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Ecosystem effects of environmental flows: modelling and experimental floods in a dryland river

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SUMMARY

1. Successful environmental flow prescriptions require an accurate understanding of the linkages among flow events, geomorphic processes and biotic responses. We describe models and results from experimental flow releases associated with an environmental flow program on the Bill Williams River (BWR), Arizona, in arid to semiarid western U.S.A.
2. Two general approaches for improving knowledge and predictions of ecological responses to environmental flows are: (1) coupling physical system models to ecological responses and (2) clarifying empirical relationships between flow and ecological responses through implementation and monitoring of experimental flow releases.
3. We modelled the BWR physical system using: (1) a reservoir operations model to simulate reservoir releases and reservoir water levels and estimate flow through the river system under a range of scenarios, (2) one- and two-dimensional river hydraulics models to estimate stage–discharge relationships at the whole-river and local scales, respectively, and (3) a groundwater model to estimate surface- and groundwater interactions in a large, alluvial valley on the BWR where surface flow is frequently absent.
4. An example of a coupled, hydrology-ecology model is the Ecosystems Function Model, which we used to link a one-dimensional hydraulic model with riparian tree seedling establishment requirements to produce spatially explicit predictions of seedling recruitment locations in a Geographic Information System. We also quantified the effects of small experimental floods on the differential mortality of native and exotic riparian trees, on beaver dam integrity and distribution, and on the dynamics of differentially flow-adapted benthic macroinvertebrate groups.
5. Results of model applications and experimental flow releases are contributing to adaptive flow management on the BWR and to the development of regional environmental flow standards. General themes that emerged from our work include the importance of response thresholds, which are commonly driven by geomorphic thresholds or mediated by geomorphic processes, and the importance of spatial and temporal variation in the

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effects of flows on ecosystems, which can result from factors such as longitudinal complexity and ecohydrological feedbacks.

Keywords: beaver, benthic macroinvertebrates, fluvial geomorphology, physical habitat modelling, riparian vegetation

Introduction

Freshwater and riparian ecosystems are at once among the most biologically diverse and seriously threatened on Earth (Dudgeon *et al.*, 2006), and as a result, substantial resources have been directed toward their restoration (Bernhardt *et al.*, 2005). Streamflow regulation has direct and indirect effects on freshwater biodiversity and can interact in important ways with other aspects of global change, such as exotic species invasions (Richardson *et al.*, 2007; Johnson, Olden & Vander Zanden, 2008) and land use (Bunn & Arthington, 2002; Andersen, Cooper & Northcott, 2007). Consequently, management of reservoirs to release river flows of appropriate quantity, quality and timing to sustain ecosystem services and biodiversity patterns (i.e. 'environmental flows') has developed into an important restoration tool (Arthington & Pusey, 2003; Postel & Richter, 2003; Arthington *et al.*, 2006; Richter & Thomas, 2007; Sophocleous, 2007).

Environmental flow prescriptions require basic understanding of relationships between streamflow and biotic response. Such understanding has advanced in recent decades (e.g. Bunn & Arthington, 2002; Nilsson & Svedmark, 2002; Merritt *et al.*, 2010) but is often qualitative or specific to certain rivers and/or species, indicating a need to develop and test quantitative and generalisable approaches that link flow and biotic responses (Whiting, 2002; Tharme, 2003; Harman & Stewardson, 2005; Anderson *et al.*, 2006; Arthington *et al.*, 2006; Petts, Morales & Sadler, 2006; Merritt *et al.*, 2010). In the context of environmental flows, models are needed to help to predict ecological responses to different managed flow scenarios, evaluate alternatives, guide implementation and inform adaptive management.

Implementing environmental flows can enable scientific examination of biotic responses to streamflow while achieving management goals related to the multiple demands on water stored in reservoirs and associated constraints on environmental flow releases. In an adaptive management framework, scientists and stakeholders design and implement flow regimes based on hypotheses about hydrology–ecology relationships and key knowledge gaps, monitor effects of the flow regimes, and then adjust future environmental flow prescriptions based on the results (Poff *et al.*, 2003; Richter *et al.*, 2006). The process should be repeated so that flow prescriptions are refined multiple times. This approach can be used to address central goals in environmental flow science, such as: (1) generating empirical response curves relating flow to physical and biotic response, (2) identifying key threshold responses and (3) identifying levels of hydrologic alteration that are acceptable for particular functions or, conversely, the quantity and quality of flow required to restore and sustain desirable system attributes (Poff *et al.*, 2010). Models and data arising from environmental flow experiments on particular rivers can then be used to address broad management goals, such as developing regional environmental flow standards for other rivers (Arthington *et al.*, 2006; Poff *et al.*, 2006, 2010).

In this paper, we present examples of models and results relating streamflow to ecological responses, drawn from recent experiences developing, implementing and evaluating environmental flows downstream of a large reservoir on the Bill Williams River (BWR), a significant tributary to the lower Colorado River in western U.S.A. (Fig. 1). Because the BWR corridor is managed largely for its natural values and to provide habitat for wildlife populations that have declined along the adjacent lower Colorado and other regional rivers (Ohmart, Anderson & Hunter, 1988), understanding the effects of different streamflow regimes on downstream aquatic and riparian ecosystems is a priority for resource managers along the river (Shafroth & Beauchamp, 2006). More generally, many of the key questions on the BWR pertain to rivers in other arid and semiarid regions around the world, such as how flow affects exotic species invasions, keystone species (including ecosystem engineers) and resistance and resilience in aquatic

