

Designing flow regimes to support entire river ecosystems

Jonathan D Tonkin^{1,2*}, Julian D Olden³, David M Merritt⁴, Lindsay V Reynolds⁴, Jane S Rogosch^{3†}, and David A Lytle²

Overcoming challenges of water scarcity necessitates creative flow management approaches that account for multiple, potentially competing water needs of plants and animals in river ecosystems. Mechanistic multispecies models can guide decision making by evaluating trade-offs associated with flow regimes designed for specific ecosystem outcomes before implementation. We investigated the cross-ecosystem effects of environmental flow regimes designed to benefit focal groups of riparian vegetation, fishes, and invertebrates. The models revealed trade-offs among different designer flow regimes with narrow taxonomic targets, which in some cases caused non-target taxa to become locally extirpated within short (decadal) timespans. By incorporating multiple flow frequencies – from intra-annual-scale pulses to large decadal-scale floods – the simulated natural flow regime enabled balanced, albeit smaller, population sizes across the three ecosystem components: 72% of that achieved by designer flow regimes, on average. Although returning to a natural flow regime may not be possible in highly flow-modified rivers, novel flow regimes must incorporate diverse flood and drought frequencies to accommodate the occasionally conflicting requirements of different taxa at different times.

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Dams and other types of human infrastructure have modified river hydrology globally and continue to do so at an unprecedented rate (Grill *et al.* 2019). Alteration of river flows comes at a major cost for biota inhabiting freshwater and riparian (hereafter “river”) ecosystems (Bunn and Arthington 2002; Tonkin *et al.* 2018), threatening the countless ecosystem services they provide (Auerbach *et al.* 2014). Maintaining functional river ecosystems under uncertain hydroclimatic futures presents a major management challenge for both existing and planned dam projects (Horne *et al.* 2019; Palmer and Ruhí 2019; Tonkin *et al.* 2019), requiring the consideration of flow prescriptions that target the health of downstream ecosystems (Acreman *et al.* 2014).

Environmental flows are increasingly used to help minimize the detrimental effects of dam management on river biota (Poff and Matthews 2013; Yarnell *et al.* 2015). Designer environmental flows range from single events designed to achieve a specific goal, such as a flood for mobilizing sediment, to entire flow regimes designed to accommodate multiple ecosystem needs (Acreman *et al.* 2014). Although increasing attention has focused on trade-offs between ecosystem and multiple human needs (domestic, agriculture, hydropower) in flow designs (eg Chen and Olden 2017; Sabo *et al.* 2017;

Tickner *et al.* 2017), the large majority of these management decisions are based on a narrow perspective of the ecosystem.

In practice, most environmental flow programs target a few important species or a particular component of the river ecosystem, such as recruitment of riparian vegetation or spawning of native fish (Olden *et al.* 2014), without directly considering secondary effects on other components of the ecosystem. For instance, a flow regime designed to maximize fish abundance or diversity may have unintended less beneficial, or even detrimental, effects for native riparian plants. This presents the question: does flow management designed to benefit one important component of the river ecosystem simultaneously protect other components, or does it involve ecological trade-offs that compromise other ecosystem components? In reality, such trade-offs are hard to avoid, but their magnitude will likely depend on the specific target of the management action.

Despite growing demand for holistic ecosystem approaches to support sustainable riverine management, robust quantitative models to underpin such efforts remain scarce. Here, we examined the responses to designer flows targeting three ubiquitous but distinct components of river ecosystems: riparian vegetation, fishes, and aquatic invertebrates. Using a mechanistic, multispecies modeling approach that links population dynamics and hydrology (WebTable 1), we designed flow regimes to maximize management outcomes for specific targets within each of the three ecosystem components: a riparian tree (cottonwood, *Populus deltoides*), native freshwater fishes, and terrestrially available aquatic invertebrates. These flow regimes had characteristic flow event frequencies ranging across intra-annual to decadal scales. The modeling approach permitted us to simultaneously design flow regimes

¹School of Biological Sciences, University of Canterbury, Christchurch, New Zealand (*jonathan.tonkin@canterbury.ac.nz); ²Department of Integrative Biology, Oregon State University, Corvallis, OR; ³School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA; [†]current address: Missouri Cooperative Fish and Wildlife Research Unit, School of Natural Resources, University of Missouri, Columbia, MO; ⁴Watershed, Fisheries, Wildlife, Air and Rare Plants Staff and the National Stream and Aquatic Ecology Center, US Department of Agriculture Forest Service, Fort Collins, CO

for a single ecosystem component as well as quantify the associated synergies or trade-offs across other ecosystem components. These approaches enable an assessment of the potential ecological benefits or deficits of designer flow prescriptions for whole river ecosystems.

