Adaptation to natural flow regimes

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Floods and droughts are important features of most running water ecosystems, but the alteration of natural flow regimes by recent human activities, such as dam building, raises questions related to both evolution and conservation. Among organisms inhabiting running waters, what adaptations exist for surviving floods and droughts? How will the alteration of the frequency, timing and duration of flow extremes affect flood- and drought-adapted organisms? How rapidly can populations evolve in response to altered flow regimes? Here, we identify three modes of adaptation (life history, behavioral and morphological) that plants and animals use to survive floods and/or droughts. The mode of adaptation that an organism has determines its vulnerability to different kinds of flow regime alteration. The rate of evolution in response to flow regime alteration remains an open question. Because humans have now altered the flow regimes of most rivers and many streams, understanding the link between fitness and flow regime is crucial for the effective management and restoration of running water ecosystems.

Natural disturbances are an integral component of most intact ecosystems. Ecologically, fires, floods, droughts, storms and disease outbreaks regulate population size and species diversity across a range of spatial and temporal scales. Over evolutionary time, organisms also evolve traits that enable them to survive, exploit and even depend on disturbances. As human activities alter natural disturbance regimes, an important conservation goal is to understand how disturbance-adapted populations might respond to novel conditions. In rivers and streams, historic cycles of flooding and drought (the natural flow regime) are being altered severely and suddenly by dams, flood-control projects and other human activities (Figure 1). This raises many issues for the management of biodiversity; in the USA alone, there are ~2.5 million water control structures, and only ~2% of rivers remain in a natural, unmodified condition [1] (Box 1).

The natural flow regime paradigm (Box 2) has become a fundamental part of the management and basic biological study of running water ecosystems [2–4]. Although some of the ecological consequences of altered natural flow regimes have been reviewed [3,5], little attention has been paid to how organisms have evolved in response to floods and droughts. Flow regime adaptations range from behaviors that result in the avoidance of individual floods or droughts, to life-history strategies that are synchronized with long-term flow patterns. Here, we review recent empirical evidence for the adaptation of aquatic and riparian organisms to natural flow regimes, and explore how various modes of adaptation have differing implications for conservation efforts in flow-altered rivers.

Adaptation: costs, benefits and tradeoffs

We focus on adaptations that enable organisms to survive larger magnitude floods and droughts because elimination of extreme flow events is often a consequence of flow regime modification by humans and, thus, a conservation concern (Figure 1). We consider larger floods to be those that spill out of the river channel and onto the floodplain because these are of sufficient magnitude to exert mortality on aquatic and riparian species by reworking geomorphic surfaces that constitute the habitats of species [6]. The more general issue of adaptation to life in flowing water has been treated elsewhere [7,8] and will not be covered here.

Adaptation to flow regimes occurs as a response to the interaction between frequency, magnitude and predictability of mortality-causing events (Box 3). The great variation among streams and rivers in terms of the temporal pattern of these events (Box 2) also presents opportunities for stream-specific adaptation. Adaptations include behaviors that enable fish to avoid displacement by floods, insect life-history strategies that are synchronized to avoid annual droughts, and plant morphologies that protect roots by jettisoning seasonal biomass during floods (Table 1). However, such adaptations can carry both costs and benefits. For example, aquatic plants that grow large roots to provide anchorage during floods might sacrifice aboveground biomass and seed production [9,10] and suffer a competitive disadvantage in the absence of floods. This cost:benefit ratio influences both the evolution and maintenance of adaptations. In turn, alteration of the natural flow regime has the potential to shift this balance, causing the costs of an adaptation to outweigh its benefits.

Putative flow regime adaptations have been identified and studied in many different ways and, for this reason, the strength of evidence for adaptation differs from case to case (Table 1). The evidence comes from four main sources.