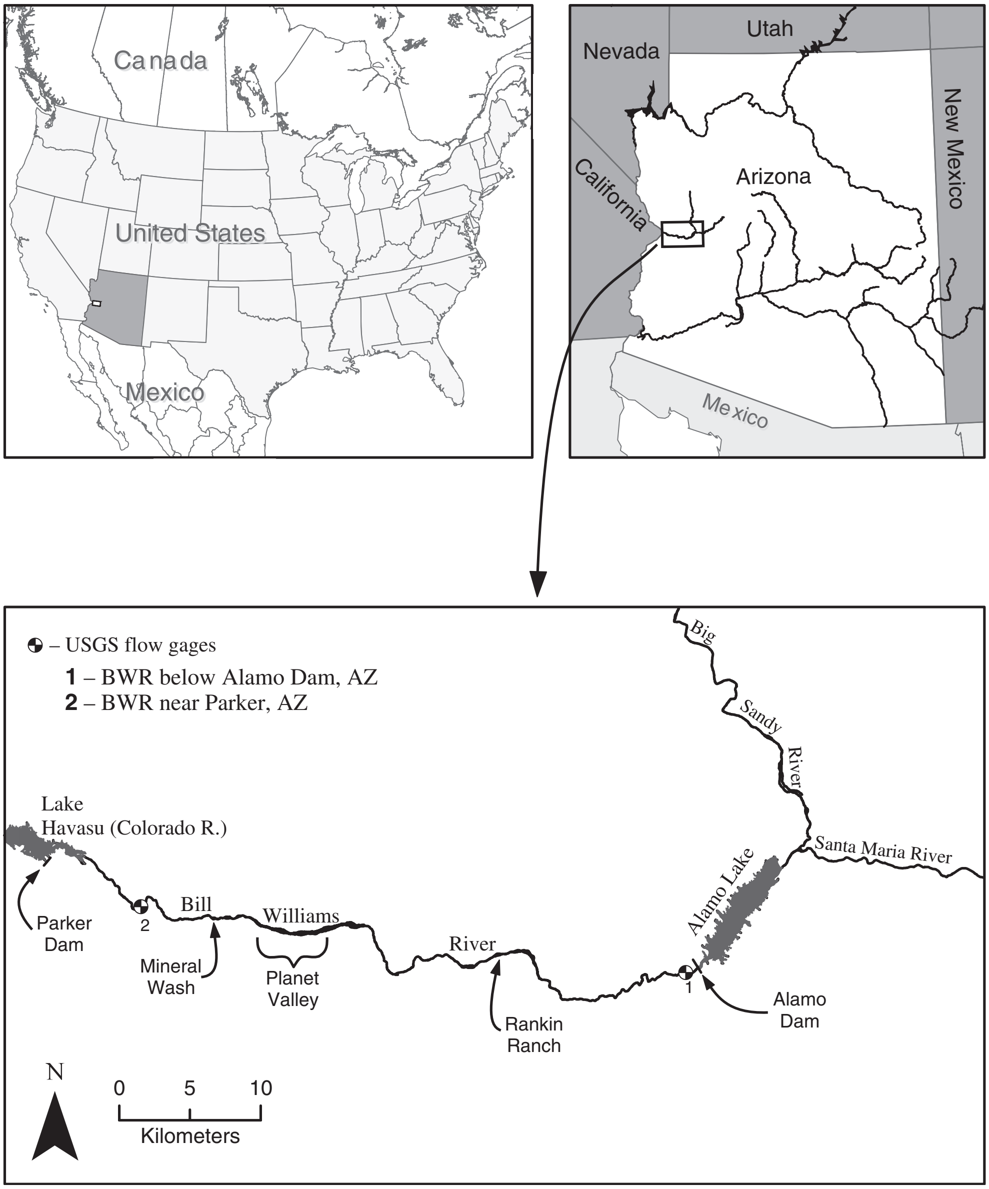

Fig. 1 Map of the Bill Williams River study area, southwestern U.S.A.

communities. By highlighting the BWR case study, we suggest that it could serve as a valuable model for environmental flow programs in other river basins. Our aim is to describe activities and approaches implemented on the BWR to illustrate how these have been linked both to support management and advance scientific understanding. The diversity of efforts on the BWR include developing conceptual flow–ecological response models; integrating reservoir simulation, hydrologic–hydraulic and biotic response models; developing empirical flow–biotic response functions for key taxa; and testing through implementation and monitoring of experimental reservoir releases. Because we describe such a wide assortment of approaches, our treatment of each is relatively brief.

Study area

The BWR drains more than 13 000 km^2 of mountain and desert terrain in the west-central portion of Arizona, U.S.A. (Fig. 1). Downstream of Alamo

Dam, a flood control structure completed in 1968, the BWR flows 58 km through a series of canyons and alluvial valleys to its confluence with the Colorado River (in Lake Havasu) at an elevation of 137 m. The BWR has an average gradient of 0.003, and no perennial tributaries enter the river downstream of Alamo Dam. The BWR is primarily a sand-bed river with coarser reaches immediately downstream of the dam. Planet Valley, a *c*. 10-km-long reach with wide, permeable channels and very deep alluvium, attenuates high flows and significantly influences base flows downstream. Average annual precipitation in the catchment ranges from approximately 40 cm in the headwaters [National Climatic Data Center (NCDC) station Bagdad] to 23 cm near Alamo Dam (NCDC station Alamo Dam) to 13 cm near the Colorado River (NCDC station Parker 6NE).

The operations of Alamo Dam, which has a reservoir storage capacity of approximately 1233×10^6 m^3, have substantially altered the downstream flow regime (Shafroth & Beauchamp, 2006). The most striking aspect of flow alteration on the BWR has been a >90% reduction in the magnitude of high flows (Fig. 2a). Timing of high flows has also changed: in the predam era, they occurred in both winter–spring and late summer–autumn, but virtually all of the latter have been eliminated since dam construction. Mean annual flows, however, often have been higher during the postdam era than in the predam period (Fig. 2b). Base flows (10% flow, or 90% exceedance) were often lower than natural during the first 10 years following dam closure, but they have been less variable and higher than natural since about 1993 (Fig. 2c). These sorts of changes to surface flows (i.e. sharp decreases in peak flow magnitudes and increases in low flows) are common effects of large dams (Graf, 2006). Although the magnitude of alteration to sediment supplies caused by Alamo Dam has not been quantified, its very large reservoir size relative to flow volumes suggests that nearly 100% of sediment from the upstream watershed is trapped by Alamo Reservoir.

Most of the land within the BWR corridor is undeveloped and managed by the U.S. Government for its natural character and high biodiversity. Active land use currently consists of a single cotton farm along a 2-km reach of the river, cattle grazing along a few river kilometers, and dispersed off-road vehicle activity. Lush riparian forests, dominated by native cottonwood (*Populus fremontii*) and willow (*Salix gooddingii*) trees, grow on floodplains of the BWR, as do extensive stands of the non-native saltcedar (*Tamarix* spp.); native mesquite (*Prosopis* spp.) trees dominate on terraces (Shafroth, Stromberg & Patten, 2002). These forests support an abundance of wildlife

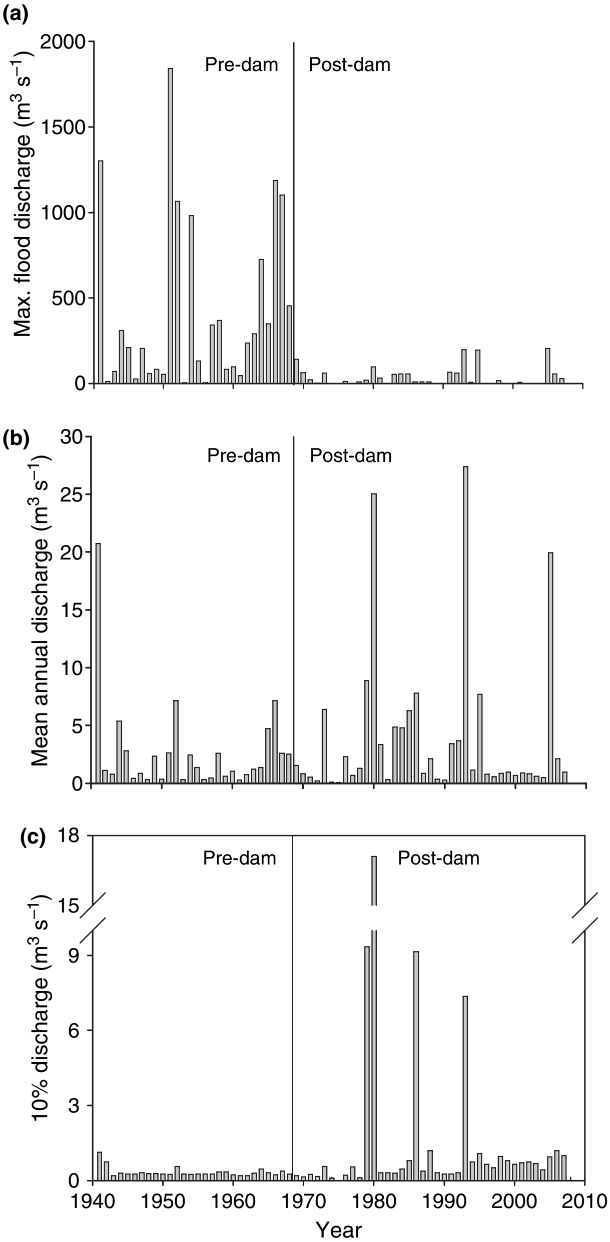

Fig. 2 Pre- and post-dam streamflow data for the Bill Williams River (1940-2007), as measured at the ''Bill Williams River below Alamo Dam'' stream gaging station. (a) Annual flood series; values are the largest peak instantaneous discharge in a given water year (Oct. 1 to Sept. 30). (b) Mean annual discharge. (c) 10% discharge (10% of flows are less than or equal to this in a given water year).

taxa (Shafroth & Beauchamp, 2006). The fish fauna of the BWR is dominated by non-native species, whereas the aquatic invertebrate fauna is typical of low-elevation, sand-bed rivers within this region (Shafroth & Beauchamp, 2006).

