A metasystem approach to designing environmental flows

Mathis L. Messager [iD], Julian D. Olden [iD], Jonathan D. Tonkin [iD], Rachel Stubbington [iD], Jane S. Rogosch [iD], Michelle H. Busch [iD], Chelsea J. Little [iD], Annika W. Walters [iD], Carla L. Atkinson [iD], Margaret Shanafield, Songyan Yu [iD], Kate S. Boersma [iD], David A. Lytle, Richard H. Walker [iD], Ryan M. Burrows [iD] and Thibault Datry [iD]

Mathis L. Messager (mathis.messager@mail.mcgill.ca) is a PhD candidate and Thibault Datry is a freshwater ecologist at the National Research Institute for Agriculture, Food and Environment (INRAE), UR RiverLy, in the Lyon-Grenoble Auvergne-Rhône-Alpes Centre, in Villeurbanne, in France. Mathis L. Messager is also affiliated with the Department of Geography at McGill University, in Montreal, Quebec, in Canada. Julian D. Olden is a professor in the School of Aquatic and Fishery Sciences at the University of Washington, in Seattle, Washington, in the United States. Jonathan D. Tonkin is an associate professor and Rutherford Discovery Fellow in the School of Biological Sciences at the University of Canterbury, with the Te Pūnaha Matatini Centre of Research Excellence in Complex Systems; and with the Bioprotection Aotearoa Centre of Research Excellence, all in Christchurch, New Zealand. Rachel Stubbington is a professor in the School of Science and Technology at Nottingham Trent University, in Nottingham, England, in the United Kingdom. Jane S. Rogosch is an assistant unit leader at the US Geological Survey's Texas Cooperative Fish and Wildlife Research Unit and an assistant professor in the Department of Natural Resources Management at Texas Tech University, in Lubbock, Texas, in the United States. Michelle H. Busch was a graduate student in the Department of Biology at the University of Oklahoma, in Norman, Oklahoma, and is currently a postdoctoral researcher at the University of Kansas Biological Survey in Lawrence, Oklahoma, both in the United States. Chelsea J. Little is an assistant professor in the School of Environmental Science at Simon Fraser University, in Burnaby, British Columbia, Canada. Annika W. Walters is an assistant unit leader at the US Geological Survey's Wyoming Cooperative Fish and Wildlife Research Unit and an associate professor in the Department of Zoology and Physiology and with the Program in Ecology at the University of Wyoming, in Larame, Wyoming, in the United States. Carla L. Atkinson is an associate professor in the Department of Biological Sciences at the University of Alabama, in Tuscaloosa, Alabama, in the United States. Margaret Shanafield is a senior research fellow in the College of Science and Engineering at Flinders University and a scientific officer at the Environmental Defenders Office, in Adelaide, South Australia, in Australia. Songyan Yu is a research fellow in the Australian Rivers Institute and the School of Environment and Science at Griffith University, in Nathan, Queensland, Australia. Kate S. Boersma is an associate professor in the Department of Biology at the University of San Diego, in San Diego, California, in the United States. David A. Lytle is a professor in the Department of Integrative Biology at Oregon State University, in Corvallis, Oregon, in the United States. Richard H. Walker is an assistant professor in the Department of *Science and Mathematics* at Upper Iowa University, in Fayette, Iowa, in the United States. Ryan M. Burrows is a research fellow in the School of Agricultural, Food and Ecosystem Sciences at The University of Melbourne, Burnley Campus, in Richmond, Victoria, in Australia.

Abstract

Accelerating the design and implementation of environmental flows (e-flows) is essential to curb the rapid, ongoing loss of freshwater biodiversity and the benefits it provides to people. However, the effectiveness of e-flow programs may be limited by a singular focus on ensuring adequate flow conditions at local sites, which overlooks the role of other ecological processes. Recent advances in metasystem ecology have shown that biodiversity patterns and ecosystem functions across river networks result from the interplay of local (environmental filtering and biotic interactions) and regional (dispersal) ecological processes. No guidelines currently exist to account for these processes in designing e-flows. We address this gap by providing a step-by-step operational framework that outlines how e-flows can be designed to conserve or restore metasystem dynamics. Our recommendations are relevant to diverse regulatory contexts and can improve e-flow outcomes even in basins with limited in situ data.

Keywords: flow management, environmental water, freshwater conservation, dispersal, Murray–Darling Basin

Rivers and streams contribute significantly to global biodiversity, biogeochemical cycles, and human well-being and are concurrently among the most threatened ecosystems on Earth (Tickner et al. 2020). To curb the decline of freshwater biodiversity and the loss of benefits to people, environmental flows (e-flows) have emerged globally as a central water resource management tool (Arthington et al. 2018). E-flows are broadly defined as "the quantity, timing, and quality of freshwater flows and levels necessary to sustain aquatic ecosystems which, in turn, support human cultures, economies, sustainable livelihoods, and well-being" (Arthington et al. 2018). Accelerating the design and implementation of e-flows is recognized as a management and policy priority to ensure ecologically sustainable water management both now and into the future (Arthington et al. 2018, Tickner et al. 2020).

E-flow assessments have historically relied on ensuring minimum instream flows for individual rivers below dams, but recent decades have witnessed a shift to e-flow standards encompassing multiple aspects of the flow regime and developed at the regional scale rather than on a river-by-river basis (Poff et al. 2017). Nonetheless, regional e-flow planning remains focused on species' responses to the local flow regime, overlooking mounting evidence that biodiversity and ecosystem functioning in river networks result from the interaction between ecological processes at local to regional scales (Gounand et al. 2018, Poff 2018, Cid et al. 2020, 2022). Standard e-flow prescriptions may therefore be less effective, for example, when the population and community dynamics within a river are strongly driven by regional processes such as species dispersal. Local communities may not recover following e-flow implementation if dispersal limitation due to river fragmentation limits recolonization from source populations elsewhere in the river network (Brooks et al. 2011, Chester et al. 2014). In such cases, adopting a metasystem perspective

Box 1. Basics of metasystem theory.

The *metasystem* concept posits that landscape-scale variability in biodiversity and ecosystem functioning results from the interaction of regional- and local-scale processes (Gounand et al. 2018, Cid et al. 2022). The regional structure of the physical landscape regulates flows of materials, energy, and organisms among the subcomponents (e.g., sites, habitat patches) of a metasystem. Each subcomponent is in turn characterized by local dynamics driven by abiotic conditions and biotic interactions. Local-scale ecological processes (e.g., within a river reach) are influenced by ecological processes operating at the regional scale (e.g., across multiple reaches in a river network or multiple basins) and vice versa, such that both scales require concurrent consideration to understand metasystems. Metasystem dynamics exist across levels of biological organization from populations to ecosystems. A *metapopulation* consists of multiple populations of a single species connected by dispersal (Hanski 1998). Such spatially structured populations may form *metacommunities*, whereby a set of local communities are connected by the dispersal of multiple potentially interacting species (Leibold et al. 2004). Finally, energy and materials, such as inorganic and organic matter or nutrients, also move through *metaecosystems* in which patches exhibit heterogeneous ecosystem functions (Gounand et al. 2018).

From a metacommunity perspective, the distribution and abundance of species across the landscape are driven by three mechanisms: trait-by-environment matching, dispersal, and stochastic ecological drift (Leibold and Chase 2017). These processes are in turn influenced by three factors: habitat heterogeneity, connectivity, and scale (Leibold and Chase 2017).

Trait-by-environment matching operates when organisms differ in their fitness (e.g., growth rate) across gradients of abiotic and biotic conditions (Leibold and Chase 2017). This is related to the concept of a species' niche, incorporating both *environmental filtering* (whereby the abiotic environment prevents the establishment or persistence of certain species) and the effects of *biotic interactions* such as competition and predation. *Dispersal* refers to the movement of individuals from one site (emigration) to another (immigration), which connects populations and communities (Leibold et al. 2004). *Ecological drift* describes the stochastic dynamics of events such as births, deaths, immigration and emigration that lead to random changes in population sizes and, therefore, species' relative abundances (Vellend 2010). All three processes structure metacommunities simultaneously. Their interactions and relative strength shape the diversity of species in space and time.

Variability within and among metacommunities is influenced by habitat heterogeneity and species identity. The relative strength of trait-by-environment matching, dispersal, and ecological drift in driving the abundance and distribution of species varies across patches, through time and among species (Leibold et al. 2022). System *connectivity* alters dispersal and ecological drift; low connectivity can have similar effects to poor dispersal ability, limiting community diversity and ecosystem functioning (Leibold and Chase 2017). Finally, the relative importance of metasystem processes and drivers varies across temporal and spatial *scales*. For example, spatial scale influences the environmental gradients organisms experience and the patchiness of the environment, whereas the connectivity of a metasystem, the dispersal ability of organisms, and ecological drift vary across both spatial and temporal scales (Leibold and Chase 2017).
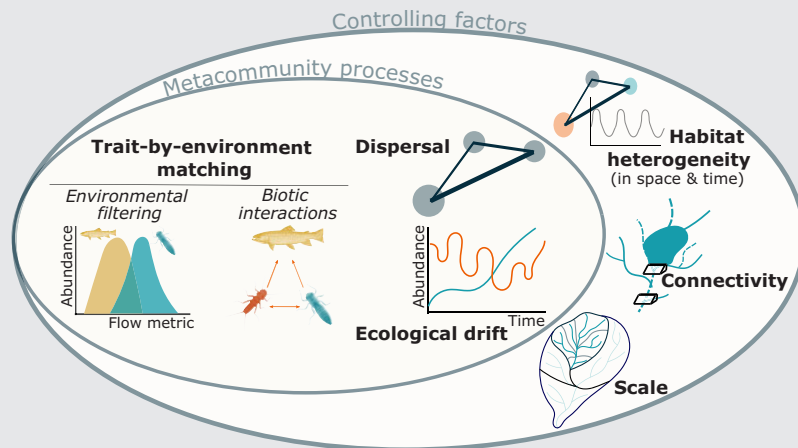
Figure 1. Processes and factors driving the distribution and abundance of species in metacommunities (on the basis of Leibold and Chase 2017). Rates of dispersal (arrow thickness) vary among habitat patches (circle size represents species or community abundance). Metacommunity processes are modulated by heterogeneity in space and time (the circle colors represent habitat heterogeneity among sites linked by dispersal); connectivity among sites, driven by habitat (e.g., continuous and dashed lines represent perennial and nonperennial river segments, respectively) and instream barriers (e.g., dams, represented by triangular prisms, creating reservoirs); and scale.

(see box 1 for background) that considers links between river flows and diverse ecological processes across local and regional scales could enhance the success of e-flow practices.

The potential for the metasystem perspective to strengthen the management, conservation, and restoration of river networks is increasingly recognized (Chase et al. 2020, Cid et al. 2020, 2022, Patrick et al. 2021), and greater integration of advances in ecology, including metacommunity ecology, into e-flow science has been widely called for (Auerbach and Poff 2011, Poff 2018). However, a framework to guide e-flow design from a metasystem perspective

and bridge the current gap between theory and practice remains elusive. In this article, we discuss how metasystem concepts and tools can be incorporated into the science and implementation of e-flows. We first demonstrate how riverine metasystem processes mediate ecological responses to flow alteration. We then provide an operational framework for designing e-flows to conserve or restore metasystem dynamics. Recognizing that the effectiveness of e-flow programs can be limited by unexamined ecological processes, our aim is to provide a conceptual basis and empirical examples, and to discuss available tools with which researchers and managers can broaden the set of ecological processes integrated into the design, implementation, and monitoring of e-flow programs and, therefore, enhance the likelihood of positive outcomes.

We focus predominantly on the metapopulation and metacommunity scales for the next generation of e-flow design (see box 1 for definitions) but stress the need for future developments in e-flow science to assess and protect metaecosystem dynamics (Gounand et al. 2018) in river networks. In addition, we focus strictly on the ecological benefits of e-flows but recognize the importance of integrating sociocultural objectives into these efforts (Anderson et al. 2019). Throughout, we illustrate the relevance of adopting a metasystem perspective for e-flow programs using examples from freshwater conservation and restoration programs, with a particular focus on the basin-wide e-flow program of the Murray–Darling Basin (MDB; box 2).

Metasystem processes mediate ecological responses to flow alteration and influence environmental flow outcomes

E-flow design currently relies on the premise that local habitat conditions, governed primarily by the flow regime, define the distribution and abundance of species through environmental filtering. Environmental filtering (see box 1, figure 1) implies that resident species that are adapted to a local flow regime become less abundant and less likely to persist at a site as flows increasingly differ from the original flow regime (Poff et al. 1997). To evaluate environmental filtering, e-flow assessments often rely on flow–ecology relationships which relate ecological responses (e.g., abundance of a species, taxonomic richness, recruitment) across sites or through time to various facets of the flow regime (e.g., figure 2; Poff et al. 2010, Freeman et al. 2022). However, metasystem dynamics other than environmental filtering, such as biotic interactions (as part of trait-by-environment matching; see box 1), dispersal, and ecological drift can cause ecological responses to altered flow regimes to deviate from those expected in isolated populations or communities. The influence of habitat heterogeneity, scale, and connectivity on these metasystem processes can also strongly mediate the observed response of species to flow alteration (box 1). Flow–ecology relationships and the resulting e-flow prescriptions are always uncertain because of the inherent complexity and stochasticity of ecosystems, but deviations resulting from overlooked metasystem processes and influencing factors can further blur or bias standard assessments and compromise the effectiveness of subsequent flow management.

Few programs monitor the outcomes of e-flow implementation and even fewer investigate the processes behind these outcomes (Souchon et al. 2008). In addition, e-flow recommendations and post-implementation evaluations are rarely published in accessible databases (Tonkin et al. 2014a). However, a few cases are documented in which metasystem factors, such as limited dispersal strength and connectivity (Reinfelds et al. 2010, Brooks et al. 2011, Chester et al. 2014, Growns 2016), may have limited the effectiveness of e-flow implementations. For example, Reinfelds and colleagues (2010) found that historical e-flow releases provided insufficient water depths for riffle passage by Australian bass (*Macquaria novemaculeata*), a migratory fish, but that small increases in flow releases could increase water depths and effectively promote connectivity. By contrast, targeted e-flows have enabled fish movement in the MDB (Beesley et al. 2014, Koster et al. 2017). Spring–summer freshes resulting from e-flow releases, for example, supported spawning-related movements by golden perch (*Macquaria ambigua*; Koster et al. 2017). Several instances also exist in which biotic interactions altered species' responses to flow alteration (Stefferud et al. 2011, Gido and Propst 2012) or to e-flow implementation (Marks et al. 2010) or where e-flow implementations have proved more beneficial to nonnative than to native species (Conallin et al. 2012). In Fossil Creek (Arizona, United States), native fish abundance did not respond to e-flows where nonnative fish were present, whereas a 50-fold increase in abundance was observed where e-flows were combined with nonnative fish removal (Marks et al. 2010). Leveraging multi-objective optimization models to design dam operation releases in the San Juan River (United States), Chen and Olden (2017) concluded that novel e-flow regimes could more efficiently benefit native species while controlling nonnative species when compared with e-flows designed to resemble historical flow conditions.