■ Methods

Management targets

Using species common to the Colorado River Basin of the southwestern US, we defined management targets that natural resource managers often seek to maximize downstream from large dams. These outcomes relate to three components of river ecosystems: cottonwood tree coverage as a percent of riparian carrying capacity, native fish species biomass as a percent of total carrying capacity (including non-native fishes), and abundance of terrestrially available benthic invertebrates (hereafter “aquatic invertebrates”). Cottonwood is an important native riparian tree that anchors riverbanks, contributes carbon to streams, and provides a range of structurally rich habitats that support diverse communities, but also suffers from the effects of flow regime modification and competition with non-natives like tamarisk (*Tamarix* spp; Merritt and Poff 2010). Native fish species are a focal management target because they provide critical ecosystem services including food-web regulation, food security, recreation, and nutrient cycling, but also face an uncertain future resulting from altered hydrology and impacts from non-native species (Chen and Olden 2017). Terrestrially available aquatic invertebrates serve as aquatic prey for fish and, upon emergence as winged adults, as terrestrial prey for birds, bats, lizards, and other riparian animals (Baxter *et al.* 2005). Using these targets, coupled with mechanistic population models, we identified flow regimes that maximized the value of each target ecosystem component and explored trade-offs in achieving positive outcomes across all three components (both target and non-target) by projecting the flow time-series for up to 200 years into the future. Detailed methods are presented in WebPanel 1.

Modeling frameworks

We modeled the three ecosystem components using three independent existing models parameterized with empirical data. Riparian vegetation and fishes were modeled using coupled, stage-structured matrix population models projected at annual time steps (Lytle *et al.* 2017; Rogosch *et al.* 2019). Informed by empirical data from a variety of sources, these “matrix community models” link the flow regime directly with population dynamics in a framework that enables an understanding of whole-community dynamics and can incorporate stochasticity by taking random draws from a sequence of river flow year types. Floods and droughts interact with vital rates, affecting

population sizes, which opens vacant space (vegetation) or biomass (fish) for recruitment during the next year if conditions are met. Both models have demonstrated a strong ability to recover known patterns on the landscape via tests against empirical data (Lytle *et al.* 2017; Rogosch *et al.* 2019).

The plant community comprised five taxa with six stage classes from seedling to reproductive adult: cottonwood (*P. deltoides*), tamarisk (*Tamarix ramosissima*), sandbar willow (*Salix exigua*), meadow grasses, and big sagebrush (*Artemisia tridentata*). These taxa are representative of dominant groups across dryland regions. The fish community consisted of seven species, each with three stage classes. Three of the species are native to the US Southwest: desert sucker (*Catostomus clarkii*), Sonora sucker (*Catostomus insignis*), and roundtail chub (*Gila robusta*); the remaining four are non-native: yellow bullhead (*Ameiurus natalis*), green sunfish (*Lepomis cyanellus*), small-mouth bass (*Micropterus dolomieu*), and red shiner (*Cyprinella lutrensis*).

Benthic invertebrates, which experience population dynamics at intra-annual timescales, were modeled using a form of the continuous logistic growth model that enables carrying capacity (K) to fluctuate through time (McMullen *et al.* 2017). Carrying capacity, in this case, responds to flood events. For flood-adapted species, carrying capacity is highest immediately post-flood. The magnitude of a flood pulse determines the magnitude of change in K , and this relationship can be modeled for events of any magnitude and for multiple, repeated events. Unlike the fish and riparian plant models, this model operates on individual populations in that the populations do not share a finite resource such as space or biomass; each population has its own carrying capacity. As representatives of a diverse range of aquatic invertebrate life histories, we modeled three invertebrate taxa: a fast life-cycle, flood-adapted mayfly (*Fallceon* spp, Ephemeroptera: Baetidae); a slow life-cycle, flood-adapted dragonfly (*Progomphus* spp, Odonata: Gomphidae); and a flood-averse ostracod seed shrimp (Crustacea: Ostracoda) (see WebPanel 1). In addition, the mayfly and dragonfly are important resources in both aquatic and terrestrial food webs owing to their aerial adult stages. Our management scenario objective was to maximize the mayfly and dragonfly population sizes, and minimize that of the ostracod.

Vital rates for all species included in the models were obtained from independent sources in the literature and from field studies (see WebPanel 1 for details). Vital rates included stage-specific mortality rates in response to flow events for fish and riparian plants, and population growth rates and flow-specific mortality rates for aquatic invertebrates.

Hydrograph details

Both the designer and natural flow regime scenarios followed the same modeling procedure. For the designer flow regimes, we generated a flow regime that maximized each target

ecosystem component. These simulations, based on parameterizations from biological field data, represent a river modeled after a generalized tributary of the Colorado River (see “Flow design” section below). We also compared the outcome of these designer flows to those based on a natural flow regime scenario. The natural flow regime scenario was generated from a real hydrograph derived from a large free-flowing river supporting riparian vegetation, fish, and aquatic invertebrate components (upper Verde River, Arizona). To do this, we sourced a 45-year (1964–2008) historical hydrograph from the upper Verde River (US Geological Survey gauge #09503700) near Paulden, Arizona. All three groups were modeled from this one central flow regime in our natural flow regime scenario, enabling a comparison of community dynamics across the whole ecosystem. We then quantified the community-wide population responses to each flow regime (three designer flows and a natural flow) across ecosystem components (Figure 1). For details of conversion of the hydrograph for each model, see WebPanel 1.