Environmental flow program on the Bill Williams River

Since the early 1990s, land and water managers along the BWR have been dedicated to a collaborative approach to managing flow releases from Alamo Dam. In 2004, the BWR and Alamo Dam became one of eight U.S. rivers and 36 dams that are part of the Sustainable Rivers Project (SRP), a collaboration between The Nature Conservancy and the U.S. Army Corps of Engineers. The SRP aims to evaluate and, where appropriate, recommend changes to dam operations to restore and protect the health of rivers and surrounding natural areas while continuing to meet human needs for services such as flood control and power generation (*http://nature.org/success/dams.html*), using a holistic approach (*sensu* Tharme, 2003) known as 'ecologically sustainable water management' (ESWM; Richter *et al.*, 2003, 2006).

Implementation of the ESWM process on the BWR has followed several steps, beginning with a summary report on pre- and post-dam hydrology, geomorphology and streamflow–biotic responses, which provided background for a flow requirements workshop (Fig. 3; Shafroth & Beauchamp, 2006). In this 3-day workshop, approximately 50 scientists and resource managers developed conceptual hydrology–ecology models for aquatic macroinvertebrates, fish, riparian plants and terrestrial fauna associated with different riparian vegetation types. These conceptual models related the magnitude, timing, duration, frequency and rate of change of flood flows and base flows to particular ecological processes or functions and were used to develop a set of unified flow requirements for the BWR (Fig. 4; Shafroth & Beauchamp, 2006).

Based on management recommendations and scientific hypotheses generated from the ecosystem flow requirements workshop, we have worked with resource managers to develop and implement models and field data collection associated with experimental flow releases to support the BWR environmental flow program. Most of these efforts began only following the 2005 ecosystem flows workshop; thus, integration and application of some of our approaches is ongoing. Our modelling and research efforts are integral parts of the more general environmental flow program (Fig. 3).

The BWR is characteristic of many managed rivers in that its natural flow and sediment regimes have been altered dramatically by dam construction and operation. The BWR is unusual, however, in that opportunities are available for conducting environmental flow experiments, largely because it is relatively free of the constraints typical of environmental flow programs on other rivers. For example, there is essentially no water withdrawn from the river or reservoir, water rights issues are not contentious, and flow is primarily through undeveloped, natural terrain on public lands. Thus, confounding effects of land and water uses other than those associated with the dam are mostly absent on the BWR, allowing for relatively clear interpretations of the effects of flow and dam operations on downstream biota and ecosystems. Further, the positive and collaborative relationships that have developed between land and water managers, stakeholders and scientists have facilitated implementation of experimental releases and the advance planning needed to measure system responses to particular flow events.

Models to simulate key hydrologic and geomorphic conditions and processes

In the context of environmental flow development and implementation on the BWR, models of river hydraulics, groundwater–surface water dynamics and reservoir operations simulation are being used to estimate key hydrological and geomorphic conditions and processes that can be linked to biotic responses through other models, software and field data collection (Fig. 3).

River hydraulics

River hydraulic models use channel topography and gradient to assess flow depths, velocities, inundated areas, shear stresses and other hydraulic conditions for various discharges. These physical metrics can be linked to requirements of riverine biota to inform environmental flows (Jowett, 1997). Both one- and two-dimensional hydraulic models are supporting environmental flow analysis on the BWR.

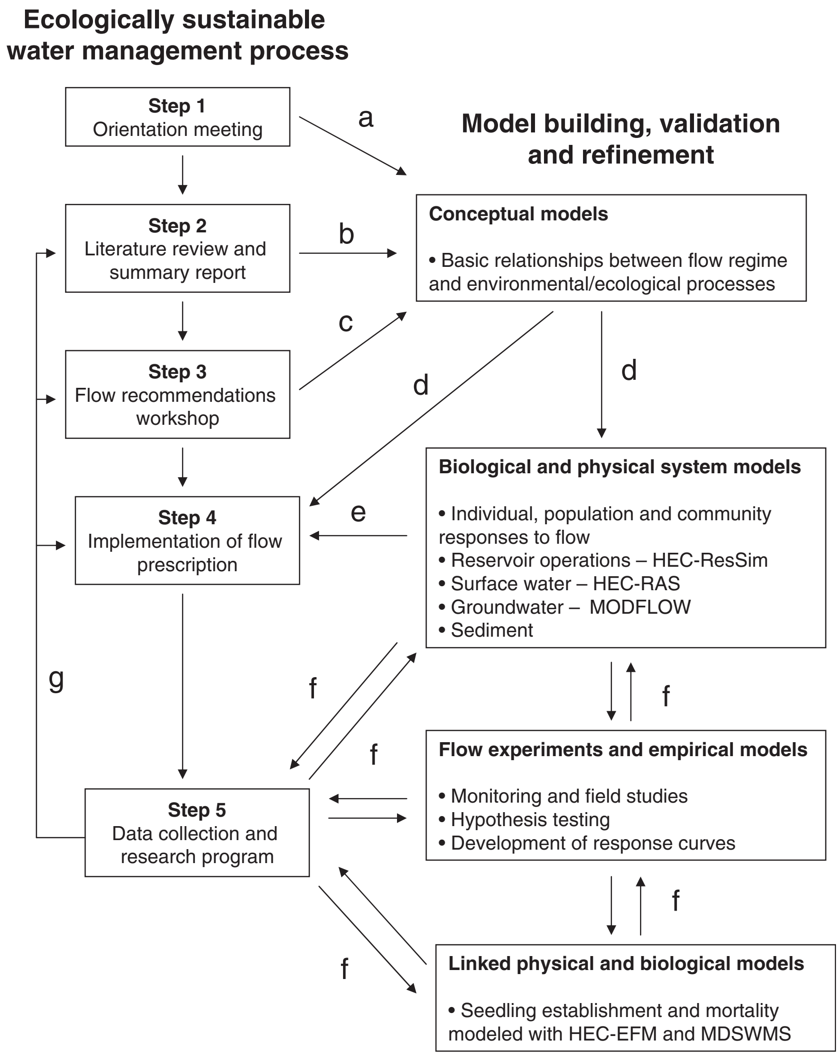

Fig. 3 Relationships between the process to define and adaptively implement environmental flows (left column; Richter *et al*., 2006) and models and experimental flows discussed in this paper. Different activities and information transfer between boxes are identified with letters adjacent to arrows (a–g) and detailed here: (a) Inform and engage stakeholders about the process and clarify the purpose. In the case of the Bill Williams River, the primary objective of developing flow recommendations was to maximise biodiversity in the below-dam reach. (b) Provide information on pre- and post-dam hydrology, geomorphology and hydrology–ecology relationships. (c) Develop conceptual hydrology–ecology models for diverse taxa including aquatic macroinvertebrates, fish, riparian plants and terrestrial fauna associated with different riparian vegetation types. (d) Define hydrology–ecology relationships (when sufficient information exists) or formulate hypotheses relating different aspects of streamflow to ecosystem components, to inform modelling efforts and flow prescriptions. (e) Use results of physical system and biological modelling to inform flow prescriptions. (f) Collect and interpret data and output from monitoring the effects of flow experiments, and from physical, biological and coupled models. Refine models. (g) Use results of the data collection and research program to update the literature review and summary report, refine hypotheses regarding ecosystem responses to streamflow, and inform changes to flow prescriptions in an adaptive management framework.