Below, we summarize how metacommunity processes, modulated by habitat heterogeneity, connectivity, and scale, may influence e-flow outcomes, and we propose a set of solutions (table 1) that we embed in an operational framework in the following section. We focus on flow–ecology relationships, but these considerations apply equally to hydraulic-habitat models, which also emphasize local conditions (Lamouroux et al. 2017).

Trait-by-environment matching: Biotic interactions

E-flow designs seldom explicitly account for biotic interactions, but competitive, trophic, and host–commensal interactions can modulate species' responses to flow alteration at local and regional scales (figure 4; Dewson et al. 2007, Bogan and Lytle 2011). Flow alterations can directly or indirectly shift the outcomes of competitive interactions, altering species' abundance and distribution. For example, the local extinction of competitors following a shift from a perennial to an intermittent flow regime was the likely cause of an 11-fold increase in the abundance of two diving beetles in a desert stream (Bogan and Lytle 2011).

The widespread occurrence of nonnative species in freshwater systems can also interact with flow alterations and fundamentally change the abundance and spatial distribution of native species (Ruhí et al. 2019), confounding flow–ecology relationships. In some cases, flow alteration can facilitate the invasion and dominance of nonnative species, which can be mitigated by e-flows. For example, nonnative riparian *Tamarix* sp. shrubs have become most dominant over native *Populus deltoides* in flow-regulated river reaches of the southwestern United States (Merritt and Poff 2010), but targeted e-flows could help to reverse this trend (Lytle et al. 2017). Equally, e-flow implementations that disregard the flow preferences of nonnative species may have a net negative effect on the ecological targets of conservation actions. For example, e-flows designed to reduce the incidence of low-flow periods in southern Victorian streams (Australia) benefitted nonnative trout at the expense of the native fish roundhead galaxias (*Galaxias*

Box 2. Existing e-flow program with a metasystem approach in the Murray–Darling Basin.

The Murray–Darling Basin (MDB) drains 1 million km^2 of southeastern Australia (figure 3), supports 40% of Australian agriculture production and is home to more than 40 First Nations. The basin supports 50 native fish and 120 waterbird species (Murray–Darling Basin Authority 2020a). Rivers across the basin are degraded by many anthropogenic stressors, including widespread overallocation of water entitlements for irrigation. The Millennium Drought (1996–2011) was a turning point in Australian river management, prompting the drafting of the Water Act (2007), which, in turn, established the Murray Darling Basin Authority (MDBA). Since 2012, the MDBA has overseen the implementation of a plan for basin-wide coordination of water resource management (Australian Government 2021). The Basin Plan establishes water diversion limits and e-flows objectives for each of the MDB's subcatchments and groundwater basins, depending on storage levels and weather conditions. Achieving the diversion limits entails the recovery of approximately 15% of average total annual water withdrawals prior to the Plan. From 2014 to 2020, a total of 9510 × 10^9 cubic meters of e-flows were delivered in the basin through 666 actions (Barbour et al. 2021b, figure 3).

The MDB e-flows program (MDBA 2020b, Barbour et al. 2021a, Commonwealth Environmental Water Office 2022) broadly aligns with the metasystem approach and framework we present herein. First, the MDB Plan takes a basin-scale perspective. It relates local outcomes of e-flow events to large-scale objectives and accounts for the interactions of various metacommunity processes and influencing factors at local and regional scales (box 1). Second, the program covers multiple main ecological targets with varying flow requirements: flow and connectivity, native fish, vegetation, and waterbirds (figure 3). Third, the program was founded on an adaptive management approach with a strong e-flow Monitoring, Evaluation and Research Program (Flow-MER; Barbour et al. 2021a), which collects spatially explicit data on hydrology, ecology and river–floodplain structure at sites across the basin, including information on longitudinal and lateral connectivity and the dispersal of species. Finally, a variety of e-flow management levers are spatially coordinated depending on the degree of regulation of rivers and management objectives.

Nonetheless, the coordination of e-flow allocations and monitoring across the basin may benefit from greater integration of concepts and tools from the field of metacommunity ecology described in our framework. For example, although efforts exist to understand the metapopulation dynamics of native fish and waterbirds, and multiple population and flow–ecology models have been developed for the fish species of the MDB, spatially explicit models that account for the role of dispersal and biotic interactions in structuring metapopulations and metacommunities are still largely missing (but see Stoffels et al. 2015 for an example). These models could inform the prioritization of water allocations for recruitment in keystone sites while promoting connections that allow fish to move among populations (see framework section). In addition, the expected outcomes of the program are mostly species and area specific and do not yet incorporate basin-wide indices of biodiversity. Several of these limitations are slated to be addressed through the Flow-MER program. The most recent evaluation and research plan outlines several projects that aim, for example, to develop a multiscale approach to evaluate biodiversity, to further evaluate flow triggers for local and regional scale fish movement, and to develop integrative models of interactions among species, basin-scale and multispecies responses (Barbour et al. 2021a).

---

anomalus, Leprieur et al. 2006). Finally, when flow alterations cause aquatic habitats to shrink, biotic interactions tend to intensify, especially if partial streambed drying occurs. During drying, organisms become confined to pools, amplifying predation and competition for declining food resources (Magoulick and Kobza 2003).

Dispersal

The relative strength of dispersal and local processes of environmental filtering and biotic interactions influences the predictive power of flow–ecology relationships. Both dispersal surplus and dispersal deficit can decrease the precision of standard flow–ecology relationships established through correlative studies (figure 4). If dispersal among sites is high, source–sink or mass effects may override local-scale processes (Leibold et al. 2004). In cases of mass effects, species may occupy sites in which they are inferior competitors or maladapted to local habitat conditions if they can continuously immigrate from nearby source sites where conditions are more favorable (Mouquet and Loreau 2003). If dispersal is limited, species may be unable to track their preferred abiotic conditions to access sites in which they would exhibit high fitness or be superior competitors (Leibold et al. 2004). Similar to situations of high dispersal, some species may persist in suboptimal sites, in this case because superior competitors are unable to colonize and outcompete them owing to dispersal limitation. For instance, an analysis of the relationships between flow magnitude and fish species richness for large-river specialists in the tributaries of the Missouri and Mississippi rivers showed that flow magnitude alone underrepresented richness in lower-flow sites accessible to dispersers and overrepresented richness in isolated sites (Dunn and Paukert 2021). Low dispersal is often thought to limit the success of local efforts to restore physical habitat (Stoll et al. 2013, Tonkin et al. 2014b), water quality (McManamay et al. 2016), and e-flows (Brooks et al. 2011).

The greatest ability to predict ecological responses to flow may manifest in metacommunities with intermediate levels of dispersal and strong environmental filtering (i.e., species sorting; Leibold et al. 2004). In such networks, species can disperse across the landscape into habitats in which environmental conditions maximize their fitness but where the local communities are not swamped by colonists from the regional species pool. Beyond accounting for dispersal in flow–ecology relationships, the effectiveness of e-flow programs could be improved by considering dispersal in their overall design (see the framework in the next section).

Flow alteration can also affect dispersal. Changes in flow regimes can either increase or decrease dispersal rates, depending on species traits and instream physical barriers with flow-dependent passability (e.g., low-head dams, natural knickpoints). Increases in discharge can boost dispersal by promoting instream drift (Naman et al. 2016), inducing nonmigratory and upstream migratory movement by fish (Taylor and Cooke 2012), increasing the passability of instream barriers by drowning them out (Marshall et al. 2021), enhancing the connectivity among river reaches during low-flow periods (Rolls et al. 2012), or providing access
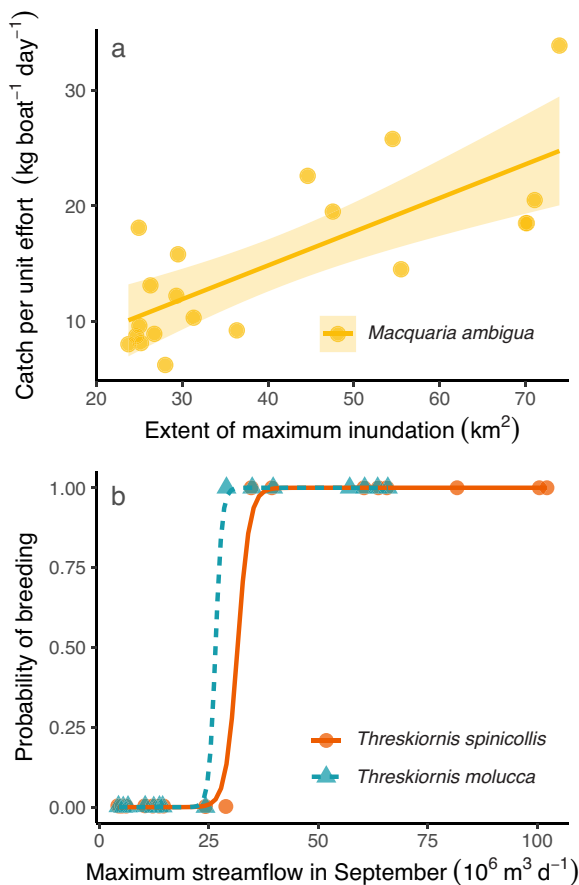
Figure 2. Standard examples of empirical flow–ecology relationships derived from monitoring data in the Murray–Darling Basin. Source: The data are from Colloff and colleagues (2018). (a) For the native fish golden perch (*Macquaria ambigua*), relationship between catch per unit effort and extent of maximum inundation in each year from 1984 to 2003, River Murray (South Australia), with line of best fit from linear regression ($R^2 = .571$, $p < .05$); (b) for waterbirds, attempted breeding by ibis (*Threskiornis* spp.) from 1978 to 2005, Lake Merreti (South Australia). The lines show logistic model fits predicting breeding success from maximum flow in the month of September.

to side channels and floodplain habitats if overbank flows occur (Stoffels et al. 2016). If increases in discharge are accompanied by high flow velocities, downstream hydraulic forces can reduce upstream dispersal or create velocity barriers, particularly in road culverts (Warren and Pardew 1998). Lower discharge generally decreases connectivity and, therefore dispersal, particularly when surface water is lost and the river network becomes fragmented, although flow decline may also trigger dispersal away from shrinking aquatic habitat (Rolls et al. 2012, Naman et al. 2016).

Beyond flow magnitude, the timing, duration, frequency, and rate of change in flow events also affect dispersal. Fish migration (Jonsson 1991), plant seed transport (Kehr et al. 2014), and insect emergence and adult dispersal (Lytle 2003) may be synchronized to coincide with (or avoid) flow events at specific times. An earlier onset of drying, for instance, may prevent access to refuges (Hwan and Carlson 2016), dispersal to spawning grounds (Scoppettone et al. 2015), and emergence of the terrestrial adults of insects with aquatic life stages (Drummond et al. 2015).

Ecological drift

Small and dispersal-limited populations and communities are often more susceptible to demographic stochasticity, genetic drift,

and inbreeding, potentially reducing the effectiveness of standard e-flow implementation to below what would be expected (Gido et al. 2016). In isolated communities composed of few individuals, ecological drift may override environmental filtering or alter the outcome of competitive interactions driving community composition (Ron et al. 2018, Siqueira et al. 2020). Flow–ecology relationships may therefore be particularly uncertain when ecological drift is dominant. In turn, flow alterations that isolate or shrink populations put them at a greater risk of stochastic decline and local extinction. Providing adequate local flow conditions may be insufficient to sustain small, isolated populations (e.g., in the MDB; Pavlova et al. 2017), such that a species may be driven to local extinction unless flow management increases its dispersal rates or is complemented with population augmentation (Ryman and Laikre 1991) or barrier removal. Alternatively, naturally isolated populations may have adapted to local habitat conditions, resulting in population viability despite small numbers and limited dispersal potential (Phillipsen and Lytle 2013). Even in such situations, particularly when selection pressures are strong and divergent across populations, the transferability of standard flow–ecology relationships and the effectiveness of the resulting e-flow management program may be limited by independent evolution among local populations.

Controlling factors: Scale and heterogeneity

The effects of scale and spatiotemporal variation in the relative strength of trait-by-environment matching, dispersal, and ecological drift are important to recognize in e-flow assessments. Flow–ecology relationships developed from data at small spatial scales and in metacommunities from networks in which habitat heterogeneity is low may be more uncertain than those developed with sites spanning a greater extent and flow gradient (figure 4; Colloff et al. 2018, Viana and Chase 2019). At large scales that span river basins with separate regional species pools, the transferability of relationships between species and environmental factors may also be limited by biogeographic barriers and recent speciation events (Heino et al. 2015). For example, whereas flow–ecology relationships developed for fish species exhibit as much transferability within as among river basins in the southwestern United States (Chen and Olden 2018), ecoregions are more effective than river classifications derived from hydrology alone for explaining the variation in fish traits across the United States (McManamay et al. 2015).

The mechanisms that shape riverine metacommunities vary over time (box 1, figure 1; Datry et al. 2016, Sarremejane et al. 2017a, Perkin et al. 2021), so e-flows designed from snapshot or seasonal ecological data may overlook important metacommunity dynamics. For example, snapshot studies may not capture the temporal synchronization of species and trait composition across sites by flow alterations such as hydropeaking, which increases the risk of population and community collapse (e.g., across the Colorado River Basin; Ruhí et al. 2018). Flow–ecology relationships are often derived from data collected during only one or two specific seasons rather than year-round—during summer or fall in temperate regions when rivers are more easily wadable (Harper et al. 2022, Morgan et al. 2022). Low-flow statistics are often strong predictors of taxonomic community composition and species' abundances during these periods of strong environmental filtering (Rolls et al. 2012, Arthington et al. 2014). However, the roles of other flow events that promote connectivity (e.g., with floodplains), flood disturbances, and community composition following recolonization in intermittent reaches are often over-

looked. Temporal variability particularly influences flow–ecology relationships in dynamic river systems, including those with extensive nonperennial river reaches (Ruhí et al. 2017, Sarremejane et al. 2017a). When a river stops flowing and dries, aquatic dispersal ceases, and the strength of environmental filtering and biotic interactions increases in remaining wet habitats. When flow resumes, dispersal and ecological drift then prevail until sufficient colonists have reached previously dry patches and environmental filtering regains dominance, provided intermediate dispersal (Datry et al. 2016, Sarremejane et al. 2017a). Sampling perennial sites in river networks with nonperennial river reaches during low-flow conditions may even yield counterintuitive results. In prairie streams, for example, the abundance of stream fish was lower during wet years compared with dry years in the same river reaches: During dry years, individuals dispersed from intermittent to perennial reaches at the onset of drying and returned to intermittent reaches when flow returned (Hedden and Gido 2020). Smaller upstream sites did not fit this pattern, potentially because of limited connectivity. Greater consideration of intra- and interannual flow variability is therefore required to capture the temporal dynamism of lotic metacommunities when building flow–ecology relationships.