Observations
The observation that a particular trait (life history, behavior or morphology) might enhance the ability of an organism to withstand flood or drought is the most common, and also the weakest, form of evidence. Although documenting this kind of close mapping between flow regime and phenotype is important for inspiring more
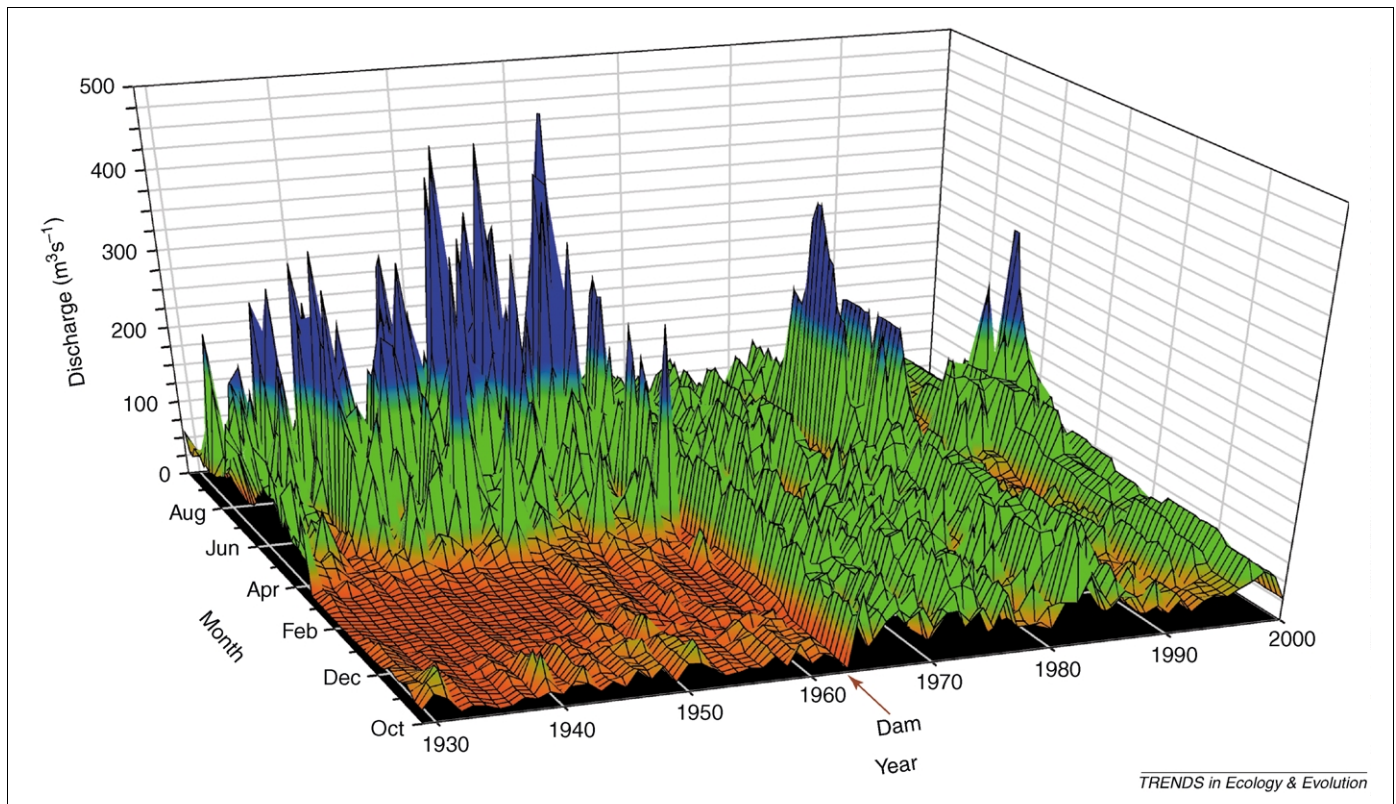
Figure 1. Hydrograph of the Green River, Utah, USA from 1929 to 2000. Before the Flaming Gorge Dam was completed in 1963 (arrow), the river experienced floods from spring snowmelt and droughts during autumn and winter. Damming truncated the flow extreme s, causing both floods and droughts to become less frequent and smaller in magnitude. Data from US Geological Survey.

detailed studies, these examples are beyond the scope of this review and therefore have been omitted.

Cross-species comparisons

Some adaptations have been examined across multiple species in a comparative or phylogenetic context, which enables researchers to ask whether the presence of a trait is correlated with the occupation of flood- or drought-prone habitats. For example, by quantifying the brittleness of twig bases across eight species of willow, Beismann *et al.* [11] showed an association between high stem brittleness (which enables the mechanical jettisoning of vegetation during floods, and also vegetative propagation via plant fragments) and occupation of flood-prone riparian habitats.