HEC-RAS [U.S. Army Corps of Engineers (USACE), 2006] is a one-dimensional hydraulic model being used to model river hydraulics and inundated areas over a range of discharges for the entire BWR corridor. The HEC-RAS model for the BWR uses cross-sections extracted from light detection and ranging (LIDAR) surveys of the river corridor. LIDAR data were collected during low flow conditions (surface water flow rates varied spatially between 0 and 0.8 m^3 s^{-1}) and very shallow associated water depths, with point spacing on the order of 1 m, and vertical accuracies of <16 cm (mean = 3.5 cm). Vegetation filtering to create

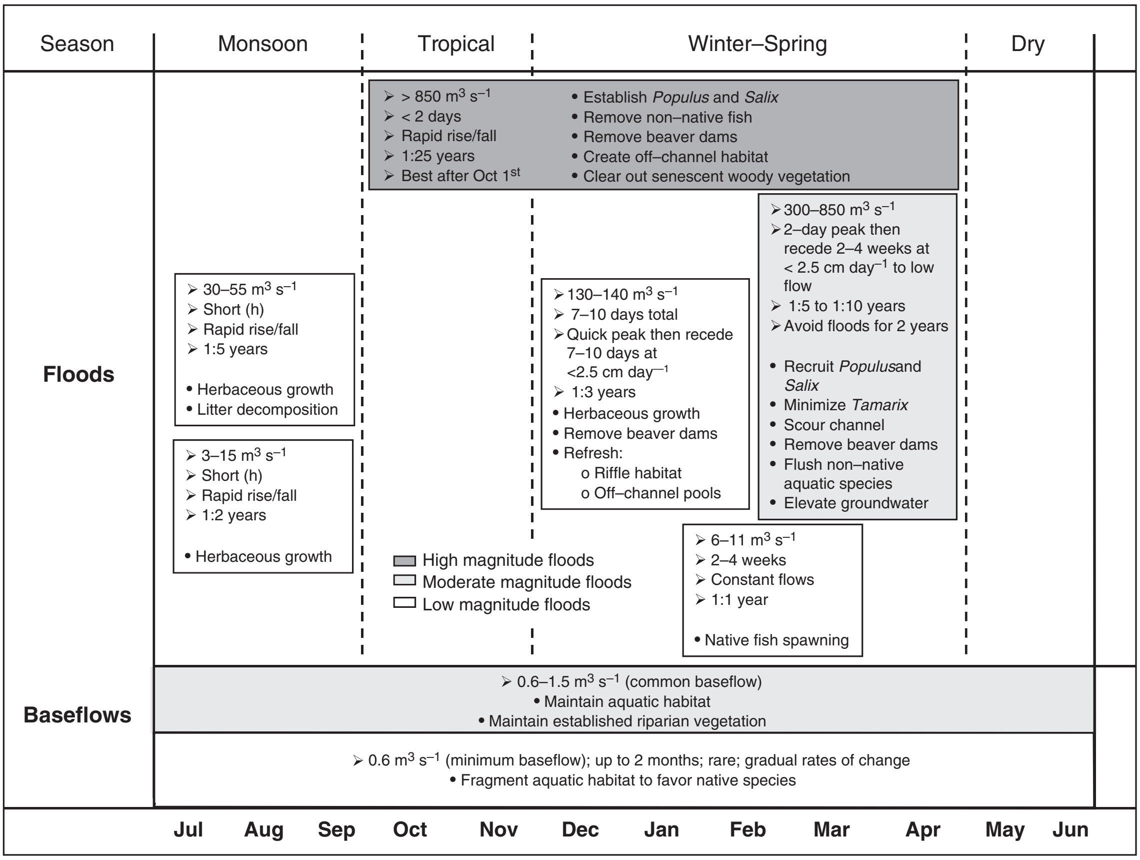

Fig. 4 Flow requirements for the Bill Williams River, developed by scientists and resource managers at a 2-day workshop. Blocks include different flood flow and baseflow regimes, within four seasons. Arrows indicate flow characteristics, such as magnitude, timing, duration, frequency and rate of change. Bullets indicate ecological functions associated with flows. See Shafroth & Beauchamp (2006) for more detailed information.

bare earth data sets was accomplished using the Bare Earth Extraction Plug-In (Version 1.0; Johns Hopkins University Applied Physics Laboratory, Laurel, MD, U.S.A.) with QUICK TERRAIN MODELER software (Applied Imagery, Silver Springs, MD, U.S.A.). HEC-RAS assumes a static channel and floodplain configuration, creating uncertainty in model prediction of large floods in which channel topography can change substantially, especially in a sand-bed river such as the BWR. Hence, re-surveying of cross-sections is required periodically to assess the degree of topographic change and potential consequences for model accuracy. HEC-RAS is being used in combination with other tools to model flow–biota connections, such as tree seedling establishment at the river segment scale, as discussed below.

More detailed hydraulic modelling is being applied to shorter reaches of interest on the BWR using the U.S. Geological Survey's Multidimensional Surface Water Modelling System (MDSWMS), which is a pre- and postprocessing application for computational models of surface-water hydraulics. Modelling with MDSWMS provides predictions of spatially distributed flow depth, velocity, shear stress and sediment mobility associated with different discharges (McDonald, Nelson & Bennett, 2005). This approach predicts flow and sediment transport characteristics relevant to investigating certain flow–biota relationships at the detailed scales of bars and vegetation patches. On the BWR, we are combining MDSWMS modelling of local-scale hydraulic forces with tree seedling monitoring to evaluate the response of seedlings to floods, as discussed below.

Surface water–groundwater interactions

Interactions between ground water and surface water systems can strongly influence surface and hyporheic flows and associated aquatic and riparian ecosystems (Boulton & Hancock, 2006; Eamus *et al*., 2006), especially in arid and semiarid regions or where permeable sedimentary groundwater basins are present. Thus, environmental flow development should incorporate considerations of ground water and groundwater–surface water interactions through the use of groundwater models and/or water budget simulations (Springer *et al*., 1999; Rains, Mount & Larsen, 2004; Sophocleous, 2007). Uncertainties in quantifying groundwater–surface water interactions and legal separation of surface water and groundwater management in many areas, however, remain an obstacle to incorporation of groundwater dynamics into flow management decisions.