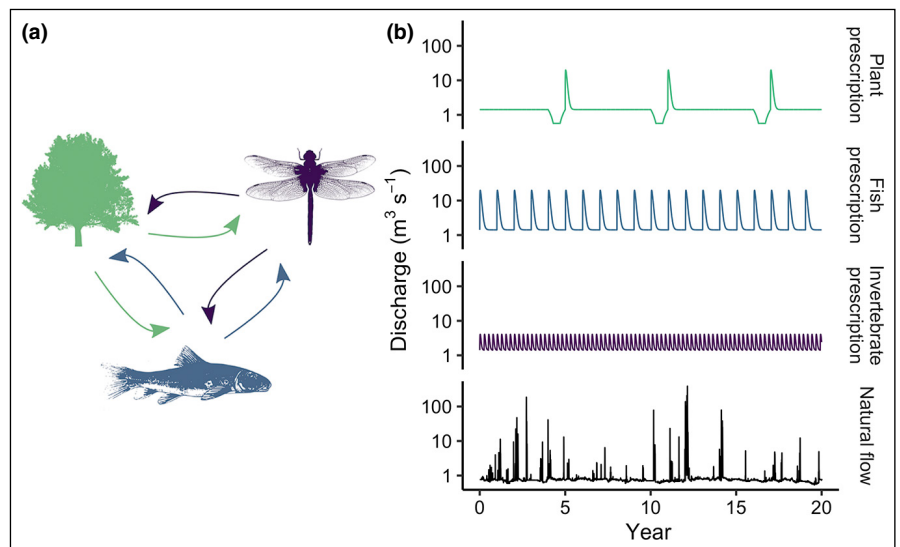


Figure 1. The modeled ecosystem components and flow regimes. (a) The three ecosystem components examined: riparian plants (target: % cottonwoods), fish (target: % native species), and aquatic invertebrates (target: % terrestrially available taxa). Arrows represent potential trade-offs associated with specific flow prescriptions. (b) A schematic of the three flow regimes designed for each target ecosystem component. We searched flow parameter space for optimal sequences of flow events that maximized each of the management targets. The plant and fish models are based on year-types and the invertebrate model responds to individual flow events, and therefore the “hydrographs” are for visual purposes only (eg the plant prescription shows a single large flood event every 6 years, preceded by a drought year). The bottom panel represents the historical hydrograph taken from the upper Verde River, in Arizona. Note the logarithmic scale on the y-axis.

Flow design

We searched flow parameter space for optimal sequences of flow events that maximized each of the management targets associated with riparian plants, native fishes, and aquatic invertebrates (see WebPanel 1). This approach was based on constrained, systematic optimization for point optima. Although our flow design approach focused on modifying the frequency of different events or year-types, each model incorporated various other components of a flow regime, including magnitude, timing, rate of change, and duration of flow events (Lytle *et al.* 2017; McMullen *et al.* 2017; Rogosch *et al.* 2019).

The approach to flow design differed for the three ecosystem components. For riparian plants and fishes, the search for an optimal flow design followed a series of steps that incrementally adjusted the frequency of particular year-types. The resulting prescribed flow regime for riparian vegetation consisted of a spring flood every 6 years, preceded by a drought year, with a series of non-event years in between (WebTable 1). These floods occurred within the spring window that enabled cottonwood and tamarisk to recruit (synchronized with seed release). The resulting prescribed flow regime for native fish consisted of a spring flood every year. In contrast to the plant and fish models, the invertebrate model operated in continuous time. Because the aquatic invertebrates we modeled do not compete directly with one another for a resource, such as space

or food, we modeled the three taxa independently so that each species had its own carrying capacity, which we scaled to 100. We sought to maximize the average value of the two terrestrially available target taxa (ie % of K) over the 20-year evaluation period. The resulting scenario that maximized the target was four small pulses per year, below the threshold of a flood in either the fish or riparian models. Therefore, the invertebrate prescription resulted in 100% of years being non-event years for the fish and riparian vegetation.

Results and discussion

We identified specific flow regimes that were highly beneficial to populations of each targeted ecosystem component – cottonwoods, native fishes, and aquatic invertebrates – by maximizing their average population sizes through time (Figures 1 and 2; WebFigures 1–3). These designer flow regimes, optimized separately for each ecosystem target, always outperformed the historical natural regime for the intended ecosystem component, suggesting that artificially imposed flow regimes can in some instances generate greater population sizes than the natural flow regime. This finding is consistent with modeling studies targeting native fish abundance in the San Juan River (US), fisheries yield in the Mekong River Basin (Southeast Asia), and cottonwood population dynamics in the Yampa