Box 1. The big picture

- Recent studies show that a wide variety of organisms have adaptations for surviving or exploiting historic cycles of flood and drought (the natural flow regime).
- However, the natural flow regime of many streams and rivers is being severely altered by dams, flood-control projects and other human activities.
- The mode of adaptation (whether an organism has evolved a life history, behavioral, or morphological strategy for coping with extreme flows) may determine whether an organism can survive flow regime alteration.
- Understanding how organisms have evolved to depend on natural flow regimes will aid the daunting task of maintaining native biodiversity in human-altered rivers and streams.

Gradients

Measuring the performance of a species across a gradient of flow regimes provides insight into the range of flow regime variability that a species can tolerate. Species introductions present a unique opportunity for quantifying the costs and benefits of flow-regime adaptations across a wide gradient of flow regimes. For example, Fausch *et al.* [12] found recently that establishment of introduced rainbow trout succeeded in rivers with flow regimes matching those of the native range, but failed otherwise, and that timing of flood events was a determining factor.

Experiments

Finally, experimental manipulations (e.g. quantification of the flood magnitude that a flexible plant stem can tolerate [13]) can be used to measure directly the benefits and, in some cases, the costs of having a flow regime adaptation.

Modes of adaptation

Flow regime adaptations involve life histories, behaviors and morphologies of plants and animals (Table 1). For each mode of adaptation, different components of the natural flow regime appear to be relevant: timing is important for many life-history adaptations, predictability for behavioral adaptations, and magnitude and frequency for morphological adaptations. Because of these differences, organisms with different modes of adaptation can show markedly different responses to the same flow regime modifications.

Box 2. The natural flow-regime paradigm

The natural flow-regime paradigm [2,3] postulates that the structure and function of a riverine ecosystem, and the adaptations of its constituent riparian and aquatic species, are dictated by the pattern of temporal variation in river flows. In ecological terms, the primary components of a flow regime are the magnitude, frequency, seasonal timing, predictability, duration and rate of change of flow conditions. From an evolutionary perspective, extreme events (floods and droughts) exert primary selective pressure for adaptation because they often represent sources of mortality. In the context of adaptation to flow regimes, a lexicon of flow regime parameters would be the following.

- Magnitude: the amount of water moving past a fixed location per unit time. The larger (or smaller) the magnitude of a flood (or drought), the greater the expected physical impact.
- Frequency: the number of events of a given magnitude per time interval (e.g. per year). For a given river or stream, frequency is typically related inversely to magnitude.
- Duration: the period of time associated with a particular flow event. Expressed in terms of number of days a flood or drought lasts.
- Timing: the date during the year that flood or drought occurs, often derived from long-term flow records.
- Predictability: the degree to which flood or drought events are autocorrelated temporally, typically on an annual cycle. Predictable events might also be correlated with other environmental signals (e.g. rainfall events, seasonal thermal extremes, sudden increases or decreases in flow).

Poff [28] looked at flow gauge data for 806 undammed streams and small rivers across the USA, and calculated natural flow-regime parameter values ranging from 0.62 to 0.91 for flood frequency (overbanking events $\cdot$ y^{-1}), 0.44 to 0.96 for flood predictability (proportion of floods falling in a common 60-day period), 2.3 to 9.9 days for average flood duration, and 0.45 to 0.81 for drought predictability (proportion of droughts falling in a common 60-day period). In a natural flow-regime classification, snowmelt-dominated streams in the Rocky Mountains have the highest predictability of seasonal flood timing (>0.95), relatively high low-flow timing (~0.75), and relatively low flood frequency (~0.60). By contrast, some streams in the Great Plains of the USA have unpredictable flood (~0.45) and low-flow timing (~0.50), and very high flood frequency (~0.90).

Life-history adaptations

Life-history adaptations typically involve the synchronization of life-cycle events, such as reproduction and growth, in relation to the occurrence of flow regime events. Many rivers and streams are seasonal, with flood or drought being more probable during certain parts of the year. Although individual flow events might be difficult or even impossible to forecast, organisms might adapt to the long-term average timing of flow events if they occur with sufficient predictability and frequency (Box 3). Life-history adaptations have been identified in fish, aquatic insects and riparian plants, and include the timing of reproduction, emergence into an aerial adult stage, and diapause (Table 1). For some organisms, life-history adaptations enable organisms to avoid mortality by escaping floods [14,15] or droughts [16,17]. Other organisms take advantage of floods or droughts by timing their reproduction to coincide with optimal conditions, thereby enhancing the fitness of their offspring [18–23].