Surface water–groundwater interactions in the BWR's Planet Valley (Fig. 1) exert strong control on depths to ground water and the re-emergence of surface flow downstream, with consequent effects on ecosystems that are partially or wholly groundwater-dependent. We used MODFLOW, a numerical (finite-difference) groundwater flow model (McDonald & Harbaugh, 1988), to simulate steady-state, three-dimensional flow in the two aquifers in Planet Valley (fluvial aquifer, basin fill aquifer). By numerically simulating the hydraulic gradient of the groundwater basin and solving for hydraulic conductivities of the two aquifers, a groundwater budget was developed that provided estimates of (1) surface flow downstream of Planet Valley, (2) sub-surface flow downstream of Planet Valley and (3) losses from the basin to evapotranspiration. The steady-state model was calibrated to June, 2001 water level measurements in 20 wells as well as stream discharge during the same period. Additionally, the model was calibrated using an iterative process that included matching transient conditions of two aquifer tests conducted in the basin. There is an ongoing effort to integrate MODFLOW and HEC-RAS, which will ultimately create a modelling tool that can simulate surface and groundwater flows and interactions.

Reservoir operations simulations

Reservoir operations models can simulate reservoir releases and reservoir water levels, and estimate flow through a river system under a range of release scenarios. In an environmental flows context, changes to reservoir levels are important because they can be related to stakeholder values and constrain flow release options. In case of the BWR, for example, a State Park and associated recreation industry depend on certain reservoir levels for access (i.e. boat ramps), and there is some concern that the rate of change in reservoir levels could impact the reservoir's sport fish populations, as well as shoreline and inflow delta geomorphology and associated riparian habitat. Thus, although reservoir simulation models are generally not used directly to tie stream flow to biotic response downstream, they are crucial for understanding the effects of different flow scenarios on reservoir operations and for performing the tradeoff analyses needed to test new operational rules designed to incorporate environmental flows. HEC-ResSim (Reservoir System Simulation; USACE, 2007) is a rule-based model being applied to the BWR. Rules are created, prioritised, and modified to make simulated releases agree with how the reservoir is actually operated. A set of rules simulates a unique operating plan and can be changed to test different reservoir management scenarios, such as implementing environmental flow releases.

Linking flows and ecological responses: models and experimental flows

Understanding and modelling key aspects of the physical system are important for developing mechanistic linkages between flow and ecological responses. Published studies and expert knowledge can inform development of conceptual or quantitative models that link flow or flow-related variables, such as habitat and water quality conditions to biological responses. This information can help to prioritise data collection to fill key gaps, generate hypotheses, or parameterise models that link flow and ecological response. In an environmental flows context, implementing experimental flow releases can effectively address these sorts of information needs.

Outcomes from the BWR ecosystem flow requirements workshop included flow recommendations and suggestions for future research to fill key hydrology–ecology knowledge gaps (Shafroth & Beauchamp, 2006). High inflows to Alamo Lake between September 2004 and March 2005 afforded opportunities to use the workshop results to guide the flood recession in 2005, plan and implement experimental flows in 2006 and 2007, and measure several system responses.

In particular, we focused on developing, testing and refining hypotheses and models relating flow to the establishment and mortality of riparian tree seedlings; the removal of beaver dams and associated lentic habitats; and the dynamics of different aquatic invertebrate guilds.

Between November 2004 and March 2005, a series of high-flow releases (between 150 and 204 $m^3 s^{-1}$) in response to wet conditions caused substantial geomorphic reworking, including scour and deposition of bars, removal of beaver dams and associated conversion of lentic to lotic habitats, planform shifts and exposure of bare substrates. The flow recession in March 2005 was managed to promote riparian tree establishment. In March 2006, a 48-h experimental flood pulse was released, which produced peak daily flows of 69 $m^3 s^{-1}$ at the stream gage immediately below the dam and 52 $m^3 s^{-1}$ at the gage *c.* 50 km downstream. After an initially sharp reduction, the recession following this peak was gradual, with flows declining approximately 0.7 m^3 s day^{-1} over 15 days, in an effort to provide conditions favourable for establishment of new riparian tree seedlings. In March 2007, a smaller magnitude, 16-h experimental flood pulse was released, which produced peak daily flows of 29 $m^3 s^{-1}$ and 6 $m^3 s^{-1}$ at the upstream and downstream gages respectively (Fig. 5).

These events were small compared with historic floods on the BWR: the 2005, 2006 and 2007 high-flow releases have recurrence intervals of approximately 3, 1.7 and 1.5 years, respectively, when compared with

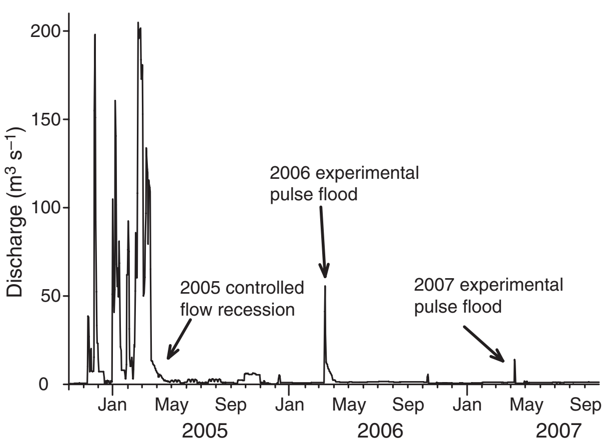

Fig. 5 Mean daily streamflow at the Bill Williams River near Alamo stream gage during a period with experimental flow releases from Alamo Dam and associated hydrology–ecology field research (from 1 Oct. 2004 to 30 Sept. 2007).

predam floods (BWR near Alamo gage). The 2005–2007 controlled floods were more significant within the postdam hydrologic regime, under which, for example, the 2006 flood represents an approximately 5-year event. The significance of these events can also be evaluated in terms of transport stage, which is the ratio of the boundary shear stress during floods to the critical shear stress for mobilisation of bed materials. The 2006 event, for example, had a transport stage on the order of 10 in two study reaches, indicating the potential for even small floods to cause significant sediment transport and bed disturbance in the BWR.

Riparian tree seedling establishment

Establishing and conserving native riparian trees in the Salicaceae family is a resource management priority throughout western U.S.A. and in parts of Europe and Central Asia (Hughes & Rood, 2003; Rood *et al.*, 2005; Thevs *et al.*, 2008). In western North America, forests dominated by *Populus* (cottonwood, poplar) and *Salix* (willow) provide important habitat for numerous wildlife taxa, including hundreds of bird species, some of which are listed as threatened or endangered (Rice, Anderson & Ohmart, 1984). Because of extensive loss and degradation of similar forests along the lower Colorado River, where riparian areas are now dominated by non-native *Tamarix* (Nagler *et al.*, 2005), maintaining cottonwood-willow forests on the BWR is a high priority and has helped guide environmental flow implementation. Environmental flows have promoted riparian *Populus* recruitment on the BWR and other North American systems (Shafroth *et al.*, 1998; Rood *et al.*, 2005), but in other cases, such as the Tarim River in western China, a lack of attention to seedling establishment requirements has made environmental flows ineffective for recruiting new *Populus* cohorts (Zhao *et al.*, 2006).

We are using the Ecosystem Functions Model (HEC-EFM; USACE, 2008) to predict ecological responses on the BWR, including locations of tree seedling establishment under specific flow scenarios. Generally, HEC-EFM helps to translate changes in a flow regime to an ecosystem response using statistical and spatial analyses. HEC-EFM uses (1) time series of daily mean flow and stage and (2) user-defined parameters for variables such as season, duration, rate of change and frequency of occurrence to compute statistics relevant to an ecological response.