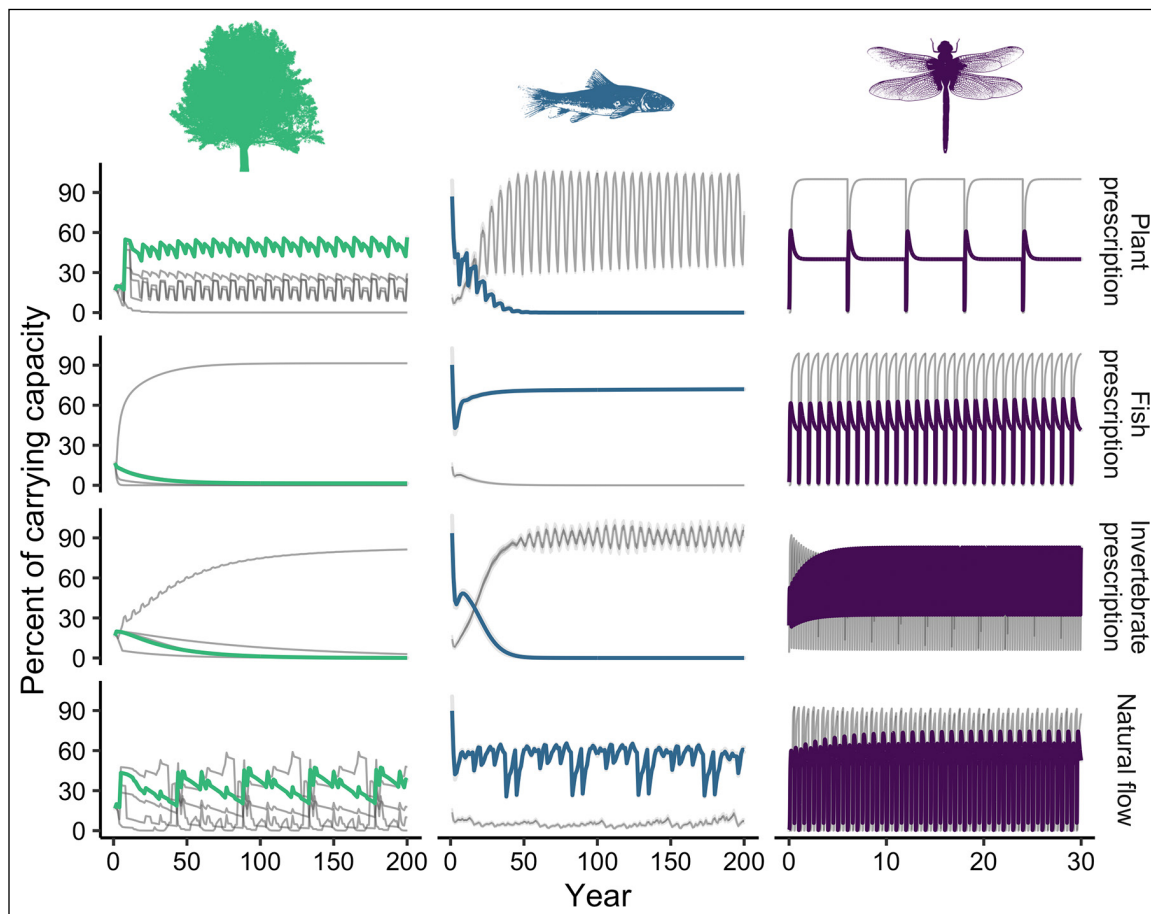


Figure 2. Results of simulations for target and non-target taxa, both within and among ecosystem components. Target taxa (plants: % cottonwoods; fish: % native species; invertebrates: % terrestrially available taxa) are shown as the colored lines and non-target taxa as gray. For plants, the four gray lines represent the four non-target plant taxa individually. For fish, the single gray line represents the four non-native fish species combined (the band around the line represents two standard errors around the mean of 100 iterations). For invertebrates, the gray line represents the non-target taxon (ostracods). See WebFigures 1–3 for full results. Model evaluation (eg Figure 3) discarded the first 10 years as a burn-in period.

River basin (US) (Chen and Olden 2017; Lytle *et al.* 2017; Sabo *et al.* 2017).

However, our results suggested that a narrow management focus on a single taxonomic group, as is commonly the case for environmental flow efforts, might come at a cost for other components of the ecosystem (Figure 3; WebFigure 4). Each scenario had at least one major losing ecosystem component: cottonwoods declined in the fish-prescribed flows (7% of natural flow %K), native fish abundance declined in the vegetation-prescribed flows (5% of natural flow %K), and both cottonwoods (10% of natural flow %K) and native fishes (6% of natural flow %K) declined in the invertebrate-prescribed flows. Thus, major ecological deficits appear to accompany environmental flow regimes that target a single ecosystem outcome.

