, implementation of these tools and principles remains rare (Acreman *et al.* 2020). Effectively integrating state-of-the-art ecological theory into environmental management will require research and capacity building. Monitoring programs should include measures of ecosystem processes across the river network, such as decomposition of leaf litter and ecosystem metabolism (Young *et al.* 2008) or measures of food web structure (Otto *et al.* 2018), which could help to identify functional hotspots (McClain *et al.* 2003). These measures could be systematically integrated into conservation planning. As different biodiversity facets, ecosystem processes, and ecosystem services may vary in their degree of spatial congruence across the river network, prioritization methods that integrate these variables simultaneously could be used to maximize their protection in a holistic way (Hermoso *et al.* 2018; Erős and Bányai 2020).

Conclusions

Meta-system theory represents a powerful framework for understanding the dynamics of populations, communities,

and ecosystems, and for guiding conservation, biomonitoring, and restoration of increasingly fragmented river networks. Yet potential applications of this approach are only beginning to emerge, and many methodological and empirical developments are urgently needed to integrate this framework into environmental policies. Guidance based on meta-system theory could improve the quality of legislation and understanding of causes and effects across spatial scales, and constitute a major step toward sustainable, adaptive management of rivers in the Anthropocene. The relevance of this framework will be even greater in the future, as climate change and escalating human demand for water exacerbate the frequency and magnitude of extreme events, such as floods and droughts, thereby rapidly altering river connectivity and producing unprecedented river network fragmentation.

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⁹Institut de Recerca de la Biodiversitat, Universitat de Barcelona, Barcelona, Spain; ¹⁰Norwegian Institute for Water Research, Oslo, Norway; ¹¹Finnish Environment Institute, Environmental Policy Centre, Helsinki, Finland

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