Parameters are typically based on hydrologic drivers of important ecosystem processes and the flow requirements of different life stages of the flora and fauna of interest. HEC-EFM computes the flow and stage (statistical results) that meet the parameters defined for the ecological responses under study. This process can be repeated for multiple flow scenarios to gain insights about how different flow regimes can influence ecosystem dynamics.

We used HEC-EFM to model seedling establishment associated with the 2006 experimental flow on the BWR, which was designed, in part, to stimulate recruitment of riparian tree seedlings, particularly *Populus fremontii* and *Salix gooddingii*. We used published information from the BWR and other relevant research on *Populus*, *Salix*, and *Tamarix* establishment to parameterise HEC-EFM. The ecology of *Populus* establishment has been well-studied, and the driving factors are similar for other pioneer trees such as *Salix* and *Tamarix*. For successful establishment, *Populus* seed release typically needs to coincide with flood recession and exposure of bare substrates, the rate of flow recession needs to be gradual enough that seedlings do not desiccate, and flows in subsequent years need to be small enough to prevent seedling removal (Mahoney & Rood, 1998). Seeds of these pioneer taxa do not remain viable for more than several weeks; thus, these conditions must be met promptly after seed dispersal. Recruitment seasons based on seed dispersal phenology and rates for the maximum stage recession that the seedlings would be able to survive were entered as statistical parameters in HEC-EFM. *Populus*, *Salix* and *Tamarix* disperse seed primarily in spring and early summer on the BWR, and their periods of dispersal are partially non-overlapping (Shafroth *et al.*, 1998). Maximum recession rates were estimated as 6 cm day^{-1} over 7 days for *Populus* and *Tamarix* and 4 cm day^{-1} for *Salix* (Shafroth *et al.*, 1998; Horton & Clark, 2001; Amlin & Rood, 2002). The HEC-EFM software was used to compute the flow and stage that met the above criteria for recruitment. These statistical results were simulated with HEC-RAS to compute water surface profiles, which were then translated to depth grids and displayed with GIS using HEC-GeoRAS (Fig. 6).

Riparian tree seedling mortality

In addition to establishing native trees, preventing or limiting the establishment of non-native trees is of global interest in the context of riparian forest restoration (Richardson *et al.*, 2007). Reducing non-native *Tamarix* establishment is often a priority along rivers in western North America (Shafroth *et al.*, 2005). Limited research has suggested that *Tamarix* may be less tolerant of flooding and associated geomorphic processes than native *Populus* and *Salix* species (Stromberg, 1997; Levine & Stromberg, 2001).

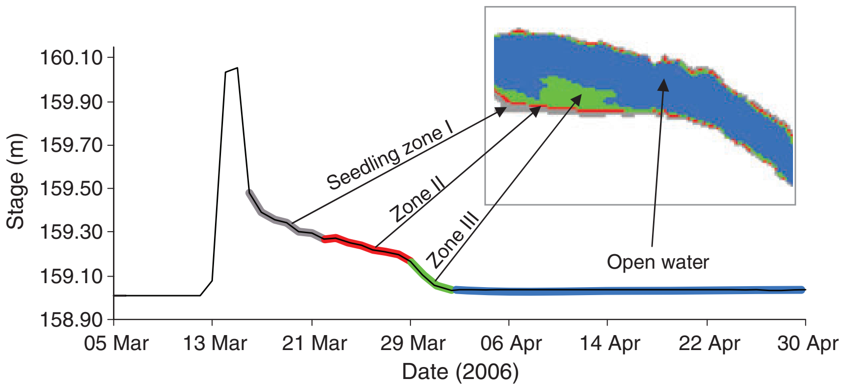

Fig. 6 Ecosystem Functions Model (HEC-EFM) analysis of simulated establishment of three riparian tree species resulting from an experimental flow release from Alamo Dam on the Bill Williams River in Spring 2006. The line figure depicts modelled river stage (dark line), three predicted seedling establishment zones and open water (coloured bands). Seedlings were predicted to become established where substrate was recently exposed, and if seed was available, and river stage recession did not exceed a species' tolerance. Zone I contains only *Populus*; Zone II contains *Populus* and *Salix*; and Zone III contains *Populus*, *Salix* and *Tamarix*. Statistical results were output to the main interface of HEC-EFM and then modelled using HEC-RAS and GeoRAS to generate spatial layers that indicate where different species mixes were predicted to occur. The inset figure (upper right) is a spatial depiction of the three zones and open water along a 75 m reach of the Bill Williams River.

In two study reaches, we collected data before and after each flood on the density, diameter and height of *Salix* and *Tamarix* seedlings; channel bed topography; and flood hydraulics. The two study reaches, Rankin Ranch (RR) and Mineral Wash (MW; Fig. 1), contained bars vegetated with seedlings that established following the 2005 floods, which, because of their differing distances downstream of Alamo Dam, experienced different water discharge and sediment supply during each of the 2006 and 2007 pulses (Figs 1 & 5).

Prior to the 2006 flood, the density of *Tamarix* seedlings that established in 2005 was much greater than that of *Salix* seedlings of the same age (Fig. 7). The diameter and height of *Salix* seedlings, however, were substantially greater than those of *Tamarix*. Both the 2006 and 2007 flood pulses resulted in much greater reductions of *Tamarix* stem density than *Salix* (Fig. 7). The greater antecedent size of the *Salix* likely produced greater resilience to flood-induced mortality from either scour, the dominant mechanism of seedling mortality in the RR reach, or burial, the dominant mechanism in the MW reach. The smaller *Tamarix* seedlings appeared to be especially impacted by burial. These results suggest that floods can increase the relative density of native *Salix* to non-native *Tamarix*, potentially lending a competitive advantage to the native species, and that such effects vary spatially as a function of geomorphic processes.

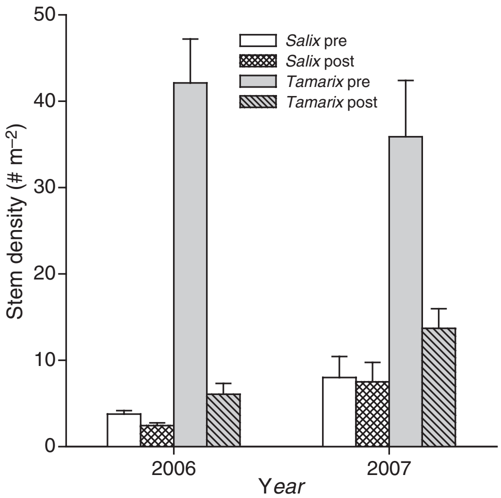

Fig. 7 Mean and standard error of pre- and postflood stem densities recorded in 1 m^2 seedling plots for *Salix* and *Tamarix*, illustrating greater flood-related mortality of *Tamarix* than *Salix* in both years. Data for 2006 are from Rankin Ranch (RR) and Mineral Wash (MW) reaches combined (no. plots = 76 for *Salix*, 71 for *Tamarix*); data for 2007 are from RR only because the 2007 event did not inundate vegetation plots in the MW reach (no. plots = 34 for *Salix*, 45 for *Tamarix*).