Each designer flow regime had a characteristic temporal frequency, reflecting the varying biology of the three ecosystem components: approximately decadal or half-decadal timescale flow events for riparian vegetation, annual or near-annual for fishes, and intra-annual for invertebrates (Figures 1 and 2; WebTable 1). Cottonwood thrives under regimes with

large recruitment floods approximately every 6 years followed by growth years (ie non-event years), with a drought year included to limit population growth of drought-intolerant competitor species (Lytle *et al.* 2017). Native fishes prosper under flow regimes with more frequent and reliable (ie annual) spawning floods and no drought (Rogosch *et al.* 2019). Bigger floods are therefore beneficial for vegetation and fishes, but the timescale of response differs. In contrast, the pulses required for maintaining aquatic invertebrates are insufficiently large to exert a positive benefit for native fishes or cottonwood; this taxonomic group responds best to flow regimes comprising many regular small pulses to maintain shallow riffle habitat. Without regular small pulses (larger pulses may also be incorporated), slower-water specialist invertebrates, many of which do not have a terrestrial lifecycle phase, become dominant (McMullen *et al.* 2017). In summary, various temporal frequencies are therefore fundamental aspects of a flow regime designed for the benefit of an entire ecosystem – a characteristic of the historical natural flow regime that is essential for the vitality of rivers (Figure 1; Poff *et al.* 1997; Naiman *et al.* 2008; Tonkin *et al.* 2019). Administering such ecosystem-level

designer flows may be challenging if single sensitive (threatened, endangered, or red listed) species provide the impetus (legal mandate) for implementation of designer flows.

Contrary to the designer flow regimes, the natural flow regime scenario resulted in species persistence for all ecosystem components, although population sizes were never as large as those achievable under designer flow regimes (vegetation: 66% of designer flow; fishes: 77%; invertebrates: 72%; Figures 2 and 3). We attribute this to the fact that most natural flow regimes exhibit an array of hydrologic events at multiple temporal frequencies (from intra-annual to interdecadal), thereby satisfying the ecological needs of diverse biological groups with often-conflicting requirements (Figures 1 and 2). Most dam operations fail to provide this diverse portfolio of flows that are important for recruitment, migration, spawning, and juvenile rearing across a broad array of taxa (Palmer and Ruhí 2019). Organisms have evolved life histories to capitalize on natural cycles of flooding and drought (Lytle and Poff 2004) (Figure 4). However, the evolutionary fine-tuning, and potential for rapid evolution, of entire ecosystems to the natural flow regime remains an important topic of inquiry, as does the interaction among the different ecosystem components that we have yet to consider (eg invertebrates are a food source for fish, plants provide organic matter for invertebrates). Maintaining these cycles is fundamental to the maintenance of diverse and resilient communities into the future (Tonkin *et al.* 2018). Flooding also plays a critical role in maintaining functional river geomorphology by creating and maintaining critical off-channel habitats, and mobilizing sediment, woody debris, and essential nutrients (Yarnell *et al.* 2015). Whether maintaining such variability is possible with environmental flows remains to be seen given the rapidly shifting state of river flows worldwide (Poff and Olden 2017; Poff 2018; Tonkin *et al.* 2019).

Interannual variability in flows supported by natural flow regimes facilitates the persistence of multiple species across diverse taxonomies (Figure 2). Simply put, some flows benefit particular suites of species in certain years to the detriment of others, but gains made during these periods enable their perseverance and coexistence with other species, often through unfavorable periods, over long timescales (Ruhí *et al.* 2016; Tonkin *et al.* 2017). Through time, the full dynamism of river hydrology accommodates higher temporal diversity, emphasizing the importance of taking a functional whole-regime approach to designing and prescribing environmental flows