Integrating a metasystem approach to environmental flow design and implementation: An operational framework

No e-flow implementation exists, to our knowledge, that explicitly aims to protect or restore metacommunities, and relatively few implementations have targeted metapopulation dynamics (box 2; e.g., Norton et al. 2010, Kendy et al. 2012, in the MDB). The prerequisites for e-flow programs to more effectively maintain or restore metasystem dynamics include focusing on preserving multiple populations or communities, incorporating spatially explicit biological and environmental information, and implementing spatially explicit management of water flows. However, achieving these requirements does not imply that e-flows maintain or restore metasystem dynamics. To do so, e-flow programs must be explicitly tailored to this objective and must encompass more factors than local abiotic conditions. Below, we propose a framework to operationalize metasystem ecology in e-flow programs, from program definition and e-flow design to implementation and monitoring (figure 5). Because e-flow programs operate under uncertainty, and because adopting a metasystem perspective adds another level of complexity to e-flow design, this framework functions as an adaptive management cycle. Accordingly, e-flow assessments function as near-term forecasts that are iteratively improved through implementation, monitoring, evaluation, and reporting (Webb et al. 2017, Dietze et al. 2018). In developing the framework, we build on standard methodological workflows for e-flow design (e.g., ELOHA; Poff et al. 2010) and previous proposals for adopting a metacommunity perspective in freshwater conservation and restoration (see in general, Bond and Lake 2003, Rolls et al. 2018, Chase et al. 2020, Patrick et al. 2021, Cid et al. 2022 and, specifically in riverine bioassessment, Cid et al. 2020). Our recommendations are also broadly consistent and complementary with other recent conceptual e-flow frameworks, such as the strictures and promoters framework by Lester and colleagues (2020) and the climate-informed ecological resilience principles and associated indicators proposed by Grantham and colleagues (2019).

Define
Ecological target(s)

Once the overall objectives of an e-flow program have been determined (King et al. 2015), the first step of this framework is to select the ecological target for which to develop e-flow recommendations and the associated indicators to monitor the outcome of e-flow implementation. This selection should be made as part of a participatory process involving diverse stakeholders (Mussehl et al. 2022) and should reflect scientific, socioeconomic, and cultural requirements (Finn and Jackson 2011, Anderson et al. 2019). Possible ecological targets range from one or more species (conservation targets such as the endangered Colorado pikeminnow *Ptychocheilus lucius*, or a small suite of umbrella species whose conservation is expected to benefit numerous co-occurring species; Obester et al. 2022) to communities (e.g., macroinvertebrates, fish), and entire ecosystems (e.g., ecosystems providing cultural value; First Nations Fisheries Council of British Columbia 2020). Current e-flow programs are usually tailored to one or a few species rather than to entire communities, species assemblages, or ecosystems (Olden et al. 2014, Tonkin et al. 2021) and to local rather than regional measures of biodiversity.

Careful selection of ecological targets is particularly important for designer e-flow programs (Acreman et al. 2014), which tailor flow regimes to specific ecosystem objectives, as opposed to e-flow approaches that attempt to mimic a natural flow regime. Designer e-flows that target only one or a few specific species risk benefiting one ecosystem component at the expense of others (Tonkin et al. 2021). From a metasystem perspective, even if two ecological targets require the same local flow regimes, their dispersal ability, refuge use, and life cycle and seasonal movements may differ. For example, the New Zealand fish Canterbury galaxias (*Galaxias vulgaris*) and upland bully (*Gobiomorphus breviceps*) differ in their refuge use and, therefore, their flow needs: Both species move upstream as flows decline prior to channel drying, but bullies migrate from riffles to deeper runs whereas galaxiids burrow into the moist substrate (Davey et al. 2006, Lake 2011). Therefore, slow but long-term drying may be more detrimental to galaxiids, whereas rapid drying would be more detrimental to bullies, even if in the short term (Lake 2011). In general, long-lived and less-mobile species are more sensitive to local flow conditions whereas strong dispersers with life stages dependent on multiple habitat types are more sensitive to impairment of flow connectivity (Patrick et al. 2021). Beyond individual species, the metapopulation dynamics and metacommunity structure of different guilds (e.g., upstream versus mainstem fish species; Ferreira et al. 2019) and organism types (fish versus macroinvertebrates; Hastings et al. 2016) may reflect contrasting levels of environmental filtering, biotic interactions and dispersal.

To avoid relying on an ecological target whose conservation or restoration does not extend to other potential targets, one option is to use multiple target organisms with varied dispersal abilities and local flow requirements (Cañedo-Argüelles et al. 2015). Using multiple organisms to develop e-flow standards may be particularly relevant if some targets are selected primarily for their socioeconomic or cultural values (Finn and Jackson 2011) with potentially little information on the metasystem dynamics driving their distribution and abundance. Databases listing the biological traits of species (e.g., macroinvertebrates, Sarremejane et al. 2020; fish, Mims and Olden 2012; diatoms, Riato et al. 2022), including dispersal traits, can help guide this choice.

Indicators of biodiversity at multiple levels may also be used to monitor the effectiveness of e-flow implementation on local and

Table 1. Possible implications of metacommunity processes other than environmental filtering and influencing factors for environmental flow (e-flow) design and proposed solutions.

Metasystem processes or factors	Possible implications for flow–ecology relationships and e-flow outcomes compared with standard expectations	Example for native fish in the Murray–Darling Basin	Proposed measures that may improve the e-flow program outcomes
Dispersal (enabled by network connectivity)	High or low dispersal can blur flow–ecology relationships and limit effectiveness of standard e-flow design.	Stocks and colleagues (2021): difficulty relating hydrological conditions to recruitment because of dispersal of juveniles in golden perch.	Quantify relative strength of dispersal in structuring a metacommunity. Account for dispersal among sites when modeling species' responses to flow.
	Different ecological targets of e-flow design (e.g., species, guilds) may have different dispersal needs.	Thiem and colleagues (2021): contrasting dispersal patterns among fish species calls for diverse management actions to promote population recovery and persistence.	Design e-flows to maintain, restore or limit dispersal for ecological targets. Select multiple ecological targets with varied dispersal traits.
Biotic interactions	Competitive or trophic interactions (e.g., from nonnative species) modulate species' responses to flow.	Stoffels and colleagues (2015): immigration of competitor following flow pulse reduces floodplain population of eel-tailed catfish despite favorable local conditions.	Account for biotic interactions when modeling species' responses to flow. Design flow regime to benefit native species at the detriment of invasive species (or balance these two objectives if trade-offs exist). If possible, design e-flow to limit dispersal of invasive species. Complement e-flow programs with invasive population reduction.
		Rolls and colleagues (2013): boost in golden perch recruitment is probably mediated by flow-induced increase in prey production.	
Ecological drift	Small, isolated populations and communities are vulnerable to stochastic processes.	Pavlova and colleagues (2017): Macquarie perch populations are small and vulnerable to stochasticity. Despite flow restoration, recolonization is impeded by insufficient physical connectivity.	Design e-flows to restore dispersal if populations and communities were naturally more connected. Complement e-flow programs with population augmentation programs or restoration of instream connectivity.
	Isolated populations may have developed divergent flow–ecology relationships.	Zampatti and colleagues (2021): substantial variability in age structure, recruitment source and movement patterns of golden perch across the basin is potentially related to reduced connectivity.	Develop separate flow–ecology relationships with time-series analysis rather than through comparison across sites. Limit e-flows that promote dispersal among naturally isolated populations and could jeopardize metapopulation resilience.
Scale and heterogeneity	Flow–ecology relationships developed at too small a spatial scale and in hydrologically homogeneous areas may not capture species' responses to a range of flow conditions.	Colloff and colleagues (2018): of 11 flow–ecology relationships for phytoplankton, invertebrates, fishes, waterbirds and vegetation, those developed at small spatiotemporal scales are weaker than at larger scales.	Collect hydrological and ecological data in heterogeneous flow conditions, across river networks (both in mainstem and headwater reaches), and throughout the year. Assess spatial autocorrelation in flow–ecology relationships.
	Flow–ecology relationships developed at too large a spatial scale may span separate regional species pools and be blurred by divergent adaptations of individual species to flow regimes.	Huey and colleagues (2011): Golden perch populations are usually highly connected by dispersal, but drying of normally perennial refuges can cause strong spatial genetic structure via genetic drift.	
	Metacommunity processes can vary in time and among different areas of a river network.		

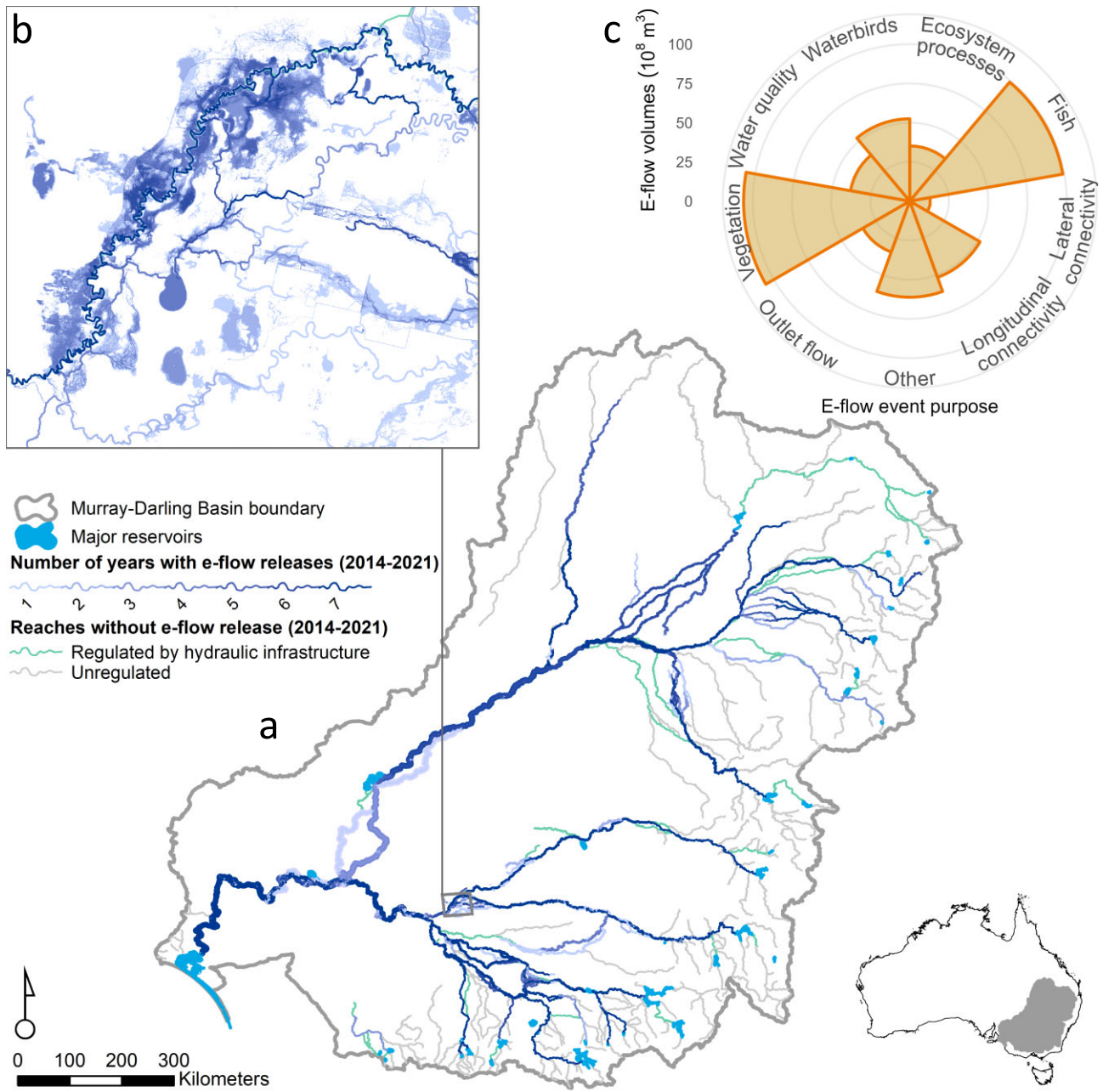*Note:* See box 1 for a description of the processes and factors.

Figure 3. Distribution of e-flow releases across the Murray–Darling Basin. Spatial distribution of e-flow releases from 2014 to 2021 across (a) the river network and (b) its floodplain. (c) E-flow volumes allocated to different ecological purposes (2013–2019; one event could have multiple purposes). The data were provided by the Commonwealth Environmental Water Office of the Australian Government and are available at https://data.gov.au/home.

regional processes. Taxonomic richness (alpha diversity) is commonly monitored but may fail to indicate substantial turnover in community composition and may partly misrepresent ecological responses to the local flow regime in cases of dispersal surplus or dispersal deficit (Cid et al. 2020). In addition, taxonomic richness cannot track basin-wide heterogeneity in community composition, changes to source–sink dynamics, or altered temporal synchrony among communities that could weaken metasystem resilience (Ruhí et al. 2017). Beta diversity describes variability in species composition in space or over time, which is particularly relevant in monitoring the effect of e-flows on metasystem dynamics (Ruhí et al. 2017). A suite of other metrics in addition to beta diversity exists to characterize regional ecological features (Cid et al. 2022). Whereas those indicators are common in

metacommunity research (Perkin et al. 2021, Larsen et al. 2021a), they are seldom used for e-flow design and monitoring. Because successful e-flow implementation depends on the involvement of multiple types of stakeholders and their coproduction of management objectives (Mussehl et al. 2022), communicating the relevance of seemingly arcane metacommunity processes and associated indicators is crucial to enable their inclusion as targets.