A theme common to most life-history adaptations is that, rather than enabling organisms to respond directly to individual flood or drought events, the life-history strategy is synchronized with the long-term average dynamics of the flow regime. This is to be expected when the timing of

Box 3. Life-history evolution under different flow regimes

Not all flow regimes favor the evolution of traits that enable flood or drought survival (Figure I). Life-history theory predicts that the magnitude, frequency and predictability of disturbance events, such as floods or droughts, can affect how organisms evolve or fail to evolve [65–68]. The predictions in Figure I are based on theory that optimizes the timing of life-history events, such as age at reproduction, with respect to the timing of flood or drought events [68]. Numbers on the axes indicate the percentage of the maximum parameter value. When extreme flows are frequent, large in magnitude and predictable, selection favors life histories that are synchronized to avoid or exploit extreme flow events (the evolutionary zone). By contrast, extreme flows that are frequent and large in magnitude but unpredictable have low selection strength for life-history timing, even though they might inflict high mortality on populations (the ecological zone). Although no optimal strategy for life-history timing can evolve to avoid the unpredictable floods or droughts, bet-hedging strategies might evolve in this case [25–27]. The lifespan of an organism might also affect selection strength (surfaces for 10 y and 0.1 y life spans are shown here) because disturbance frequency, and thus selection strength, occurs relative to the lifespan of an organism (e.g. a long-lived cottonwood tree experiences annual snowmelt-driven floods many times during a lifetime, whereas a mayfly larva in the same river system might never experience one).
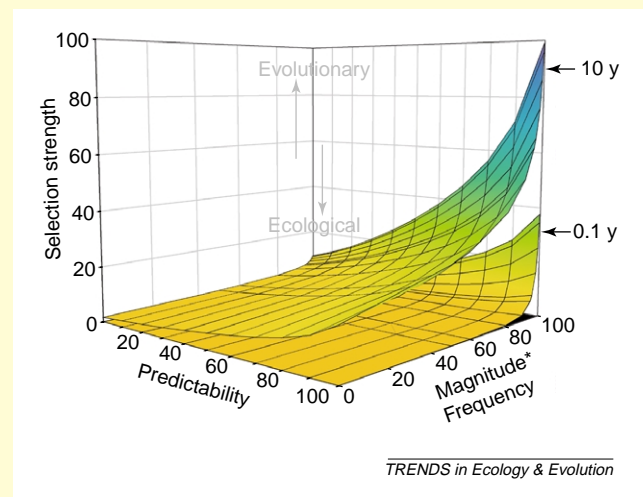

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Figure I.

floods or droughts is sufficiently predictable among years. For example, the timing of cottonwood seed maturation is relatively constant from year to year [24]. This adaptation succeeds in most years because snowmelt floods are fairly predictable; however, significant mortality costs result when flow events happen to be early or late. For some life-history timing strategies, a more subtle cost arises from the missed opportunity for further growth to avoid extreme flows. This is apparent in aquatic insects that enter a nonfeeding adult or diapause stage to avoid floods or droughts that might not occur on an annual basis [14,16,17].

In cases where flood or drought timing occurs with little or no predictability, theory suggests that bet-hedging strategies might evolve, where a parent produces diverse offspring types that correspond to different possible future environmental states [25–27]. Indeed, many rivers and streams can be characterized as having relatively unpredictable flood regimes [6,28]. Although bet hedging in response to unpredictable flow regimes has not been

Table 1. Adaptations to flooding and drought, and their costs and benefits[a]