Two-dimensional flow modelling with the MDSWMS model described above was used to characterise the local shear stresses affecting vegetation patches in the RR reach during the 2006 flood. Modelled shear stresses do not show a relationship with measures of vegetation response such as *Tamarix* mortality, however. This was contrary to our expectations based on (1) observations of scour as an important mortality mechanism by us and in studies of vegetation removal along other rivers (Friedman & Auble, 1999; Hooke & Mant, 2000; Trush, McBain & Leopold, 2000; Dixon & Turner, 2006) and (2) the well-documented influence of local shear stress on scour (e.g. Nelson, Bennett & Wiele, 2003; Parker, 2008). Modelling the complex relationships among hydraulics, vegetation and bed evolution remains a fundamental challenge (e.g. Darby, 1999; Nepf, 1999; Yager & Schmeeckle, 2007).

Beaver dams

The role of beaver (*Castor canadensis* Kuhl) as ecosystem engineers is well documented (e.g. Naiman, Johnston & Kelley, 1988). Beaver directly affect riparian plants through herbivory and cutting to obtain dam construction materials, and their dams alter local surface and ground water hydrology, channel morphology and associated aquatic and riparian habitats (Baker & Hill, 2003; Butler & Malanson, 2005). Little is known, however, about the influence of river flow regimes on beaver, including the scouring effects of high flows on beaver dams (but see Butler & Malanson, 2005) and beaver sensitivity to extreme low flows.

Beaver lured fur trappers to desert streams in southwestern U.S.A. in the early 1800s (Warren, 1927). In fact, the BWR is named after William S. Williams (1787–1849), who spent much of his life beaver trapping, hunting and exploring or guiding other explorers in the western United States, including the BWR drainage (Favour, 1962). Nevertheless, historical reports and diaries do not provide specific evidence of beaver abundance in the BWR (e.g. Möllhausen, 1858; Favour, 1962). The pre-Alamo Dam hydrologic regime may have been unfavourable to beavers, including intermittent baseflows and extreme floods (Fig. 2a) that would have destroyed dams, dens, food resources and possibly the beaver themselves. Perhaps as a result of the hydrologic changes induced by Alamo Dam, however, beaver have become abundant and geomorphically significant on the BWR in the postdam era. For example, our counts of beaver dams from aerial photographs and ground surveys indicated *c*. 2 dams km^{-1} of river in 2002, after a 7-year long flood-free period with stable baseflows, causing substantial conversion of lotic to lentic aquatic habitat. The BWR beaver appear to den primarily in banks rather than lodges, with sediment excavated during den construction adding to the bedload and suspended material captured in the beaver pond. Although a beaver dam will clearly reduce the rate of downstream sediment transport at lower discharge levels (Pollock, Beechie & Jordan, 2007), it is unclear how dams affect decadal and longer transport rates, which are affected by dam age, flood frequency and the relationships among flood character, dam integrity, and the shear force required to mobilise the pond sediment. Understanding the influence of flows on beaver number, distribution and beaver-related feedback effects is therefore a research priority on the BWR that has implications for other beaver-influenced rivers.

We have hypothesised linkages and are developing empirical models to couple BWR flows to beaver dam and pond dynamics, based on measurements of the effects of experimental flow releases in 2005, 2006 and 2007 (Fig. 5). Aerial photography and field observations indicate that the high flows in 2004–2005 resulted in the breaching or complete removal of all 100+ beaver dams then present. However, new or rebuilt dams were already present by December 2005. The 2006 experimental flood resulted in complete destruction of four of 11 dams selected for intensive monitoring and caused breaches to form in two. No dams were destroyed by the smaller 2007 experimental flood, but two of five dams were breached, resulting in full or partial impoundment drainage. We used these results to relate estimates of the probability of a beaver dam being breached to flow magnitude. Given that all dams can tolerate small floods, floods above some threshold peak discharge destroy all dams, and a sharp threshold in dam vulnerability to breaching is unlikely, we mathematically conceptualised the relationship using a sigmoid curve (Fig. 8). We hypothesize that the probability curve for individual dams will shift to the right or left,

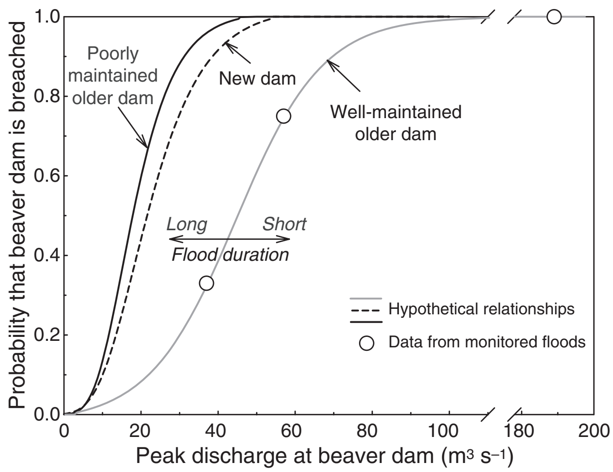

Fig. 8 Semi-quantitative, conceptual model of the relationship between flood pulse peak discharge at a beaver dam and the probability that the dam fails (gray line). The curve is a 4-parameter sigmoid generated using data from three floods on the Bill Williams River (37, 57 and 189 m^3 s^{-1}; open circles) and assumes that all dams are unaffected by a small flow pulse (peak discharge = 0.5 m^3 s^{-1}) and that floods with a peak discharge >189 m^3 s^{-1} result in failure of all dams. The curve could shift to the right or left for individual dams, depending on their structural strength and integrity (black and dashed curves) and on flood attributes other than peak discharge (e.g. flood duration).

depending on dam age, level of maintenance and other factors affecting dam strength and integrity (Fig. 8). Change in flood attributes other than peak discharge also will shift the curve. For example, increasing flood duration shifts the curve to the left, increasing the probability of a dam being breached at a given discharge (Fig. 8).

Aquatic invertebrates

A major habitat feature for aquatic invertebrates is flow variability. While highly-fluctuating flow regimes may decrease overall invertebrate abundance, constant flows and abundant beaver ponds may favour taxa that are suited to stable habitats (Cortes *et al.*, 2002; Robinson, Aebischer & Uehlinger, 2004). Relatively steady baseflow discharges on the BWR between 1996 and 2004 (Fig. 2) may have facilitated increased population survival and growth of taxa adapted to constant flow conditions, and in turn decreased populations of native desert–riverine taxa adapted to more variable flow regimes. Changes in invertebrate populations and their densities could have important implications for riverine food webs, as invertebrates and their aerial life stages are key food sources for fish, birds and other taxa (Nakano & Murakami, 2001; Schindler & Scheuerell, 2002; Baxter, Fausch & Saunders, 2005).

The BWR harbours a diversity of aquatic invertebrate species that could be divided into three groups based on life history, morphological and behavioural traits that influence their expected response to flooding disturbance (Lytle & Poff, 2004). 'Susceptible' taxa experience high rates of mortality from floods and low rates of recovery postflood (i.e. low resistance and low resilience, *sensu* Grimm & Fisher, 1989). Traits of susceptible taxa may include the lack of an aerial life stage, long life cycle, rarity, or lack of morphological or behavioural adaptations for flood survival. Ostracods inhabiting the BWR below Alamo Dam exhibit some of these traits, in particular the lack of an aerial stage that could provide a refuge from flooding. 'Resistant' taxa have some adaptations for surviving floods, although they may experience mortality from larger flood events. Resistant taxa (e.g. Odonata: Gomphidae) may have longer life-cycles, medium to low relative abundance and some adaptive mechanism for surviving floods, such as the use of positive rheotaxis to return towards the main channel from side channels during flood recession (Lytle, Olden & McMullen, 2008). 'Opportunistic' taxa may have rapid postflood recovery, even though they can experience high mortality from floods (i.e. high resilience; Grimm & Fisher, 1989). Typical traits of opportunistic taxa (e.g. Ephemeroptera in the families Baetidae and Leptohyphidae) include fast life cycles, year-round reproduction, an aerial adult stage, high abundance and morphological adaptations for surviving floods, such as hydrodynamic streamlining or protective cases (Lytle & Poff, 2004).