Whether e-flows can be designed for broader targets than individual species or locations depends largely on the legal framework mandating the provision of e-flows. E-flow implementations in the United States often aim to fulfill mitigation requirements for threatened and endangered fish species listed under the federal Endangered Species Act (Harwood et al. 2018). In Europe, the Water Framework Directive (WFD) does not mandate
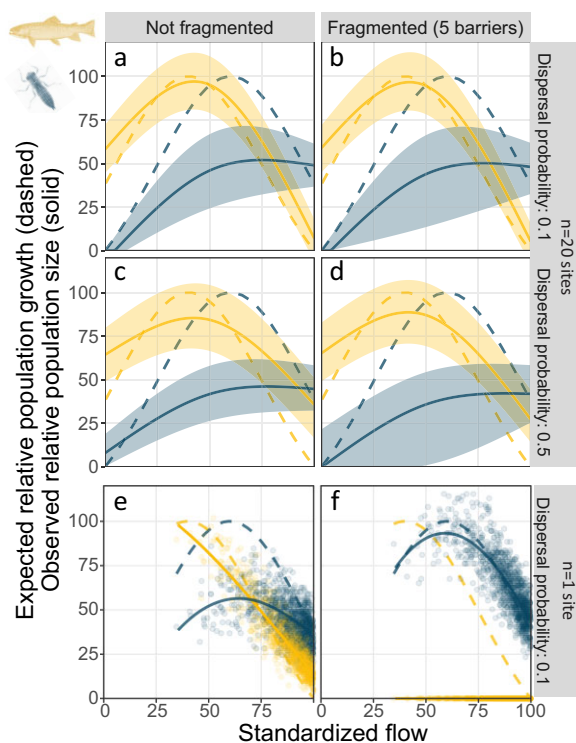
Figure 4. Metacommunity processes can cause empirical flow–ecology relationships to differ from relationships expected from only environmental filtering. A general metacommunity model (Thompson et al. 2020) was developed to simulate the population dynamics of two interacting species across 100 river sites in a synthetic river network (Carraro et al. 2020a) with spatiotemporally autocorrelated flow conditions. This model shows how the presence of a predator (light yellow) may decrease, shift, and blur the observed flow–abundance relationship (the solid line) of a prey species (dark blue) compared with its expected flow–population growth relationship (the dashed line). The effect of biotic interaction is stronger with decreased dispersal ability (modeled as decreased dispersal probability; panel (a) compared with panel (c)) and greater fragmentation (panel (b) compared with panel (a)). With high dispersal ability, mass effect may lead a species to be abundant in sites where it is maladapted (the solid yellow line extending beyond the dashed line in panels (c)–(d)). Flow–ecology relationships derived from monitoring at a single site (e–f) may provide a biased view of the flow preferences of species compared with relationships from multiple sites ($n = 20$) (a)–(d). In a fragmented context, stochasticity may even lead to the local extirpation of a species without possible recolonization despite moderately favorable conditions (f). Individual points in panels (e) and (f) represent the species' relative population abundance at different monthly time steps. The solid lines, lower and upper uncertainty bounds show fits from quantile general additive models (GAM) of population size for the 0.5, 0.1, and 0.9 quantiles, respectively. The expected population growth as a function of flow (the dashed line) was standardized from 0–5 to 0–100. The population size (the solid line) was standardized separately for $n = 20$ sites and $n = 1$ site by the maximum value across scenarios of the fitted median GAM.

the implementation of e-flows unless needed to prevent or reverse ecological degradation as indicated by indices representing community health (it requires that riverine flow regimes provide conditions "consistent with the achievement of the environmental objectives of the WFD"; European Commission 2015). Although vague, this requirement broadly aligns with metasystem thinking. In the MDB e-flow program, annual water management plans are required by law to establish e-flow allocation priorities across four main categories (river flows and connectivity, native vegetation, waterbirds, and fish), but additional objectives are also included

in e-flow design (figure 3). These include, for example, supporting populations of other native aquatic species (e.g., invertebrates, amphibians, platypus) and ecosystem functions (e.g., nutrient and carbon cycling, salt flushing). Widening the scope of e-flow policies to explicitly include multiple species and communities as ecological targets would help operationalize a metasystem perspective in e-flow programs. However, if the regulatory context requires that a narrow ecological target (e.g., a single species) be used to design the e-flow program, other aspects of this framework (e.g., metapopulation dynamics) can still be applied to support or restore metasystem dynamics for this target.

Compile available data and define monitoring needs

Designing and implementing e-flow recommendations from a metasystem perspective requires considerable data on the structure, hydrology, and ecology of the river basin. Compared with standard e-flow design frameworks, the main additional requirement is for most data to be spatially explicit. In other words, data should ideally be distributed across the region of study and the spatial relationships among sites (straight-line and river distances, structural and hydrological connectivity) considered.

Structural data consist of a ground-truthed map of river reaches and other water bodies, natural and anthropogenic instream barriers, flow-altering structures and water withdrawal points, and land cover and land use. Information on the characteristics of flow-altering features (e.g., dams, flow diversions, wastewater treatment plants) is also important—for example, their operating curves and release capacity, as well as permitted and actual water withdrawals. This data compilation process should produce a map of a diversity of management levers that may be used for e-flow provision, depending on the financial and legal tools available to water resource managers. Because most e-flow assessments still deal with individual rivers downstream of a dam (Olden et al. 2014, Ramos et al. 2018), such data on spatially distributed water sources are rarely collected.

E-flow design requires a hydrological foundation: time series representing simulated naturalized baseline conditions and the current human-influenced hydrology of the system (Poff et al. 2010). Hydrological models should ideally be developed to generate discharge time series for all reaches in the river network rather than for individual sites. In river networks with extensive nonperennial reaches, long-term observational data describing in-channel conditions (e.g., flow, low flow, no flow, dry) of river reaches across a network can indicate how conditions change in space and time. The resulting information on temporary fragmentation and ecologically important features such as persistent aquatic refuges (Sefton et al. 2019) is key to conserve metasystem dynamics. Historical observations of this type are rare (Jaeger et al. 2021), but several citizen science initiatives (e.g., Allen et al. 2019), governmental programs (e.g., Sefton et al. 2019), and improvements in remote sensing (e.g., Marshall et al. 2021) and modeling (e.g., Yu et al. 2022) of surface water presence are rapidly improving our ability to design e-flows for nonperennial systems. Finally, projections of the future hydrology of the system are useful to ensure that e-flow recommendations are climate ready—that is, compatible with potential future water availability (Judd et al. 2022).

Biological data are usually the most limiting type of data in e-flow assessments. Spatially distributed community data depicting the distribution or abundance of species across the river network form the basis of metacommunity analyses that can underpin e-flow design. Ideally, ecological and hydrological data collection sites should be colocated. To capture the spatiotemporal vari-
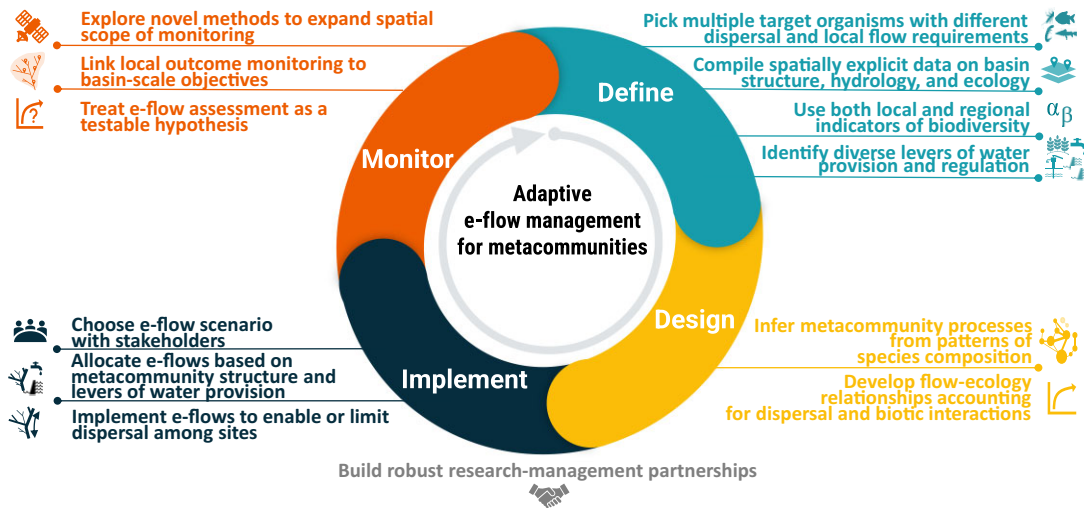
Figure 5. Operational framework for integrating a metasystem perspective in environmental flow (e-flow) design.

ability of metacommunity processes, sampling should ideally be distributed in space and time with information on straight-line and river distance among sites, across gradients of flow variability, alteration, and connectivity, and spread from mainstems to headwaters (with high dispersal often characterizing mainstem reaches and environmental filtering being more dominant in headwaters; Brown and Swan 2010). Time-series data describing taxonomic community composition enable more advanced analyses (see the next section; Ruhí et al. 2017, Jabot et al. 2020) and are therefore preferable to static snapshots. Macroinvertebrate community data collected by biomonitoring programs can provide a useful basis to conduct metacommunity analyses (Patrick et al. 2021) and can be supplemented with additional data collection to meet these spatiotemporal criteria (see the monitoring step).

Although statistical methods can estimate the role of dispersal in structuring metapopulations and metacommunities (in the design stage), quantitative measures of the dispersal rates of species in a basin can provide valuable information for species- and site-specific assessments (Heino et al. 2015). However, field-based methods are costly and, therefore, mainly applicable to systems with considerable resources or high conservation stakes (e.g., protected species). In most cases, dispersal metrics calculated from species traits (e.g., fish, Radinger and Wolter 2014; macroinvertebrates, Sarremejane et al. 2017b) can serve as useful proxies (Peredo Arce et al. 2021). In addition to quantitative estimates, trait information on the mode (aquatic, aerial, or terrestrial; active or passive), strength, timing, and direction (upstream, downstream, lateral) of species dispersal can also inform e-flow designs from a metasystem perspective (Sarremejane et al. 2017b).

Most rivers are insufficiently studied to determine the relative roles of metacommunity processes, the influence of flow alterations on these processes, or the contribution of individual river sites to metasystem health. However, intensive monitoring is already taking place in many river networks and could be adapted to meet the needs of the framework we propose. For instance, 4 years of seasonal fish community data were sufficient to estimate the effects of flow on local extinction, colonization, and recruitment probabilities for the metapopulations of 42 fish species across 23 streams of the karstic lower Flint River Basin, Georgia (United States; Peterson and Shea 2015). In addition, designing e-flows from a metasystem perspective can begin with-

out comprehensive data. Data availability inevitably constrains analytical approaches, but simple methods can be informative and guide initial e-flow recommendations (see the "Implement" section). Additional monitoring can then generate new data as part of an adaptive management approach (Webb et al. 2017) whereby e-flow recommendations are periodically adjusted. As such, this step of the framework both compiles available knowledge and data and identifies gaps to fill.

Assess the relative need for e-flows

Although flow alteration is a ubiquitous cause of ecosystem degradation, river systems are subject to multiple additional stressors, which may undermine the effectiveness of e-flow programs if not also addressed (see Stewardson et al. 2017 for examples). Physical barriers to movement, invasive species, pollution, overfishing, increasing temperatures, sediment regime disruption, and riparian clearance may have additive or interactive (e.g., antagonistic, synergistic) effects with flow alteration (Birk et al. 2020). Targeted e-flows can alleviate the impact of some of these stressors by, for example, providing passage over barriers, flushing nutrients and other pollutants, regulating sediment load and controlling invasive species. However, given the cost of designing and implementing e-flows, it is critical to identify whether efforts may be better allocated to addressing another overriding stressor rather than flow alteration. If resources allow, managers can evaluate the benefit of complementing e-flows with other management actions (as was suggested in table 1; Nicol et al. 2021) as part of an integrated basin management approach (Stewardson et al. 2017). Such a multipronged approach is already being explored in the MDB (Nicol et al. 2021) and other water-limited regions. In the San Diego River basin of California (United States), for example, multiple management actions were spatially prioritized in partnership with stakeholders to implement e-flows, protect habitat, and improve water quality across the basin (Stein et al. 2017).

Design
Infer metacommunity structure

This step aims to determine the relative strengths of metacommunity processes structuring community composition across the river network. Is the distribution and abundance

of species strongly driven by environmental filtering, biotic interactions, dispersal, and/or ecological drift? How strongly are communities and populations linked, and are there source–sink dynamics among sites? Which sites are refuges during extreme flow events? Are species governed by different processes? An increasingly diverse toolbox is available to address these questions, depending on the quantity and characteristics of observational data and the resources available for conducting scientific analyses.

Most empirical studies infer metacommunity processes by statistically analyzing patterns of species distribution or abundance among sites (Logue et al. 2011). An alternative approach involves reproducing the focal metacommunity using a spatially explicit mechanistic simulation model and testing a range of model parameters that control the relative strength of metacommunity processes, generating different scenarios of species distribution (e.g., Valente-Neto et al. 2018). The parameters associated with the scenario for which the generated patterns best match the observations are considered to most accurately reflect the processes structuring the system. Simulation models may better disentangle the relative roles of processes in empirical data, because similar ecological patterns can be driven by different processes (Valente-Neto et al. 2018). Once calibrated, such models can also simulate the effects of alternative water management scenarios on the metacommunity (Freeman et al. 2013). However, these models are currently too onerous for most management contexts in terms of data, expertise, and setup time. Therefore, we consider them unrealistic for a general operational e-flow framework and do not discuss them further.

Because the relative strength of metacommunity dynamics varies with spatial scale (see the "Controlling factors: Scale and heterogeneity" section), the units of analysis must be delineated. The biota of large basins such as the MDB is structured as potentially discrete metapopulations and metacommunities, depending on the dispersal capacity of the ecological targets and the connectivity of the system. In such cases, the basin must be divided into separate management units. For instance, population genetic studies have identified various levels of gene flow among fish species in the MDB: Golden perch exhibit high contemporary gene flow across most of the MDB, such that it should be managed as a single metapopulation (Attard et al. 2018). Other species, such as the eel-tailed catfish (*Tandanus tandanus*), exhibit genetic structure among catchments of the MDB but high levels of gene flow within those catchments (e.g., the Moonie River catchment, 15,000 square kilometers [km^2]), indicating that catchments of this size likely represent an adequate scale of analysis for e-flows and other management programs (Huey et al. 2011). Finally, for other species with small and demographically isolated populations displaying low genetic diversity, such as the threatened river blackfish (*Gadopsis marmoratus*), genetic studies can assist in the delineation of small management units within which to prioritize restoration measures (Lean et al. 2017). The scale of management must also be considered within basins. Focusing only on the communities within a fraction of the basin (e.g., only in the mainstem and larger tributaries) could overlook crucial spatial links (e.g., with headwater reaches that provide propagules and spawning grounds). Data describing the connectivity among reaches and subcatchments, whether potential (inferred from the landscape structure and the dispersal ability of ecological targets) or realized (inferred from actual dispersal or genetic structure), can enable selection of an appropriate scale (Hughes et al. 2013, Cid et al. 2022).