Adaptation	Organism	Benefit	Cost	Evidence	Refs
Life history					
Seed release synchronized with timing of spring-flood recession	Willows and cottonwoods	Ideal germination conditions (scoured, moist substrates)	Late floods can remove seedlings	E,G,C	[20[b],39[b]]
Rapid root elongation after germination	Willows and cottonwoods	Reduced drought mortality during flood recession	Possible reduction in shade tolerance	E,G,C	[39[b]]
Diapause stage synchronized with drought season	Stoneflies and other aquatic insects	Reduced drought mortality	Unknown	C	[16[b],17[b]]
Asynchronous hatching of a fraction of individuals within a brood	Stoneflies	Possible bet-hedging against floods	Unknown	G,C	[16[b],17[b],29,30]
Metamorphosis synchronized with average timing of flood season	Caddisflies in desert streams	Aerial adults avoid flood mortality in most years	Reduced fecundity (fewer eggs) relative to larvae that risk floods to continue feeding	E,G	[15]
Fast development to aerial adult stage	Mayflies and other aquatic insects in desert streams	Rapid recolonization after floods	Small body size at maturity, possible reduced fecundity	C	[14]
Early release of larvae before wet season peak flows	Atyid shrimp	Increased survivorship of young	Unknown	G	[19]
Egg-laying synchronized with seasonal low flows	Gammarid amphipod	Increased survivorship of young	Unknown	G,C	[18]
Spawning or fry emergence timed to occur in season with low flood probability	Salmonid fish	Reduced flood mortality	Unknown	G,C	[12,50,51]
Ovarian development depends on flood cue	Golden perch	Post-flood environment favorable to offspring	Unknown	G,	[37]
Straying to non-natal streams	Salmonid fish	Buffer against inter-annual habitat variability (including floods and droughts)	Risk of inferior conditions relative to natal stream	G,C	[32[b]]
Behavioral					
Movement from exposed surfaces during high flows	Glossosomatid caddisflies	Reduced flood mortality	Unknown	E	[c]
Use of rainfall as a cue to abandon streams	Giant waterbugs (Belostomatidae)	Flash flood avoidance	Desiccation and predation in terrestrial environment	E,C	[34]
Egg hatching cued by spring floods	Coregonine fish	Optimal hatch timing (abundant prey) when floods are correlated with ice breakup	Hatching in response to early floods might result in starvation	E,C	[52]
Post-flood spawning	Fish (several species)	Juvenile fish buffered from drought conditions	Unknown	C	[23,36,53,54]
Orientation into floods, movement to sheltered stream margins	Fish (several species)	Reduced flood mortality, displacement of non-native fishes	Unknown	E,C	[33,44,55,56]
Egg pockets excavated deeper than flood scour depth	Salmonid fish	Reduced flood mortality of eggs	Possible energetic cost, entombment of fry	G,C	[41,42[b],40,43,57]
Morphological					
Significant allocation to belowground biomass	Aquatic macrophytes	Anchorage during flooding, ability to resprout from roots	Possible reduction in aboveground biomass, reduced dispersal by flood-borne fragments	G,C	[10]
High bending stability, narrow leaf shape, adventitious rooting	Willows and cottonwoods	Ability to withstand floods	Unknown	G,C	[38,39[b]]
Resprouting from both roots and shoots	Willows and cottonwoods	Dispersal by vegetative fragments	Unknown	G,C	[38,39[b]]
Branch sacrifice	Cottonwoods	Enhanced drought survival	Loss of biomass	E,G,C	[58,59]
Flexible stems (relative to terrestrial species)	Aquatic buttercup	Bending during floods	Loss of biomass	E,C	[13]
Brittle twig bases that enable living stems to break free	Crack willow and other *Salix* spp., aquatic buttercup	Protection of root and trunk biomass, dispersal by flood-borne fragments	Loss of biomass	E,C	[11,13]
Flood-induced changes in root physiology (e.g. anaerobic stress proteins, aerenchyma, lenticels)	Riparian plants (many species)	Allows respiration during floods	Unknown	E,C	[60[b],61]
Buoyant seeds that expand in water	Trees in seasonally flooded Panamanian forests	Increased seed survivorship and dispersal during floods (relative to terrestrial species)	Unknown	E,C	[62]
Flood-tolerant eggs and other features for surviving underwater	Springtails (Collembola) and other terrestrial floodplain invertebrates	Survival of seasonal flood inundation	Unknown	G,C	[63,64[b]]

[a]Types of evidence for adaptation: C, comparison of trait across related taxa; G, measurement of trait performance across a natural gradient of different flow regimes (natural experiments); E, experiments used to quantify benefits and/or costs of trait directly.
[b]Review paper.
[c]S.S. Brooks, PhD Thesis, Monash University, 1998.