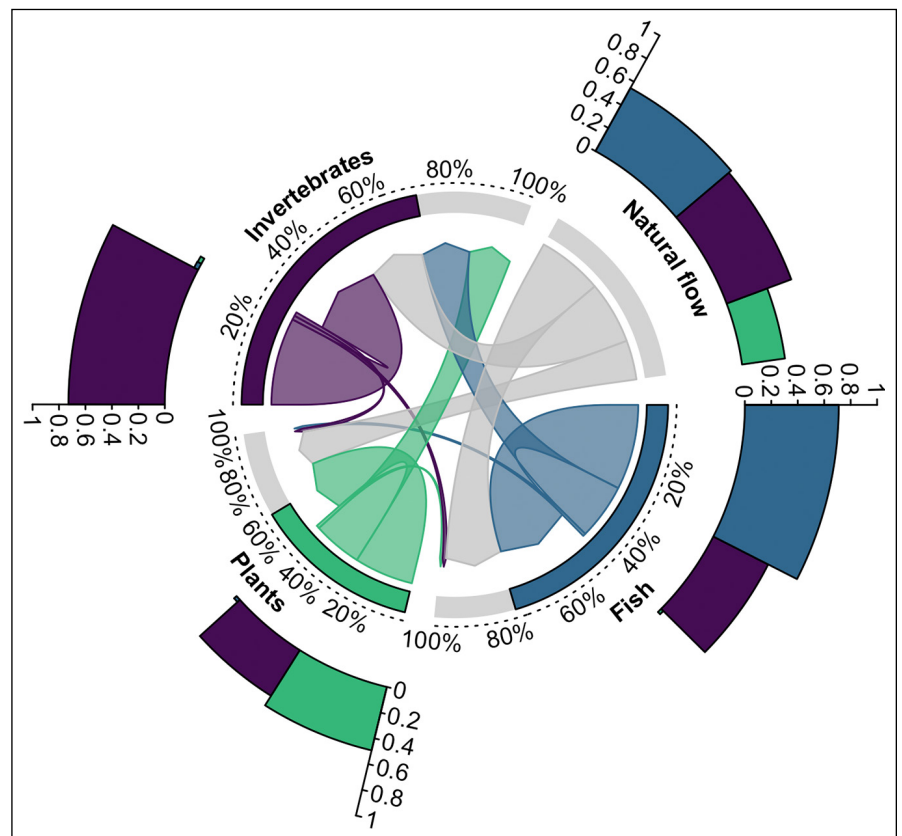


Figure 3. The ecosystem-wide effects of designer and natural flow regimes. Each of the four figure sectors represents a particular flow regime and/or ecosystem component: the natural flow regime and three designer flow regimes (riparian vegetation, fishes, and invertebrates). The effects of designer flow regimes on each component are shown, both targeted (arrow returns to same figure sector; eg fish to fish) and non-targeted (arrow from one sector to another; eg fish to plants), as well as the natural flow regime. Arrow widths correspond to the relative effects of a particular flow scenario (source of arrow) on all other components (arrow endpoint; larger widths equal more positive responses). These values are shown as proportions of maximum in the outermost bars (1 = maximum; eg native fish biomass at 100% of carrying capacity). For instance, when designing flows to most benefit native fishes, fish respond strongly (large arrow and outer bar) but plants perform poorly (small arrow and outer bar). The inner bar (tracking the circumference of the center arrows) represents the difference between the natural and prescribed flow for the group in that sector (given in percentage). For example, under the natural flow regime, fish achieve 77% of the biomass achieved under the designer flow.

(Yarnell *et al.* 2015). In long-lived species, such as riparian vegetation, desired outcomes may only manifest in response to flow prescriptions that operate over multiple years or decades. In summary, plants and animals are committed to long-term flow regimes, and humans similarly need to be committed to long-term flow management.

The mechanisms that produced undesired non-target outcomes were specific to each ecosystem component. For fishes, native species were projected to become locally extirpated within approximately 50 years due to a complete lack of flood recruitment events reflected in the invertebrate flow prescription, or a combination of droughts with too-infrequent flood events reflected in the riparian flow prescription, both of which allowed non-native fishes to dominate the community



Figure 4. The Virgin River in Zion Canyon, Utah, which enters the Colorado River at Lake Mead. The Virgin River comprises diverse riparian, fish, and invertebrate assemblages similar to those used in the present analysis, many of which have evolved life histories to capitalize on natural cycles of flooding and drought. Fremont cottonwood (*Populus fremontii*) and sand-bar willow (*Salix exigua*) are visible in the active riparian zone. Fishes in the basin include the native desert sucker (*Catostomus clarkii*) (and other native sucker and chub species), as well as the non-native red shiner (*Cyprinella lutrensis*) and green sunfish (*Lepomis cyanellus*), and related bullhead catfish and bass species.

(Figure 2; WebFigure 2). This finding is supported by empirical research in the US Southwest (Ruhí *et al.* 2016; Chen and Olden 2017; Rogosch *et al.* 2019). Cottonwoods collapsed in response to native fish-prescribed flows due to phreatophytic, flood-tolerant willow species dominating at high flood frequencies. In response to a lack of recruitment flood events under the invertebrate flow prescription, cottonwoods were replaced by non-riparian upland species such as sagebrush (Figure 2; WebFigure 1), representing a loss of riparian trees and shrubs that comprise essential and high-quality habitat for diverse terrestrial fauna (Merritt and Bateman 2012). The target invertebrates exhibited much greater fluctuations in population abundance than fish or vegetation (Figure 2; WebFigure 3). Both the fish and riparian prescriptions did not meet the needs of the aquatic invertebrates due to a lack of regularly spaced pulses required to maintain open habitat for the two target taxa: the flood-resilient mayfly (*Fallceon* spp) and flood-resistant dragonfly (*Progomphus* spp) (McMullen

et al. 2017). These clear trade-offs reflect situations where flows are targeted not for an entire community response (eg community evenness), but a specific component of each community. Different outcomes may be apparent with alternative ecological targets, but the important implication of this research is that narrowly targeting individual ecological outcomes with specific flows may have broader ecosystem-wide negative impacts.