The method most widely applied to infer metacommunity dynamics from observed patterns is variation partitioning (Peres-Neto et al. 2006). This approach decomposes the variation in occurrence- or abundance-based taxonomic composition among local communities into three components: nonspatially structured environmental variation, spatially structured environmental variation, and pure spatial variation. The purely spatial component is hypothesized to reflect the effect of dispersal processes and ecological drift, whereas the nonspatially structured environmental variation expresses environmental filtering; and the spatially structured environmental variation can result from multiple processes (Peres-Neto and Legendre 2010). Although straightforward, this method can present statistical biases (Peres-Neto and Legendre 2010) and allows limited inference of metacommunity processes if applied to a snapshot data set of species distribution (Guzman et al. 2022). Analyzing temporal variability in community composition, including through temporal approaches to variation partitioning, is therefore crucial to correctly infer metacommunity processes (Jabot et al. 2020, Guzman et al. 2022). Furthermore, applying multiple methods and analyzing multiple summary statistics, both descriptive (e.g., diversity metrics) and model-based (e.g., variation partitioning fractions), strongly increases the ability to infer metacommunity processes (Ovaskainen et al. 2019, Guzman et al. 2022).

Two promising approaches for informing e-flow design are time-series analyses of spatial beta diversity and joint species distribution models (JSDMs). Temporal analyses of spatial beta diversity can be used both to infer the relative strength of metacommunity processes (e.g., through path analysis; Jabot et al. 2020) and to identify keystone sites (i.e., that consistently support high local diversity and contributing colonists to other sites, or containing unique species; Ruhí et al. 2017). Beta diversity analyses only require data on community composition. JSDMs are community-level extensions of standard species distribution models that leverage correlation in abundance (or co-occurrence) across taxa (Warton et al. 2015). As well as demonstrating high predictive performance in inferring metacommunity structure, JSDMs can reveal the potential strength of biotic interactions, expressed as residual species-to-species correlations (Ovaskainen et al. 2019, Guzman et al. 2022). In addition to data on community composition, JSDMs require hydrological and other environmental data as predictors of species distribution.

Develop flow–ecology relationships

Developing flow–ecology relationships requires flow regime characteristics to be related to the ecological indicators of interest while accounting for dispersal and biotic interactions. First, indices describing the flow regime and flow alterations are computed from discharge time series (e.g., Mathews and Richter 2007). These metrics can be used as predictors of the ecological responses following a statistical (Olden and Poff 2003) or expert-based preselection process (e.g., the functional flows approach; Yarnell et al. 2020). To capture the influence of dispersal, spatial autocorrelation in species composition is modeled by the statistical tool used to develop the flow–ecology relationship. Multiple model types can fulfill this requirement, notably JSDMs (Warton et al. 2015), spatial stream-network (SSN) models (Isaak et al. 2014), and multivariate autoregressive state-space (MARSS) models (Holmes et al. 2012).

JSDMs provide a well-developed way to establish relationships between flow statistics and species occurrence while accounting for the spatial distribution of sites and interactions among species (Ovaskainen et al. 2019). SSN models (Isaak et al. 2014), which are beginning to be used to develop flow–ecology relationships (Bruckerhoff et al. 2019, Larsen et al. 2021b), can account for

autocorrelation that arises along both straight-line and network distances and from different dispersal modes. Differences in aquatic dispersal mode are modeled in SSNs by separately considering network distances among flow-connected (unidirectional flow, reflecting drift) and flow-unconnected sites (that are potentially on different streams and reflecting active instream dispersal; Isaak et al. 2014). Finally, MARSS models (Holmes et al. 2012) are particularly well suited to concurrently model the effects of temporal autocorrelation, spatial autocorrelation, and among-species correlation (provided sufficient sites and samples), as is evidenced by studies linking river flow regimes to metapopulation (Sarremejane et al. 2021) and metacommunity structure (Ruhí et al. 2018). MARSS models can also characterize the relationships between flow metrics and spatial beta diversity over time, and between flow metrics and site-specific contributions to beta diversity (Legendre and De Cáceres 2013). Such analysis can identify how flow variability may create phases in which the metacommunity is dominated by regional dispersal versus local environmental filtering (Datry et al. 2016, Ruhí et al. 2017) or change the relative contribution of some sites to network-wide diversity (e.g., sites acting as refuges in different seasons or years).

In river networks with extensive nonperennial reaches, in which low-flow refuge sites may play a key role in structuring metacommunities, temporary fragmentation among sites by drying could be incorporated into flow–ecology models if observations of in-channel conditions (e.g., flow, low flow, no flow, dry) are available (Sarremejane et al. 2021). Additional hydrological metrics, such as time series of pool area and volume, could also be used to predict ecological responses. If these additional predictors are used to develop flow–ecology relationships, links between discharge and in-channel conditions at monitored sites may need to be established to implement e-flow conservation actions (e.g., the amount by which surface or groundwater withdrawal must be reduced to maintain connectivity among pools). Finally, in those systems in which baseflow is particularly influenced by groundwater withdrawals and in which groundwater wells can be regulated, groundwater simulations can establish links among groundwater withdrawal, flow alterations, and community responses (Falke et al. 2011).

Implement

Conserving or restoring metacommunity dynamics entails allocating water optimally across a river network and managing for dispersal in addition to meeting species' local flow needs—the typical focus of standard e-flow design. Even small-scale e-flows, when they are well targeted across a network, can fulfill network-wide objectives (e.g., in the MDB, Gawne et al. 2018).

A few flow management projects already aim to maintain or restore dispersal among habitat patches for a particular species or to trigger fish migration, sometimes with explicit mention of metapopulation dynamics. These are mainly documented for fish in the United States and Australia, two countries with heavily altered hydrology and a long history of e-flow implementations (Poff et al. 2017). For example, e-flows have been implemented across the Susquehanna River Basin (7.1×10^4 km², northeastern United States) to conserve brook trout (*Salvelinus fontinalis*) metapopulation dynamics by promoting connectivity among habitat patches during summer low flows (Kendy et al. 2012). Similarly, e-flows maintain summer baseflow for passage over shallow riffles by endangered Colorado pikeminnow (*Ptychocheilus lucius*) in the Upper Colorado River Basin (2.9×10^5 km²; US Fish and Wildlife Service 2020). Such movement increases access to suitable habitat and

may contribute to maintaining gene flow between subpopulations. In the Lower Canning River (Western Australia), flow pulses (21.6×10^3 cubic meters per day over 5 days) during summer aim to maintain water quality and provide sufficient depth over barriers to enable upstream migration by the freshwater cobbler (*Tandanus bostocki*; Norton et al. 2010). *T. bostocki* is the largest-bodied freshwater fish species in southwestern Australia, so these flows may also facilitate passage for other species. Across the MDB, e-flows are commonly implemented to promote connectivity and dispersal, including to enable access to refuges during low flows, to drown out barriers, to trigger migratory movements, to enable recolonization of river reaches from neighboring ones after local disturbance, to facilitate gene flow among subpopulations by long-distance dispersers, and to reconnect channels and floodplains with high flows (Gawne et al. 2018, Commonwealth Environmental Water Office 2022). Facilitating dispersal is therefore already an occasional objective of e-flow design in line with a metasystem approach and could be included in more programs.

Appropriate target sites for e-flow provision depend on the metacommunity structure. If analyses indicate naturally limited dispersal among communities (or populations) and identify no keystone sites, then e-flow design should focus on maintaining a suitable flow regime across many sites (as determined by flow–ecology relationships) and providing flows that support that level of dispersal (Ruhí et al. 2017). But if analyses identify keystone sites that play a central role in supporting the metacommunity, then managers may prioritize e-flow provision at these crucial sites while maintaining sufficient flow for dispersal to the rest of the network. In the MDB, for instance, the Mid-Murray Floodplain Recovery Reach fish recovery plan focuses on ensuring suitable local habitat conditions for species whose populations are mainly driven by local recruitment, whereas e-flows are designed to trigger dispersal and ensure longitudinal connectivity for populations that rely on colonists from outside the local scale (Cornell et al. 2021, Lyon et al. 2021). Dispersal corridors that connect multiple sites through high dispersal rates, in particular, should be targeted for e-flow provision that maintains suitable abiotic conditions and connectivity for dispersal (Patrick et al. 2021). In the theoretical case in which insufficient water is available for e-flows to provide suitable conditions for two sites connected by high levels of dispersal, it may be preferable to provide adequate flow to one site—which can become a source of colonists for the other—rather than to provide unsuitable flows to both sites. Similarly, e-flow provision should prioritize promoting access to dry-phase refuges (e.g., perennial pools in naturally nonperennial rivers) during the drying period and their maintenance throughout the dry period (Rayner et al. 2009). Additional refuges may be restored (e.g., through targeted water pumping) to provide dispersal stepping stones between communities (Archdeacon and Reale 2020). During droughts, which reduce water availability in river networks at a regional scale, even locally constrained e-flow releases may reduce the synchronous pressure exerted by the drought and enhance metasystem-wide viability (Marshall et al. 2021). Once sites have been selected, flow–ecology relationships can inform selection of the flow regime elements to conserve or restore.

In the same way that designer e-flows can meet the local habitat needs of native species to the detriment of nonnative invasive species (e.g., Chen and Olden 2017), designer e-flows may be tailored to promote and impair the dispersal of native and nonnative species, respectively. For example, restoring the timing of high flows can benefit the waterborne seed dispersal of native plant species whose phenology is adapted to a natu-

ral flow regime and limit the proliferation of invasive species (Lytle et al. 2017). If flow-dependent barriers to dispersal are present (e.g., rapids, low-head dams), evaluating whether their passability should be increased (e.g., to restore dispersal among communities; Marshall et al. 2021) or decreased (e.g., to prevent a nonnative species from expanding its range) through e-flow provision, and when, is important.

E-flows may also be designed to support biotic interactions other than competition and predation. For example, several mussel species in the MDB depend on host fish to complete their life cycle and colonize new sites, such that e-flows must be designed both to support critical mussel life stages in synchronicity with fish host species' needs and also provide pathways for host fish dispersal (Wright et al. 2022).

The choice of scenario depends not only on stakeholder input (Mussehl et al. 2022) but also on the hydrology of the basin and the available management levers of water provision. For example, some perennial river pools that act as refuges in arid regions depend on occasional surface flows to persist throughout the dry season whereas others are primarily groundwater fed (Hamilton et al. 2005). Regulation of upstream surface water withdrawal or periodic releases from reservoirs may be needed for the former, whereas limits to groundwater withdrawal could be used to conserve the latter. The location of flow regulation structures, the ability to regulate surface and groundwater withdrawals and to alter land use will all influence where, how and at what cost e-flows can be allocated. To move beyond a strictly local approach, a diversity of management levers other than flow releases downstream of a single dam can be used for e-flow provision. Examples already exist of alternative sources of water for e-flow provision and include system-wide coordinated reservoir operation (Opperman et al. 2019); regulation of surface and groundwater withdrawals (e.g., in the United States, Kendy et al. 2012; in the United Kingdom, Gustard et al. 1987, implemented at least since 1963), including switching from surface to groundwater sources (McCoy et al. 2018); moving a diversion downstream (McCoy et al. 2018) or modifying the timing of withdrawal (European Commission 2015); land use planning (e.g., switching to crops requiring less water, or temporarily or permanently taking land out of agricultural production; McCoy et al. 2018); targeted improvements in conveyance or irrigation efficiency (Opperman et al. 2019); release of wastewater treatment plant effluent (Hamdhani et al. 2020); diversion of domestic water from urban or suburban water supply networks (Norton et al. 2010); and even experimental storage of spring runoff in aquifers for later instream use (McCoy et al. 2018). Which water source can more easily be used for e-flow provision strongly depends on the legal and political context. Water withdrawal limits can be legally imposed in some countries and localities, whereas other administrations rely on the buyback or leasing of water rights by government and nongovernmental organizations from willing sellers (Opperman et al. 2019). Finally, new coordination of e-flow releases across entire river basins can be achieved by strategically targeting hydropower dams undergoing relicensing through a centralized process. In the United States, for example, over 300 hydropower projects are expected to undergo relicensing between 2016 and 2026 (Schramm et al. 2016), providing an opportunity to coordinate e-flow objectives among dams with a metasystem perspective. In the MDB, environmental water is recovered to meet both local and basin-wide objectives with measures ranging from targeted infrastructure investments (e.g., efficiency gains from off-farm conveyance systems, on-farm irrigation, reservoir evaporation and seepage, urban water management) to voluntary surface and groundwater

entitlement purchases (Murray–Darling Basin Authority 2018). Then, specific e-flow targets are achieved by timing reservoir releases with unregulated streamflow, and by coordinating operating rules and withdrawals within and among catchments (box 2; Stewardson and Guarino 2018, Murray–Darling Basin Authority 2020b). The increasing use of spatially distributed sources of water for e-flow provision is both a departure from the longstanding focus on single reservoir operation and another key requisite for metasystem approaches.

Monitor

Monitoring of e-flow implementations is pivotal to improve future management, to demonstrate the benefits of public investment to decision-makers and the public, and to inform ecohydrological science in general (King et al. 2015). E-flow programs are costly and often contentious, so their legitimacy hinges on transparent reporting of their benefits (O'Donnell and Garrick 2017). The MDB plan, for example, will cost the Australian government approximately US$9 billion from 2012 to 2026 (Ross and Connell 2016). Despite their cost, most habitat and flow restorations go unmonitored, limiting the opportunities to develop evidence-informed best practices (Souchon et al. 2008). Nonetheless, guidelines and methods for monitoring the outcomes of standard e-flows are well established (Souchon et al. 2008, King et al. 2015, Webb et al. 2017).