demonstrated conclusively for an aquatic organism, several studies have found patterns that are consistent with bet-hedging strategies. For example, certain stonefly species are known to produce egg clutches that hatch asynchronously [16,17,29,30] and, in one species, hatching asynchrony is higher in a population that experiences a more variable flood regime, as predicted by theory [29]. Some zooplankton and aquatic plant species also survive drought in temporary wetlands via persistent egg or seed banks, which might be considered a form of evolutionary bet hedging [31]. Straying to non-natal streams by salmonid fish might also be a bet-hedging response to interannual variation in local flow regimes [32].

Behavioral adaptations

Behavioral adaptations enable animals to respond directly to individual floods or droughts, often by reacting to a correlated environmental cue. Behavioral adaptations include movement to protected areas during floods, drought avoidance by reproducing after floods, and the excavation of deep egg nests to avoid flood scouring (Table 1). Fish native to desert streams are particularly adept at responding to flash floods, which are preceded by a sudden increase in water velocity that the fish use as a cue to move quickly to sheltered areas along stream margins [33]. Similarly, because torrential downpours often precede floods, giant waterbugs (Belostomatidae) use rainfall as a cue to abandon streams before flash floods [34]. The predictability of floods from antecedent cues dictates the fitness of these behaviors. If the cue and the consequence become decoupled as a result of flow regime alteration, organisms could suffer false alarms by reacting to floods that never arrive (e.g. small water releases from dams that do not cause floods, but still induce fish to seek cover or spawn). In the case of giant waterbugs, individuals might also fail to react in streams where flash floods are generated by distant storms that arrive with no antecedent rainfall. The cost of a false alarm versus the cost of a failure to react, in the context of the flow regime, determines the fitness of any given behavioral strategy. Signal detection theory [35] is a promising framework for exploring the evolutionary consequences of these tradeoffs.

Unlike life-history adaptations, many behavioral adaptations enable organisms to react on a per-event basis rather than synchronizing with long-term flow regime dynamics. This is especially important for organisms in rivers and streams where the seasonal timing of floods or droughts is not predictable. Fish native to Great Plains (USA) streams, where flood timing has low predictability [28], use high-flow pulses that occur during warm months as a cue for egg laying [36]. Golden perch native to Australian dryland rivers actually require floods (which occur unpredictably) as a cue to spawn; otherwise, the developing eggs are resorbed into somatic tissue [37]. This ability to respond to cues regardless of the predictability of seasonal timing might also be important in rivers and streams with altered flow regimes because organisms might still be able to respond behaviorally to individual flow events even if they occur outside the normal range of timing, frequency or magnitude.

Morphological adaptations

Morphological adaptations to flow regime events include body shapes that reduce drag during floods, mechanical devices for shedding vegetative growth, flood-induced physiological changes, and allocation of biomass to different organs (Table 1). Many morphological adaptations of plants involve a tradeoff between allocation of biomass to flood- or drought-susceptible tissues or to protected tissues such as roots [10,38,39]. (Such tradeoffs are sometimes discussed in the context of life-history strategies). In conjunction with these allocation strategies, some plants have brittle twig or stem bases that jettison biomass during extreme floods or droughts (so-called mechanical fuses [13]), thereby protecting the remaining plant tissue from further damage [11,13]. Detached plant fragments from some willow and cottonwood species are transported downstream where they resprout, thereby serving as a dispersal function [11,38,39]. A tradeoff also exists between allocation to root biomass, which enhances resprouting ability, and to aboveground biomass, which enhances the ability to disperse via flood-borne fragments [10]. For many of these adaptations, the magnitude and frequency of flow events are important because they might determine the optimal allocation of belowground biomass or the ease with which biomass is shed.