Different frequencies of response to flows among taxa present unique challenges when setting out to optimally manage rivers in an environmental flows context. Experimental flood programs have in some cases demonstrated benefits to non-target ecosystem components (eg River Spöl, Switzerland [Robinson *et al.* 2018]; Bill Williams River, US [Shafroth *et al.* 2010]). However, the potential ecosystem-wide impacts of narrowly prescribed flow regimes emphasize the need to consider entire ecosystems as the ultimate management goal, rather than focus on single physical (eg sediment) or biological (eg fish) outcomes (Olden *et al.* 2014). Considering whole-ecosystem integrity will inevitably require mimicking some functional components of natural hydrologic variability (Yarnell *et al.* 2015) – most notably the presence of multiple frequencies and magnitudes of flow events over extended timescales – while minimizing unnatural frequencies like daily hydropowering (Kennedy *et al.* 2016). However, hydroclimatic nonstationarity, where the envelope of variability in which a river flow regime fluctuates no longer remains fixed (Milly *et al.* 2008), means returning to the inherently dynamic natural flow regime as a management target may no longer be the most beneficial option (Acreman *et al.* 2014; Poff 2018; Tonkin *et al.* 2019). Overcoming the physical limits of dam operations under nonstationarity therefore requires creative approaches to flow management (Poff and Olden 2017) and a coherent modeling approach that forecasts the effects of management actions on multiple ecosystem components simultaneously.

The unprecedented magnitude at which river flows are being altered across the developing world, combined with the already large proportion of dammed rivers in the developed world, puts into question the long-term sustainability of freshwater ecosystems (Poff and Matthews 2013; Grill *et al.* 2019). Environmental flow regimes targeting single ecological outcomes may help to alleviate some detrimental effects, but we urge caution in their application due to the potential of unintended collateral impacts on other components of the ecosystem. How can entire ecosystems be better considered in modern-day flow management strategies? We assert that designing flows for the benefit of entire ecosystems requires long-term perspectives that embrace hydrologic dynamism involving critical flow events that occur at multiple temporal frequencies. Both mechanistic and statistical modeling tools are critical for better managing dammed rivers, particularly when embedded in an iterative cycle that includes prediction, testing, and improvement as new evidence emerges (Konrad *et al.* 2011; Dietze *et al.* 2018; Tonkin *et al.* 2019). Although

returning to the historical natural flow regime in managed rivers is an increasingly distant option in a nonstationary world, environmental flows must remain founded on the principles of the natural flow regime paradigm by incorporating the variability to which native species and communities have evolved.

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Data availability statement

Code and data (Tonkin 2021) used in the analysis are available on doi.org/10.5281/zenodo.4671112.