Within an adaptive management cycle, monitoring can continuously contribute to reducing uncertainties and adjusting e-flow recommendations and objectives (Webb et al. 2017). Analyses of metacommunity dynamics and flow–ecology relationships can provide quantitative forecasts that represent testable hypotheses to iteratively refine e-flows as they are implemented (Dietze et al. 2018). Monitoring should therefore verify the actual delivery of water allocations (i.e., were discharge objectives attained?), the effectiveness of both short-term flow events (on, e.g., dispersal, recruitment) and the long-term flow regime (on, e.g., species distribution), and the validity of the assumptions and models underlying e-flow design (Souchon et al. 2008, King et al. 2015). In addition to previous assessments of stressors (see "Define" section), the monitoring stage can include continued assessment of whether nonflow stressors (e.g., water quality, instream barriers) may be affecting the ecological targets, compromising the evaluation of e-flow outcomes, and indicating the need for complementary non-flow-based measures (Nicol et al. 2021).

Reflecting management targets, e-flow monitoring has historically focused on documenting the effects of discrete flow events on local habitat conditions (Souchon et al. 2008, Olden et al. 2014). To our knowledge, the only explicitly basin-scale, long-term e-flows monitoring programs are the Glen Canyon Dam Adaptive Management Program (although mostly focused on the mainstem effects of e-flows from a single dam; Melis et al. 2015), the Victorian Environmental Flows Monitoring and Assessment Program (Webb et al. 2010), and Flow-MER in the MDB (see box 2; Gawne et al. 2020, Barbour et al. 2021a). Flow-MER uses monitoring data in seven areas across the MDB to assess both area-scale outcomes for river reaches and associated wetlands within the area and their contribution to the achievement of basin-scale objectives (i.e., outside of the spatial scope of individual flow releases). E-flow outcomes are compared with modeled scenarios that represent what outcomes would have been without e-flows, accounting for water availability each year. This annual evaluation considers how e-flow design could be altered to improve flow management outcomes. Additional funding is also allocated to novel research on ecological responses to e-flows (box 2). The ultimate aim of the

program is to improve understanding of basin-scale processes by comparing outcomes from isolated e-flow events with coordinated e-flow provision across areas (Gawne et al. 2020). Although Flow-MER (2019–2022) and preceding monitoring programs in the MDB (2014–2019) represent the largest e-flow monitoring effort in the world, the budget for their 2014–2022 implementation was approximately US\$35 million (Hart and Butcher 2018, Barbour et al. 2021a), or less than 0.5% of the overall MDB Basin Plan 15-year budget, underscoring the modest cost of monitoring relative to the total investment for e-flow implementation.

Assessing the outcomes of e-flow programs beyond a few sites across a river basin is cost prohibitive using traditional data collection methods, but several novel data sources can be combined to increase the spatial coverage and density of e-flow monitoring. First, DNA-based monitoring could expand the spatial scope and density of community sampling across river networks (Carraro et al. 2020b). Second, citizen scientists could generate abundant monitoring data to inform management and increase buy-in by diverse stakeholders (Mussehl et al. 2022). Lastly, satellite remote sensing can be used to track the delivery of e-flows and their effects on the distribution of and connectivity among habitats, and on the distribution and composition of riparian plant communities across the river network. All three of these approaches are already being trialed or implemented as part of the e-flow monitoring and research program in the MDB (e.g., Watts et al. 2019, Murray–Darling Basin Authority 2020b). With sufficient representative sampling, the results from high-quality monitoring could be extrapolated to unmonitored sites for a truly basin-scale assessment (Webb et al. 2017).

Applicability of the proposed framework

We do not propose that every e-flow program should or could adopt all components of our proposed framework. It is unrealistic to fully cater to the specific metasystem dynamics of every river basin considering the cost of achieving this objective. Moving beyond simple hydrological rules of thumb (e.g., a fixed percentage of mean annual flow) toward greater ecological realism is already a major challenge for e-flow science (Poff 2018). The development of transferable flow–ecology relationships is another key research priority for regional e-flow implementation (Poff et al. 2010). However, we contend that adopting a metasystem perspective from program definition and design to monitoring and evaluation could increase the effectiveness of most e-flow programs.

This framework best suits e-flow programs focused on preserving multiple populations or communities linked by dispersal, equipped with spatially explicit data and multiple water management levers. Examples of e-flow programs with substantial resources already exist in many river basins, and system-wide approaches are increasingly adopted (Opperman et al. 2019). The substantial political and governance hurdles to integrating a metasystem perspective and managing flows across scales will probably be easiest to clear for such programs, which will then provide proofs of concept for other basins. Nonetheless, benefits can be gained from a metasystem perspective even when those conditions are not met, or where resources are limited.

When a lack of data hinders analyses of metacommunity structure and processes, for example, managers still have multiple options. They can synthesize knowledge from experts, including local stakeholders, and existing research to develop conceptual models that could guide target setting and identify potential ecological processes and factors that may influence the effectiveness of e-flow implementation. Planning can also be supported by con-

ceptual and practical consideration of key ecological questions, such as: Do the species of interest require multiple habitats to complete their life cycle? If so, when and at what scale? Are there flow-dependent barriers to longitudinal or lateral movement? Are there nonnative species that may benefit from e-flows? Network analysis using topographic and remote sensing data can provide a priori assessments of barriers and key sites acting as refuges or connectivity hubs that could be targeted for more detailed e-flow assessments (Marshall et al. 2021, Yu et al. 2022). These assessments can be combined with knowledge of the life histories of the ecological targets to infer potential dispersal structure among populations or communities, which can help identify relevant management units (as demonstrated for more than 100 Australian aquatic species by Hughes et al. 2013). In the absence of ecological data, e-flows can also target natural spatiotemporal variability in flow regimes across a river network, rather than using flow metrics at a single site, to promote regional heterogeneity and resilience. In heavily fragmented systems, dispersal may still be possible for some species (e.g., golden perch in the MDB; Huey et al. 2011), and assessing the structure of the metasystem can help prioritize e-flows among sites. Finally, even if management is restricted to a single flow regulation structure for a single species, e-flows can still be designed to account for more than local habitat conditions, and trigger movement to other habitats, facilitate passage over barriers, or control invasive species.

Conclusions

Growing human water demand and ongoing global changes accentuate the competition for water among uses and make long-term implementation of e-flows programs increasingly uncertain. In most cases then, the main obstacle to e-flow implementation will remain political, not scientific (Owusu et al. 2022, Dourado et al. 2023). This difficulty in implementing e-flows further raises the stakes for program outcomes; whether the objectives of using scarce water for the environment are met affects the legitimacy of the programs and can determine their continued viability (O'Donnell et al. 2019). Therefore, careful design and robust monitoring that leverage advances in ecology to maximize the effectiveness of e-flow implementations are key to guaranteeing continued e-flows implementation. In this article, we specifically propose that managing for metasystem dynamics beyond local environmental filtering—namely, biotic interactions, dispersal, and ecological drift—and accounting for connectivity, scale, and heterogeneity can increase the effectiveness of e-flow implementations. To achieve this objective, strong partnerships among researchers and managers are required that facilitate the integration of recent ecological research in management and enable program codevelopment through multiple adaptive management cycles (Webb et al. 2010). Incorporating metasystem dynamics in e-flow design may even increase the transferability of flow–ecology relationships by controlling for confounding factors. Although applications of metasystem concepts and models in conservation are still in their infancy (Chase et al. 2020, Patrick et al. 2021, Cid et al. 2022), we posit that increased adoption of this perspective will in turn fuel the development of streamlined methods and transferable knowledge that will increasingly facilitate metasystem e-flow assessments.

Acknowledgments

Supplemental material

R codes and simulated data used in this study are available from https://github.com/messamat/metacom_EF_sim.

References cited

Acreman M, Arthington AH, Colloff MJ, Couch C, Crossman ND, Dyer F, Overton I, Pollino CA, Stewardson MJ, Young W. 2014. Environmental flows for natural, hybrid, and novel riverine ecosystems in a changing world. *Frontiers in Ecology and the Environment* 12: 466–473.

Allen DC, Kopp DA, Costigan KH, Datry T, Hugueny B, Turner DS, Bodner GS, Flood TJ. 2019. Citizen scientists document long-term streamflow declines in intermittent rivers of the desert southwest, USA. *Freshwater Science* 38: 244–256.

Anderson EP, et al. 2019. Understanding rivers and their social relations: A critical step to advance environmental water management. *WIREs Water* 6: e1381.

Archdeacon TP, Reale JK. 2020. No quarter: Lack of refuge during flow intermittency results in catastrophic mortality of an imperiled minnow. *Freshwater Biology* 65: 2108–2123.

Arthington AH, Rolls RJ, Sternberg D, Mackay SJ, James CS. 2014. Fish assemblages in subtropical rivers: Low-flow hydrology dominates hydro-ecological relationships. *Hydrological Sciences Journal* 59: 594–604.

Arthington AH, et al. 2018. The Brisbane declaration and global action agenda on environmental flows (2018). *Frontiers in Environmental Science* 6: 45.

Attard CRM, Brauer CJ, Sandoval-Castillo J, Faulks LK, Unmack PJ, Gilligan DM, Beheregaray LB. 2018. Ecological disturbance influences adaptive divergence despite high gene flow in golden perch (*Macquaria ambigua*): Implications for management and resilience to climate change. *Molecular Ecology* 27: 196–215.

Auerbach DA, Poff NL. 2011. Spatiotemporal controls of simulated metacommunity dynamics in dendritic networks. *Journal of the North American Benthological Society* 30: 235–251.

Australian Government. 2021. Basin Plan 2012. Australian Government. Report no. F2021C01067. www.legislation.gov.au/Details/F2021C01067.

Barbour E, et al. 2021a. *Flow-MER Basin-Scale Evaluation and Research plan: Flow-MER Program*. Commonwealth Environmental Water Office: Monitoring, Evaluation and Research Program, Department of Agriculture, Water and the Environment, Australia.

Barbour E, et al. 2021b. *Basin-Scale Evaluation of 2019–20 Commonwealth Environmental Water*. Commonwealth Environmental Water Office: Monitoring, Evaluation and Research Program, Department of Agriculture, Water and the Environment, Australia.

Beesley L, King AJ, Gawne B, Koehn JD, Price A, Nielsen D, Amtstaetter F, Meredith SN. 2014. Optimising environmental watering of floodplain wetlands for fish. *Freshwater Biology* 59: 2024–2037.

Birk S, et al. 2020. Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. *Nature Ecology and Evolution* 4: 1060–1068.

Bogan MT, Lytle DA. 2011. Severe drought drives novel community trajectories in desert stream pools. *Freshwater Biology* 56: 2070–2081.

Bond NR, Lake PS. 2003. Local habitat restoration in streams: Constraints on the effectiveness of restoration for stream biota. *Ecological Management and Restoration* 4: 193–198.

Brooks AJ, Russell M, Bevitt R, Dasey M. 2011. Constraints on the recovery of invertebrate assemblages in a regulated snowmelt river during a tributary-sourced environmental flow regime. *Marine and Freshwater Research* 62: 1407–1420.

Brown BL, Swan CM. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology* 79: 571–580.

Bruckerhoff LA, Leasure DR, Magoulick DD. 2019. Flow–ecology relationships are spatially structured and differ among flow regimes. *Journal of Applied Ecology* 56: 398–412.

Cañedo-Argüelles M, Boersma KS, Bogan MT, Olden JD, Phillipsen I, Schriever TA, Lytle DA. 2015. Dispersal strength determines metacommunity structure in a dendritic riverine network. *Journal of Biogeography* 42: 778–790.

Carraro L, Bertuzzo E, Fronhofer EA, Furrer R, Gounand I, Rinaldo A, Altermatt F. 2020a. Generation and application of river network analogues for use in ecology and evolution. *Ecology and Evolution* 10: 7537–7550.

Carraro L, Mächler E, Wüthrich R, AF 2020b. Environmental DNA allows upscaling spatial patterns of biodiversity in freshwater ecosystems. *Nature Communications* 11: 3585.

Chase JM, Jeliazkov A, Ladouceur E, Viana DS. 2020. Biodiversity conservation through the lens of metacommunity ecology. *Annals of the New York Academy of Sciences* 1469: 86–104.

Chen W, Olden JD. 2017. Designing flows to resolve human and environmental water needs in a dam-regulated river. *Nature Communications* 8: 2158.

Chen W, Olden JD. 2018. Evaluating transferability of flow–ecology relationships across space, time and taxonomy. *Freshwater Biology* 63: 817–830.

Chester ET, Matthews TG, Howson TJ, Johnston K, Mackie JK, Strachan SR, Robson BJ. 2014. Constraints on the response of fish and crayfish to environmental flow releases in a regulated headwater stream network. *PLOS ONE* 9: e91925.

Cid N, Bonada N, Heino J, Cañedo-Argüelles M, Crabot J, Sarremejane R, Soininen J, Stubbington R, Datry T. 2020. A metacommunity approach to improve biological assessments in highly dynamic freshwater ecosystems. *BioScience* 70: 427–438.

Cid N, et al. 2022. From meta-system theory to the sustainable management of rivers in the Anthropocene. *Frontiers in Ecology and the Environment* 20: 49–57.

Colloff MJ, et al. 2018. The use of historical environmental monitoring data to test predictions on cross-scale ecological responses to alterations in river flows. *Aquatic Ecology* 52: 133–153.

Commonwealth Environmental Water Office. 2022. Water Management Plan 2022–2023. Commonwealth Environmental Water Office. www.dcceew.gov.au/water/cewo/publications/water-management-plan-2022-23.

Conallin AJ, Smith BB, Thwaites LA, Walker KF, Gillanders BM. 2012.

Environmental water allocations in regulated lowland rivers may encourage offstream movements and spawning by Common Carp, *Cyprinus carpio*: Implications for wetland rehabilitation. *Marine and Freshwater Research* 63: 865–877.

Cornell G, Hale R, Amtstaetter F, Conallin J, Stuart I. 2021. *Mid-Murray Floodplain Recovery Reach Fish Recovery Plan*. Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water and Planning. https://finterest.com.au/wp-content/uploads/2021/11/Draft-Mid-Murray-Fish-Recovery-Plan-November-2021.pdf.

Datry T, Bonada N, Heino J. 2016. Towards understanding the rganization of metacommunities in highly dynamic ecological systems. *Oikos* 125: 149–159.

Davey AJH, Kelly DJ, Biggs BJF. 2006. Refuge-use strategies of stream fishes in response to extreme low flows. *Journal of Fish Biology* 69: 1047–1059.

Dewson ZS, James ABW, Death RG. 2007. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society* 26: 401–415.

Dietze MC, et al. 2018. Iterative near-term ecological forecasting: Needs, opportunities, and challenges. *Proceedings of the National Academy of Sciences* 115: 1424–1432.

Dourado GF, Rallings AM, Viers JH. 2023. Overcoming persistent challenges in putting environmental flow policy into practice: A systematic review and bibliometric analysis. *Environmental Research Letters* 18: 043002.