Conclusions

Different modes of adaptation (life history, behavioral or morphological) appear to evolve in response to very different components of the natural flow regime. For organisms that use life-history strategies to avoid floods or droughts, the seasonal timing of flow events (in particular, the predictability of seasonal timing) is an important flow-regime parameter. This occurs because many life-history adaptations involve the synchronization of a life stage to long-term flow regime dynamics, rather than an immediate response to individual flow events. Life-history adaptations are particularly important for organisms with complex or migratory life cycles that enable temporary escape from flood- or drought-prone environments (e.g. aquatic insects with aerial adult stages or migratory fish). By contrast, many organisms with behavioral adaptations can cope with extreme flows on a per-event basis, and long-term average flow dynamics might not play as important a role. For most of these behaviorally adapted organisms, the ability to predict large-magnitude flow events from some environmental cue is crucial. For plants with morphological adaptations involving biomass allocation, the frequency and magnitude of flood events are important because they determine the optimal allocation between above- and belowground biomass.

From a conservation perspective, organisms with life-history adaptations could be affected by flow-regime modifications that redistribute extreme flow events to different times of the year. Water projects, such as floodwater storage and irrigation works often alter the seasonal timing of floods or droughts [2,3]. Because most life-history adaptations are constitutive (i.e. they are implemented regardless of whether an extreme flow event occurs eventually), organisms with these adaptations might also suffer a fitness cost from activities that eliminate

floods and droughts from the flow regime. In this case, adapted organisms could forego growth to avoid a flood or drought that never arrives, which is a flawed strategy that might leave them vulnerable to competition from invading species that lack adaptations to extreme flows. Although life-history strategies can sometimes evolve rapidly in response to novel conditions (in as few as 13 generations for some fish [40]), adaptation in response to a human-altered flow regime remains to be demonstrated for any species.

Most behavioral adaptations, in contrast to life-history adaptations, appear robust to an alteration in the seasonal timing of flow events because they are triggered by individual floods or droughts, rather than performed constitutively. (An exception is for those salmonid fishes that excavate egg pockets before seasonal floods, regardless of whether a flood occurs eventually [41–43]). Wholesale removal of floods or droughts might not pose a problem for these behaviorally adapted organisms because costs are incurred only when the behaviors are performed. However, it is not known whether there are intrinsic costs to having the ability to respond to floods or droughts even if they occur rarely, or if organisms are unable to respond behaviorally to flow events that occur far outside the seasonal timing of the natural flow regime.

Prospects
Flow regime alteration, especially by large dam projects that eliminate floods and droughts, has facilitated invasions by non-native organisms that might not otherwise survive extreme flows [3–5]. If adaptation to natural cycles of flood and drought is widespread among aquatic and riparian species, restoration of natural flow regimes might act as a selective sieve that remove invaders thereby enabling adapted native species to persist. This might be easiest to accomplish in systems that experience large-magnitude floods and droughts regularly (e.g. those in desert climates [44,45]), but even subtle differences in flow regime could determine the success or failure of an invader (e.g. differences in seasonal flood timing [12]). On the flip side, however, if species are finely tuned to particular flow regimes, they might be vulnerable to flow regime alteration. For example, manipulation of flood and drought timing in regulated rivers can change fish distributions by favoring species that spawn only during certain times of the year [22,46].

One problem in inferring potential adaptations of species to natural flow regimes is a general lack of knowledge of the full range of natural flow regime types that species can occupy. Within the geographic range of the species, there can be a variety of flow-regime types, as defined by different combinations of flood and drought magnitude, frequency, timing and predictability [8,28]. A better accounting of how species with identified flow-regime adaptations assort themselves across gradients of variation in flow regimes could provide insights into possible cost:benefit ratios of different adaptive strategies.

The most direct approach to predicting how the removal of extreme flow events could affect populations would be to conduct experiments that identify both the costs and the benefits of flow regime adaptations. Some natural experiments have occurred already. The damming of western USA rivers has revealed one cost of flood adaptation: a lack of spring snowmelt floods has halted recruitment of riparian cottonwoods, which had evolved to depend on these predictable seasonal events [47,48]. Another issue is whether populations can keep evolutionary pace with current rates of flow-regime alteration [49]. This is imperative because flow-regime modification by humans can be sudden and severe – instantaneous in the case of some dam projects (Figure 1) – providing little or no time for populations to adapt gradually to novel conditions. Although it is clear that some organisms have evolved life histories, behaviors, and morphologies that enable their survival during or exploitation of naturally occurring floods and droughts, it remains to be seen whether these adaptations function adequately as natural flow regimes become increasingly altered by humans.

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