References

- Acreman M, Arthington AH, Colloff MJ, *et al.* 2014. Environmental flows for natural, hybrid, and novel riverine ecosystems in a changing world. *Front Ecol Environ* **12**: 466–73.
- Auerbach DA, Deisenroth DB, McShane RR, *et al.* 2014. Beyond the concrete: accounting for ecosystem services from free-flowing rivers. *Ecosyst Serv* **10**: 1–5.
- Baxter CV, Fausch KD, and Saunders WC. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biol* **50**: 201–20.
- Bunn SE and Arthington AH. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environ Manage* **30**: 492–507.
- Chen W and Olden JD. 2017. Designing flows to resolve human and environmental water needs in a dam-regulated river. *Nat Commun* **8**: 2158.
- Dietze MC, Fox A, Beck-Johnson LM, *et al.* 2018. Iterative near-term ecological forecasting: needs, opportunities, and challenges. *P Natl Acad Sci USA* **115**: 1424–32.
- Grill G, Lehner B, Thieme M, *et al.* 2019. Mapping the world's free-flowing rivers. *Nature* **569**: 215–21.
- Horne AC, Nathan R, Poff NL, *et al.* 2019. Modeling flow–ecology responses in the Anthropocene: challenges for sustainable riverine management. *BioScience* **69**: 789–99.
- Kennedy TA, Muehlbauer JD, Yackulic CB, *et al.* 2016. Flow management for hydropower extirpates aquatic insects, undermining river food webs. *BioScience* **66**: 561–75.
- Konrad CP, Olden JD, Lytle DA, *et al.* 2011. Large-scale flow experiments for managing river systems. *BioScience* **61**: 948–59.
- Lytle DA, Merritt DM, Tonkin JD, *et al.* 2017. Linking river flow regimes to riparian plant guilds: a community-wide modeling approach. *Ecol Appl* **27**: 1338–50.
- Lytle DA and Poff N. 2004. Adaptation to natural flow regimes. *Trends Ecol Evol* **19**: 94–100.
- McMullen LE, De Leenheer P, Tonkin JD, and Lytle DA. 2017. High mortality and enhanced recovery: modelling the countervailing effects of disturbance on population dynamics. *Ecol Lett* **20**: 1566–75.
- Merritt DM and Bateman HL. 2012. Linking stream flow and groundwater to avian habitat in a desert riparian system. *Ecol Appl* **22**: 1973–88.
- Merritt DM and Poff NL. 2010. Shifting dominance of riparian *Populus* and *Tamarix* along gradients of flow alteration in western North American rivers. *Ecol Appl* **20**: 135–52.
- Milly PCD, Betancourt J, Falkenmark M, *et al.* 2008. Stationarity is dead: whither water management? *Science* **319**: 573–74.
- Naiman RJ, Latterell JJ, Pettit NE, and Olden JD. 2008. Flow variability and the biophysical vitality of river systems. *C R Geosci* **340**: 629–43.
- Olden JD, Konrad CP, Melis TS, *et al.* 2014. Are large-scale flow experiments informing the science and management of freshwater ecosystems? *Front Ecol Environ* **12**: 176–85.
- Palmer M and Ruhí A. 2019. Linkages between flow regime, biota, and ecosystem processes: implications for river restoration. *Science* **365**: eaaw2087.
- Poff NL. 2018. Beyond the natural flow regime? Broadening the hydro–ecological foundation to meet environmental flows challenges in a non-stationary world. *Freshwater Biol* **63**: 1011–21.
- Poff NL, Allan JD, Bain MB, *et al.* 1997. The natural flow regime. *BioScience* **47**: 769–84.
- Poff NL and Matthews JH. 2013. Environmental flows in the Anthropocene: past progress and future prospects. *Curr Opin Environ Sust* **5**: 667–75.
- Poff NL and Olden JD. 2017. Can dams be designed for sustainability? *Science* **358**: 1252–53.
- Robinson CT, Siebers AR, and Ortlepp J. 2018. Long-term ecological responses of the River Spöl to experimental floods. *Freshw Sci* **37**: 433–47.
- Rogosch JS, Tonkin JD, Lytle DA, *et al.* 2019. Increasing drought favors nonnative fishes in a dryland river: evidence from a multispecies demographic model. *Ecosphere* **10**: e02681.
- Ruhí A, Olden JD, and Sabo JL. 2016. Declining streamflow induces collapse and replacement of native fish in the American Southwest. *Front Ecol Environ* **14**: 465–72.
- Sabo JL, Ruhí A, Holtgrieve GW, *et al.* 2017. Designing river flows to improve food security futures in the Lower Mekong Basin. *Science* **358**: eaao1053.
- Shafroth PB, Wilcox AC, Lytle DA, *et al.* 2010. Ecosystem effects of environmental flows: modelling and experimental floods in a dry-land river. *Freshwater Biol* **55**: 68–85.
- Tickner D, Parker H, Moncrieff CR, *et al.* 2017. Managing rivers for multiple benefits – a coherent approach to research, policy and planning. *Front Environ Sci* **5**: 4.
- Tonkin J. 2021. [jdtonkin/flow-tradeoffs](https://github.com/jdtonkin/flow-tradeoffs): final pre-publication in FREE (version v1.0). Zenodo. doi.org/10.5281/zenodo.4671112. 8 April 2021.
- Tonkin JD, Bogan MT, Bonada N, *et al.* 2017. Seasonality and predictability shape temporal species diversity. *Ecology* **98**: 1201–16.
- Tonkin JD, Merritt DM, Olden JD, *et al.* 2018. Flow regime alteration degrades ecological networks in riparian ecosystems. *Nat Ecol Evol* **2**: 86–93.

Tonkin JD, Poff NL, Bond NR, *et al.* 2019. Prepare river ecosystems for an uncertain future. *Nature* **570**: 301–03.

Yarnell SM, Petts GE, Schmidt JC, *et al.* 2015. Functional flows in modified riverscapes: hydrographs, habitats and opportunities. *BioScience* **65**: 963–72.

Supporting Information

Additional, web-only material may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/fee.2348/supinfo>



One size fits some

The size of seeds may determine not only how likely they are to be dispersed or consumed and to germinate but also how competitive their seedlings may be. In the case of oaks (*Quercus* spp), acorns are dispersed by jays and magpies (both in the Corvidae family) if they fit in the bird's bill. Similarly, rodents select acorns of sizes they can carry to hoarding sites. Yet acorns are more likely to resist desiccation and tend to produce taller seedlings if they are large. Owing to divergent pressures on acorn size across life stages, acorn mass can vary by two orders of magnitude within a species.

While each oak parent tree produces acorns of relatively similar sizes, there is remarkable variability among individual trees, as demonstrated in this image by acorns sorted in groups of three “siblings” from each of nine holm oak (*Quercus ilex*) parents. Offspring may be most competitive under the conditions in which the parent estab-

lished, and high variability in acorn size across parents may result from, and persist under, heterogeneous conditions.

Curiously, inter-parent variability also applies to acorn shapes. What are the dispersal implications of acorns being elongated, spherical, or thick at the bottom? What consequences could reforestation programs, which select for large acorns due to their greater probability of emergence, have on tree development and survival over generations? How is intraspecific diversity of oak populations affected if defaunation removes certain acorn disperser or consumer guilds? Does the ongoing oak colonization of conifer-dominated ecosystems under climate change select for certain acorn characteristics, and what does this imply for acorn-feeding guilds in these new communities?

Alexandro B Leverkus¹ and Francisco B Navarro²

¹Department of Ecology, University of Granada, Spain;

²Area of Agriculture and Environment, IFAPA Centro Camino de Purchil, Granada, Spain
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