Drummond LR, McIntosh AR, Larned ST. 2015. Invertebrate community dynamics and insect emergence in response to pool drying in a temporary river. *Freshwater Biology* 60: 1596–1612.

Dunn CG, Paukert CP. 2021. Accounting for dispersal and local habitat when evaluating tributary use by riverine fishes. *Ecosphere* 12: e03711.

European Commission. 2015. Ecological flows in the implementation of the Water Framework Directive. European Commission. Guidance document no. 31.

Falke JA, Fausch KD, Magelky R, Aldred A, Durnford DS, Riley LK, Oad R. 2011. The role of groundwater pumping and drought in shaping ecological futures for stream fishes in a dryland river basin of the western Great Plains. *Ecohydrology* 4: 682–697.

Ferreira FC, Souza UP, Cetra M, Petrere M. 2019. Rhithronic and potamonic fishes coexist in wadeable streams under distinct metacommunity processes. *Ecology of Freshwater Fish* 28: 85–96.

Finn M, Jackson S. 2011. Protecting indigenous values in water management: A challenge to conventional environmental flow assessments. *Ecosystems* 14: 1232–1248.

First Nations Fisheries Council of British Columbia. 2020. Environmental flow needs: A primer for First Nations. First Nations Fisheries Council of British. www.fnfisheriescouncil.ca/wp-content/uploads/2022/01/WFF-ENVIRONMENTAL-FLOW-NEEDS-2020.pdf.

Freeman MC, et al. 2013. Linking river management to species conservation using dynamic landscape-scale models. *River Research and Applications* 29: 906–918.

Freeman MC, et al. 2022. Toward improved understanding of streamflow effects on freshwater fishes. *Fisheries* 47: 290–298.

Gawne B, Capon SJ, Hale J, Brooks SS, Campbell C, Stewardson MJ, Grace MR, Stoffels RJ, Guarino F, Everingham P. 2018. Different conceptualizations of river basins to inform management of environmental flows. *Frontiers in Environmental Science* 6: 111.

Gawne B, et al. 2020. Monitoring of environmental flow outcomes in a large river basin: The Commonwealth Environmental Water Holder's long-term intervention in the Murray–Darling Basin,

Australia. *River Research and Applications* 36: 630–644.

Gido KB, Propst DL 2012. Long-term dynamics of native and nonnative fishes in the San Juan River, New Mexico and Utah, under a partially managed flow regime. *Transactions of the American Fisheries Society* 141: 645–659.

Gido KB, Whitney JE, Perkin JS, Turner TF 2016. Fragmentation, connectivity and fish species persistence in freshwater ecosystems. Pages 292–323 in Closs G, Krkosek M Olden J, eds. *Conservation of Freshwater Fishes*. Cambridge University Press.

Gounand I, Harvey E, Little CJ, Altermatt F. 2018. Meta-ecosystems 2.0: Rooting the theory into the field. *Trends in Ecology and Evolution* 33: 36–46.

Grantham TE, Matthews JH, Bledsoe BP. 2019. Shifting currents: Managing freshwater systems for ecological resilience in a changing climate. *Water Security* 8: 100049.

Growns I. 2016. The implementation of an environmental flow regime results in ecological recovery of regulated rivers. *Restoration Ecology* 24: 406–414.

Gustard A, Cole G, Marshall D, Bayliss A. 1987. A study of compensation flows in the UK. Institute of Hydrology. https://nora.nerc.ac.uk/id/eprint/6040.

Guzman LM, et al. 2022. Accounting for temporal change in multiple biodiversity patterns improves the inference of metacommunity processes. *Ecology* 103: e3683.

Hamdhani H, Eppehimer DE, Bogan MT. 2020. Release of treated effluent into streams: A global review of ecological impacts with a consideration of its potential use for environmental flows. *Freshwater Biology* 65: 1657–1670.

Hamilton SK, Bunn SE, Thoms MC, Marshall JC. 2005. Persistence of aquatic refugia between flow pulses in a dryland river system (Cooper Creek, Australia). *Limnology and Oceanography* 50: 743–754.

Hanski I. 1998. Metapopulation dynamics. *Nature* 396: 41–49.

Harper M, et al. 2022. How do changes in flow magnitude due to hydropower operations affect fish abundance and biomass in temperate regions? A systematic review. *Environmental Evidence* 11: 1–39.

Hart B, Butcher R. 2018. *Commonwealth Long Term Intervention Monitoring Project: Stage 1 Midterm Review and Evaluation*. Water Science, Moama, and Water's Edge Consulting.

Harwood AJ, Tickner D, Richter BD, Locke A, Johnson S, Yu X. 2018. Critical factors for water policy to enable effective environmental flow implementation. *Frontiers in Environmental Science* 6: 37.

Hastings RP, Meiners SJ, Colombo RE, Thomas TE. 2016. Contrasting impacts of dams on the metacommunity structure of fish and macroinvertebrate assemblages. *North American Journal of Fisheries Management* 36: 1358–1367.

Hedden SC, Gido KB. 2020. Dispersal drives changes in fish community abundance in intermittent stream networks. *River Research and Applications* 36: 797–806.

Heino J, Melo AS, Siqueira T, Soininen J, Valanko S, Bini LM. 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. *Freshwater Biology* 60: 845–869.

Holmes EE, Ward EJ, Kellie W. 2012. MARSS: Multivariate autoregressive state-space models for analyzing time-series data. *R Journal*. 4: 11.

Huey JA, Schmidt DJ, Balcombe SR, Marshall JC, Hughes JM. 2011. High gene flow and metapopulation dynamics detected for three species in a dryland river system. *Freshwater Biology* 56: 2378–2390.

Hughes JM, Huey JA, Schmidt DJ. 2013. Is a realised connectivity among populations of aquatic fauna predictable from potential connectivity? *Freshwater Biology* 58: 951–966.

Hwan JL, Carlson SM. 2016. Fragmentation of an intermittent stream

during seasonal drought: Intra-annual and interannual patterns and biological consequences. *River Research and Applications* 32: 856–870.

Isaak DJ, et al. 2014. Applications of spatial statistical network models to stream data. *Wiley Interdisciplinary Reviews: Water* 1: 277–294.

Jabot F, Laroche F, Massol F, Arthaud F, Crabot J, Dubart M, Blanchet S, Munoz F, David P, Datry T. 2020. Assessing metacommunity processes through signatures in spatiotemporal turnover of community composition. *Ecology Letters* 23: 1330–1339.

Jaeger KL, et al. 2021. Beyond streamflow: Call for a national data repository of streamflow presence for streams and rivers in the United States. *Water* 13: 1627.

Jonsson N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. *Nordic Journal of Freshwater Research* 66: 20–35.

Judd M, Bond N, Horne AC. 2022. The challenge of setting "climate ready" ecological targets for environmental flow planning. *Frontiers in Environmental Science* 10: 21.

Kehr JM, Merritt DM, Stromberg JC. 2014. Links between primary seed dispersal, hydrochory and flood timing in a semi-arid region river. *Journal of Vegetation Science* 25: 287–300.

Kendy E, Apse C, Blann K. 2012. A Practical Guide to Environmental Flows for Policy and Planning. *Nature Conservancy*. www.conservationgateway.org/ConservationByGeography/NorthAmerica/UnitedStates/edc/Documents/ED_freshwater_envflows_Practical%20Guide%20Eflows%20for%20Policy.pdf

King AJ, Gawne B, Beesley L, Koehn JD, Nielsen DL, Price A. 2015. Improving ecological response monitoring of environmental flows. *Environmental Management* 55: 991–1005.

Koster WM, Dawson DR, Liu C, Moloney PD, Crook DA, Thomson JR. 2017. Influence of streamflow on spawning-related movements of golden perch *Macquaria ambigua* in south-eastern Australia. *Journal of Fish Biology* 90: 93–108.

Lake PS. 2011. *Drought and Aquatic Ecosystems: Effects and Responses*. Wiley.

Lamouroux N, Hauer C, Stewardson MJ, LeRoy Poff N. 2017. Physical habitat modeling and ecohydrological tools. Pages 265–285 in Horne AC, Webb JA, Stewardson MJ, Richter B Acreman M, eds. *Water for the Environment: From Policy and Science to Implementation and Management*. Academic Press.

Larsen S, et al. 2021a. The geography of metapopulation synchrony in dendritic river networks. *Ecology Letters* 24: 791–801.

Larsen S, Majone B, Zulian P, Stella E, Bellin A, Bruno MC, Zolezzi G. 2021b. Combining hydrologic simulations and stream-network models to reveal flow-ecology relationships in a large alpine catchment. *Water Resources Research* 57: e2020WR028496.

Lean J, Hammer MP, Unmack PJ, Adams M, Beheregaray LB. 2017. Landscape genetics informs mesohabitat preference and conservation priorities for a surrogate indicator species in a highly fragmented river system. *Heredity* 118: 374–384.

Legendre P, De Cáceres M. 2013. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. *Ecology Letters* 16: 951–963.

Leibold MA, et al. 2004. The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters* 7: 601–613.

Leibold MA, Chase JM. 2017. Metacommunity Ecology. *Monographs in Population Biology*, vol. 59. Princeton University Press.

Leibold MA, Rudolph FJ, Blanchet FG, De Meester L, Gravel D, Hartig F, Peres-Neto P, Shoemaker L, Chase JM. 2022. The internal structure of metacommunities. *Oikos* 2022: e08618.

Leprieur F, Hickey MA, Arbuckle CJ, Closs GP, Brosse S, Townsend CR. 2006. Hydrological disturbance benefits a native fish at the expense of an exotic fish. *Journal of Applied Ecology* 43: 930–939.

Lester RE, McGinness HM, Price AE, MacQueen A, Poff NL, Gawne B. 2020. Identifying multiple factors limiting long-term success in environmental watering. *Marine and Freshwater Research* 71: 238–254.

Logue JB, Mouquet N, Peter H, Hillebrand H. 2011. Empirical approaches to metacommunities: A review and comparison with theory. *Trends in Ecology and Evolution* 26: 482–491.

Lyon JP, Bird T, Tonkin Z, Raymond S, Sharley J, Hale R. 2021. Does life history mediate discharge as a driver of multi-decadal changes in populations of freshwater fish? *Ecological Applications* 31: e02430.

Lytle DA. 2003. Reconstructing long-term flood regimes with rainfall data: Effects of flood timing on caddisfly populations. *Southwestern Naturalist* 48: 36–42.

Lytle DA, Merritt DM, Tonkin JD, Olden JD, Reynolds LV. 2017. Linking river flow regimes to riparian plant guilds: A community-wide modeling approach. *Ecological Applications* 27: 1338–1350.

Magoulick DD, Kobza RM. 2003. The role of refugia for fishes during drought: A review and synthesis. *Freshwater Biology* 48: 1186–1198.

Marks JC, Haden GA, O'Neill M, Pace C. 2010. Effects of flow restoration and exotic species removal on recovery of native fish: Lessons from a dam decommissioning. *Restoration Ecology* 18: 934–943.

Marshall JC, Lobegeiger JS, Starkey A. 2021. Risks to fish populations in dryland rivers from the combined threats of drought and instream barriers. *Frontiers in Environmental Science* 9: 671556.

Mathews R, Richter BD. 2007. Application of the indicators of hydrologic alteration software in environmental flow setting. *JAWRA Journal of the American Water Resources Association* 43: 1400–1413.

McCoy AL, Holmes SR, Boisjolie BA. 2018. Flow restoration in the Columbia river basin: An evaluation of a flow restoration accounting framework. *Environmental Management* 61: 506–519.

McManamay RA, Bevelhimer MS, Frimpong EA. 2015. Associations among hydrologic classifications and fish traits to support environmental flow standards. *Ecohydrology* 8: 460–479.

McManamay RA, Jett RT, Ryon MG, Gregory SM, Stratton SH, Peterson MJ. 2016. Dispersal limitations on fish community recovery following long-term water quality remediation. *Hydrobiologia* 771: 45–65.

Melis TS, Walters CJ, Korman J. 2015. Surprise and opportunity for learning in Grand Canyon: The Glen Canyon dam adaptive management program. *Ecology and Society* 20: 26270262.

Merritt DM, Poff NLR. 2010. Shifting dominance of riparian *Populus* and *Tamarix* along gradients of flow alteration in western North American rivers. *Ecological Applications* 20: 135–152.

Mims MC, Olden JD. 2012. Life history theory predicts fish assemblage response to hydrologic regimes. *Ecology* 93: 35–45.

Morgan B, Asce M, Lane B. 2022. Accounting for uncertainty in regional flow–ecology relationships. *Journal of Water Resources Planning and Management* 148: 05022001.

Mouquet N, Loreau M. 2003. Community patterns in source-sink metacommunities. *American Naturalist* 162: 544–557.

Murray–Darling Basin Authority. 2018. Sustainable Diversion Limits. Murray–Darling Basin Authority. https://www.mdba.gov.au/water-use/water-limits/sustainable-diversion-limits.

Murray–Darling Basin Authority. 2020a. The Basin Plan 2020 Evaluation. Murray–Darling Basin Authority. https://www.mdba.gov.au/sites/default/files/publications/bp-eval-2020-full-report.pdf.

Murray–Darling Basin Authority. 2020b. Basin-Wide Environmental Watering Strategy, 2nd ed, revised. Murray–Darling Basin Authority. https://www.mdba.gov.au/sites/default/files/publications/basin-wide-environmental-watering-strategy-second-edition.

pdf.

Mussehl ML, Horne AC, Webb JA, Poff NL. 2022. Purposeful stakeholder engagement for improved environmental flow outcomes. *Frontiers in Environmental Science* 9: 749864.

Naman SM, Rosenfeld JS, Richardson JS. 2016. Causes and consequences of invertebrate drift in running waters: From individuals to populations and trophic fluxes. *Canadian Journal of Fisheries and Aquatic Sciences* 73: 1292–1305.

Nicol S, et al. 2021. Evaluating the ecological benefits of management actions to complement environmental flows in river systems. *Environmental Management* 67: 1–14.

Norton S, Storer T, Galvin L 2010. *Ecological Study of the Lower Canning River Environmental Water Releases*. Department of Water, Government of Western Australia.Water Science Technical Series report no. 35.

Obester AN, Lusardi RA, Santos NR, Peek RA, Yarnell SM. 2022. The use of umbrella fish species to provide a more comprehensive approach for freshwater conservation management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 32: 112–128.

O'Donnell EL, Garrick DE. 2017. Defining success: A multicriteria approach to guide evaluation and investment. Pages 625–645 in Horne AC, Webb JA, Stewardson MJ, Richter B Acreman M, eds. *Water for the Environment: From Policy and Science to Implementation and Management*. Academic Press.

O'Donnell EL, Horne AC, Godden L, Head B. 2019. Cry me a river: Building trust and maintaining legitimacy in environmental flows. *Australasian Journal of Water Resources* 23: 1–13.

Olden JD, Poff NL. 2003. Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. *River Research and Applications* 19: 101–121.

Olden JD, et al. 2014. Are large-scale flow experiments informing the science and management of freshwater ecosystems? *Frontiers in Ecology and the Environment* 12: 176–185.

Opperman JJ, Kendy E, Barrios E. 2019. Securing environmental flows through system reoperation and management: Lessons from case studies of implementation. *Frontiers in Environmental Science* 7: 104.

Ovaskainen O, Rybicki J, Abrego N. 2019. What can observational data reveal about metacommunity processes? *Ecography* 42: 1877–1886.

Owusu A, Mul M, van der Zaag P, Slinger J. 2022. May the odds be in your favor: Why many attempts to reoperate dams for the environment stall. *Journal of Water Resources Planning and Management* 148: 04022009.

Patrick CJ, Anderson KE, Brown BL, Hawkins CP, Metcalfe A, Saffarinia P, Siqueira T, Swan CM, Tonkin JD, Yuan LL. 2021. The application of metacommunity theory to the management of riverine ecosystems. *Wiley Interdisciplinary Reviews: Water* 8: e1557.

Pavlova A, et al. 2017. Severe consequences of habitat fragmentation on genetic diversity of an endangered Australian freshwater fish: A call for assisted gene flow. *Evolutionary Applications* 10: 531–550.

Peredo Arce A, Hörren T, Schletterer M, Kail J. 2021. How far can EPTs fly? A comparison of empirical flying distances of riverine invertebrates and existing dispersal metrics. *Ecological Indicators* 125: 107465.

Peres-Neto PR, Legendre P. 2010. Estimating and controlling for spatial structure in the study of ecological communities. *Global Ecology and Biogeography* 19: 174–184.

Peres-Neto PR, Legendre P, Dray P, Borcard D. 2006. Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology* 87: 2614–2625.

Perkin JS, Papraniku IF, Gibbs WK, Hoeinghaus DJ, Walker DM.

2021. Temporal trajectories in metacommunity structure: Insights from interdisciplinary research in intermittent streams. *WIREs Water* 8: e1531.

Peterson JT, Shea CP. 2015. An evaluation of the relations between flow regime components, stream characteristics, species traits, and meta-demographic rates of warm-water-stream fishes: Implications for aquatic resource management. *River Research and Applications* 31: 1227–1241.

Phillipsen IC, Lytle DA. 2013. Aquatic insects in a sea of desert: Population genetic structure is shaped by limited dispersal in a naturally fragmented landscape. *Ecography* 36: 731–743.

Poff NL. 2018. Beyond the natural flow regime? Broadening the hydro-ecological foundation to meet environmental flows challenges in a non-stationary world. *Freshwater Biology* 63: 1011–1021.

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime. *BioScience* 47: 769–784.

Poff NL, et al. 2010. The ecological limits of hydrologic alteration (ELOHA): A new framework for developing regional environmental flow standards. *Freshwater Biology* 55: 147–170.

Poff NL, Tharme RE, Arthington AH. 2017. Evolution of environmental flows assessment science, principles, and methodologies. Pages 203–236 in Horne AC, Webb JA, Stewardson MJ, Richter B Acreman M, eds. *Water for the Environment: From Policy and Science to Implementation and Management*. Academic Press.

Radinger J, Wolter C. 2014. Patterns and predictors of fish dispersal in rivers. *Fish and Fisheries* 15: 456–473.

Ramos V, Formigo N, Maia R. 2018. Environmental flows under the WFD implementation. *Water Resources Management* 32: 5115–5149.

Rayner TS, Jenkins KM, Kingsford RT. 2009. Small environmental flows, drought and the role of refugia for freshwater fish in the Macquarie Marshes, arid Australia. *Ecohydrology* 2: 440–453.

Reinfelds I, Lincoln-Smith M, Haeusler T, Ryan D, Growns I. 2010. Hydraulic assessment of environmental flow regimes to facilitate fish passage through natural riffles: Shoalhaven river below Tallowa Dam, New South Wales, Australia. *River Research and Applications* 26: 589–604.

Riato L, Hill RA, Herlihy AT, Peck DV, Kaufmann PR, Stoddard JL, Paulsen SG. 2022. Genus-level, trait-based multimetric diatom indices for assessing the ecological condition of rivers and streams across the conterminous United States. *Ecological Indicators* 141: 109131.

Rolls RJ, Leigh C, Sheldon F. 2012. Mechanistic effects of low-flow hydrology on riverine ecosystems: Ecological principles and consequences of alteration. *Freshwater Science* 31: 1163–1186.

Rolls RJ, Growns IO, Khan TA, Wilson GG, Ellison TL, Prior A, Waring CC. 2013. Fish recruitment in rivers with modified discharge depends on the interacting effects of flow and thermal regimes. *Freshwater Biology* 58: 1804–1819.

Rolls RJ, Heino J, Ryder DS, Chessman BC, Growns IO, Thompson RM, Gido KB. 2018. Scaling biodiversity responses to hydrological regimes. *Biological Reviews* 93: 971–995.

Ron R, Fragman-Sapir O, Kadmon R. 2018. Dispersal increases ecological selection by increasing effective community size. *Proceedings of the National Academy of Sciences* 115: 11280–11285.

Ross A, Connell D. 2016. The evolution and performance of river basin management in the Murray–Darling Basin. *Ecology and Society* 21: 26269970.

Ruhí A, Datry T, Sabo JL. 2017. Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. *Conservation Biology* 31: 1459–1468.

Ruhí A, Dong X, McDaniel CH, Batzer DP, Sabo JL. 2018. Detrimental

effects of a novel flow regime on the functional trajectory of an aquatic invertebrate metacommunity. *Global Change Biology* 24: 3749–3765.

Ruhí A, Catford JA, Cross WF, Escoriza D, Olden JD. 2019. Understanding the nexus between hydrological alteration and biological invasions. Pages 45–64 in Sabater S, Elosegi A, Ludwig R, eds. *Multiple Stressors in River Ecosystems: Status, Impacts, and Prospects for the Future.* Elsevier.

Ryman N, Laikre L. 1991. Effects of supportive breeding on the genetically effective population size. *Conservation Biology* 5: 325–329.

Sarremejane R, Cañedo-Argüelles M, Prat N, Mykrä H, Muotka T, Bonada N. 2017a. Do metacommunities vary through time? Intermittent rivers as model systems. *Journal of Biogeography* 44: 2752–2763.

Sarremejane R, Mykrä H, Bonada N, Aroviita J, Muotka T. 2017b. Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. *Freshwater Biology* 62: 1073–1082.

Sarremejane R, et al. 2020. DISPERSE: A trait database to assess the dispersal potential of European aquatic macroinvertebrates. *Scientific Data* 7: 386.

Sarremejane R, Stubbington R, England J, Sefton CEM, Eastman M, Parry S, Ruhí A. 2021. Drought effects on invertebrate metapopulation dynamics and quasi-extinction risk in an intermittent river network. *Global Change Biology* 27: 4024–4039.

Schramm MP, Bevelhimer MS, DeRolph CR. 2016. A synthesis of environmental and recreational mitigation requirements at hydropower projects in the United States. *Environmental Science and Policy* 61: 87–96.

Scoppettone GG, Rissler PH, Fabes MC, Shea SP. 2015. Population dynamics of the Cui-ui of Pyramid Lake, Nevada: A potamodromous catostomid subject to failed reproduction. *North American Journal of Fisheries Management* 35: 853–864.

Sefton CEM, Parry S, England J, Angell G. 2019. Visualising and quantifying the variability of hydrological state in intermittent rivers. *Fundamental and Applied Limnology* 193: 21–38.

Siqueira T, et al. 2020. Community size can affect the signals of ecological drift and niche selection on biodiversity. *Ecology* 101: e03014.

Souchon Y, et al. 2008. Detecting biological responses to flow management: Missed opportunities: Future directions. *River Research and Applications* 24: 506–518.

Stefferud JA, Gido KB, Propst DL. 2011. Spatially variable response of native fish assemblages to discharge, predators and habitat characteristics in an arid-land river. *Freshwater Biology* 56: 1403–1416.

Stein ED, Sengupta A, Mazor RD, McCune K, Bledsoe BP, Adams S. 2017. Application of regional flow-ecology relationships to inform watershed management decisions: Application of the ELOHA framework in the San Diego River watershed, California, USA. *Ecohydrology* 10: e1869.

Stewardson MJ, Shang W, Kattel GR, Webb JA 2017. Environmental water and integrated catchment management. Pages 519–536 in Horne AC, Webb JA, Stewardson MJ, Richter B Acreman M, eds. *Water for the Environment: From Policy and Science to Implementation and Management.* Academic Press.

Stewardson MJ, Guarino F. 2018. Basin-scale environmental water delivery in the Murray–Darling, Australia: A hydrological perspective. *Freshwater Biology* 63: 969–985.

Stocks JR, Davis S, Anderson MJ, Asmus MW, Cheshire KJM, van der Meulen DE, Walsh CT, Gilligan DM. 2021. Fish and flows: Abiotic drivers influence the recruitment response of a freshwater fish community throughout a regulated lotic system of the Murray–Darling Basin. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 3228–3247.

Stoffels RJ, Robert Clarke K, Linklater DS, Rick Stoffels CJ, Murray–Darling T. 2015. Temporal dynamics of a local fish community are strongly affected by immigration from the surrounding metacommunity. *Ecology and Evolution* 5: 200–212.

Stoffels RJ, Rehwinkel RA, Price AE, Fagan WF. 2016. Dynamics of fish dispersal during river-floodplain connectivity and its implications for community assembly. *Aquatic Sciences* 78: 355–365.

Stoll S, Sundermann A, Lorenz AW, Kail J, Haase P. 2013. Small and impoverished regional species pools constrain uciusation of restored river reaches by fishes. *Freshwater Biology* 58: 664–674.

Taylor MK, Cooke SJ. 2012. Meta-analyses of the effects of river flow on fish movement and activity. *Environmental Reviews* 20: 211–219.

Thiem JD, et al. 2021. Contrasting natal origin and movement history informs recovery pathways for three lowland river species following a mass fish kill. *Marine and Freshwater Research* 73: 237–246.

Thompson PL, Guzman LM, De Meester L, Horváth Z, Ptacnik R, Vanschoenwinkel B, Viana DS, Chase JM. 2020. A process-based metacommunity framework linking local and regional scale community ecology. *Ecology Letters* 23: 1314–1329.

Tickner D, et al. 2020. Bending the curve of global freshwater biodiversity loss: An emergency recovery plan. *BioScience* 70: 330–342.

Tonkin JD, Jähnig SC, Haase P. 2014a. The rise of riverine flow-ecology and environmental flow research. *Environmental Processes* 1: 323–330.

Tonkin JD, Stoll S, Sundermann A, Haase P. 2014b. Dispersal distance and the pool of taxa, but not barriers, determine the uciusation of restored river reaches by benthic invertebrates. *Freshwater Biology* 59: 1843–1855.

Tonkin JD, Olden JD, Merritt DM, Reynolds LV, Rogosch JS, Lytle DA. 2021. Designing flow regimes to support entire river ecosystems. *Frontiers in Ecology and the Environment* 19: 326–333.

US Fish and Wildlife Service. 2020. Species Status Assessment Report for the Colorado Pikeminnow *Ptychocheilus lucius*. US Fish and Wildlife Service. www.fws.gov/sites/default/files/documents/Colorado_Pikeminnow-PeerReviewPlan_508.pdf.

Valente-Neto F, Durães L, Siqueira T, Roque FO. 2018. Metacommunity detectives: Confronting models based on niche and stochastic assembly scenarios with empirical data from a tropical stream network. *Freshwater Biology* 63: 86–99.

Vellend M. 2010. Conceptual synthesis in community ecology. *Quarterly Review of Biology* 85: 183–206.

Viana DS, Chase JM. 2019. Spatial scale modulates the inference of metacommunity assembly processes. *Ecology* 100: e02576.

Warren ML, Pardew MG. 1998. Road crossings as barriers to small-stream fish movement. *Transactions of the American Fisheries Society* 127: 637–644.

Warton DI, Blanchet FG, O'Hara RB, Ovaskainen O, Taskinen S, Walker SC, Hui FKC. 2015. So many variables: Joint modeling in community ecology. *Trends in Ecology and Evolution* 30: 766–779.

Watts RJ, Bond NR, Grace MR, Healy S, Howitt JA, Liu X, McCasker NG, Thiem JD, Trethewie JA, Wright DW. 2019. *Commonwealth Environmental Water Office Long Term Intervention Monitoring Project: Edward/Kolety-Wakool River System Selected Area Technical Report 2018–19.* Commonwealth Environmental Water Office, Commonwealth of Australia.

Webb JA, et al. 2010. Negotiating the turbulent boundary: The

challenges of building a science–management collaboration for landscape-scale monitoring of environmental flows. *Marine and Freshwater Research* 61: 798–807.

Webb JA, Watts RJ, Allan C, Warner AT. 2017. Principles for monitoring, evaluation, and adaptive management of environmental water regimes. Pages 599–623 in Horne AC, Webb JA, Stewardson MJ, Richter B, Acreman M, eds. *Water for the Environment: From Policy and Science to Implementation and Management*. Academic Press.

Wright D, Thiem J, Blackman E, Beatty S, Lymbery A, Davis S. 2022. Desiccation tolerance of river and floodplain mussels in the Murray–Darling Basin. *NSW DPI Technical Report to the Commonwealth Environmental Water Office*. www.dcceew.gov.au/sites/default/files/documents/desiccation-tolerance-river-floodplain-mussels-murray-darling-basin.pdf.

Yarnell SM, Stein ED, Webb JA, Grantham T, Lusardi RA, Zimmerman J, Peek RA, Lane BA, Howard J, Sandoval-Solis S. 2020. A functional flows approach to selecting ecologically relevant flow metrics for environmental flow applications. *River Research and Applications* 36: 318–324.

Yu S, Rose PM, Bond NR, Bunn SE, Kennard MJ. 2022. Identifying priority aquatic refuges to sustain freshwater biodiversity in intermittent streams in eastern Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems* 32: 1584–1595.

Zampatti BP, et al. 2021. Population demographics of golden perch (*Macquaria ambigua*) in the Darling River prior to a major fish kill: A guide for rehabilitation. *Marine and Freshwater Research* 73: 223–236.