As part of the environmental flow studies in the BWR, we are investigating how flow magnitude and variability influence aquatic invertebrates and the spatial variation in invertebrate response to peak flows. We sampled two sites before and after the 2007 pulse flow on the BWR (RR and MW; Fig. 1). At each site five transects were sampled, approximately 200 m apart, and four, timed D-net kick samples were taken and pooled. Invertebrates were stored in 95% ethanol, subsampled to at least 300 organisms per transect, and identified to genus or lowest possible taxonomic level. Abundances were estimated by multiplying the number of organisms identified by the inverse of the fraction subsampled and divided per habitat area. We quantified flood effects using log response ratio (log of postflood over preflood density) because it accounts for deviations around the mean for both pre- and postflood samples and linearises the sampling distribution (Hedges, Gurevitch & Curtis, 1999).

After the 2007 experimental flood, ostracod populations were severely reduced and did not recover even after 2 weeks (Fig. 9). While both Gomphidae and Ephemeroptera experienced flood-induced mortality, both groups rebounded in numbers after 2 weeks (Fig. 9). We attribute the rapid return of gomphids to their ability to move back to the active stream channel, even when they were displaced into high flow channels that dried out postflood. Recovery of Ephemeroptera was likely because of recruitment from aerial adults that were present during the flood. For example, one abundant taxon, *Fallceon quilleri* (Baetidae), can complete its life cycle in only 9–11 days (Gray, 1981). Ephemeroptera recovery

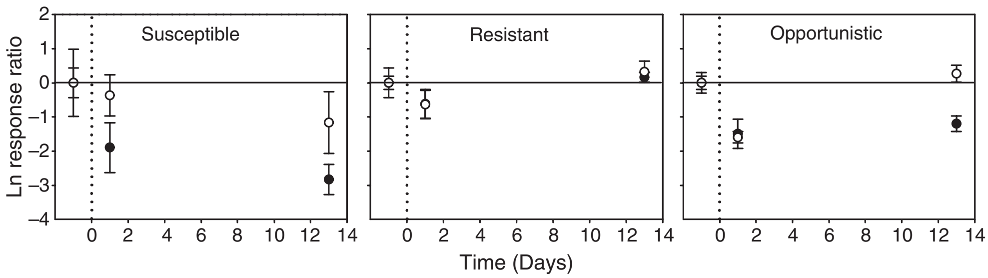

Fig. 9 Natural log of the response ratio (postflood over preflood density) for susceptible (Ostracoda), resistant (Odonata: Gomphidae) and opportunistic (Ephemeroptera) taxa relative to the 2007 flood event at two sites in the BWR. Solid circles represent Rankin Ranch and open circles represent Mineral Wash. Error bars denote variance of log response ratio. Negative values indicate postflood reduction, and positive values indicate postflood increase.

differed at RR versus MW, possibly because of other differences in the habitat such as substrate characteristics or downstream attenuation of flood magnitude and duration.

Discussion

The BWR is proving to be an outstanding natural laboratory for investigating relationships between river flows, geomorphic processes and biotic responses. A diverse set of physical system models and linked, physical–biological response models are being tested, validated and refined through the implementation of regular, experimental flow releases. Results are being reported to land and water managers along the BWR to help to guide adaptive reservoir management (Fig. 3). We anticipate that our applications of existing (e.g. HEC-RAS, MDSWMS and MODFLOW) and new (HEC-EFM) models to the context of environmental flows will be transferable to other situations, such as rivers in North America, Europe and Central Asia where *Populus* forest restoration is desirable. As well, our field observations and associated models of flow–biota relationships can serve as hypotheses to be tested on other rivers.

The hydrology–ecology relationships we describe in this paper (riparian seedling establishment, seedling mortality, beaver dam persistence and invertebrate guild dynamics) all exhibit responses to flow that are non-linear and include important thresholds. Articulating these types of thresholds can be instrumental for managing river-specific or regional environmental flow programs (Poff *et al.*, 2010). In riverine systems, threshold responses can be complex and related to various aspects of flow such as magnitude, duration, frequency, timing and rate of change. In the case of riparian seedling establishment, for example, rapid rates of stage decline and hence desiccation may cross thresholds for seedling survival (Mahoney & Rood, 1991). For beaver dams, crossing particular flow thresholds (and associated physical force thresholds) could lead to a shift from minor or modest damage to complete removal of dams.

Many of the types of threshold relationships among river flows and biota are driven by geomorphic thresholds (Bull, 1979; Church, 2002). Initiation of bed-particle motion is one such threshold that is fundamental to sediment transport and geomorphic change (e.g. Church, 2006). Bed-mobility thresholds are exceeded by relatively frequent flows in the sand-bedded BWR, and, for example, appear to trigger mortality of benthic invertebrates, as documented following the 2007 flood (1.5-year recurrence interval). A different set of flow and shear stress thresholds apply to seedling mortality, such that mortality occurs where flows are large enough to scour low-elevation bars in the active channel to a depth sufficient to cause vegetation scour (Friedman & Auble, 1999; Dixon & Turner, 2006; Sandercock, Hooke & Mant, 2007). Aggradation-induced seedling mortality may be driven by thresholds of the depth of sediment deposition in relation to seedling height (Levine & Stromberg, 2001; Gurnell & Petts, 2006; Polzin & Rood, 2006). Because key thresholds such as those associated with bed mobilisation are easily exceeded in sand-bed rivers such as the BWR [see for example Church's (2006) discussion of 'labile' channels], even modest environmental flow releases can be geomorphically and ecologically effective. This effectiveness is restricted to low-elevation areas of the channel, however. Thresholds associated with scour of larger trees and channel widening across the historic floodplain, as occurred during large floods in the predam era, are no longer exceeded on the BWR. On dammed rivers in general, environmental flow releases are unlikely to attain sufficient magnitudes to reverse changes to floodplain areas that have become inactive as a result of dam construction (Graf, 2006).

Although the effects of dams on geomorphic processes are well documented (e.g. Williams & Wolman, 1984; Graf, 2006; Schmidt & Wilcock, 2008), many environmental flow programs attempt to make direct linkages between flow and biotic response without considering the mediating effect of geomorphic processes and consequent habitat structure and dynamics, with notable exceptions such as studies on the Trinity River, California (Kondolf & Wilcock, 1996; Trush *et al.*, 2000) and the Colorado River in Grand Canyon, Arizona (Schmidt *et al.*, 2001). Incorporation of modelling approaches that account for geomorphic processes, including models of sediment transport, channel migration and sediment budgets, holds great potential for advancing efforts to link flow variables and flow regime change to biotic responses and thereby strengthen the scientific basis of environmental flow assessments and implementation strategies.

Significant spatial and temporal complexity in hydrology–ecology relationships can result from longitudinal hydrologic and geomorphic variation downstream of an environmental flow release point and from ecohydrological feedbacks. On the BWR, for example, attenuation of experimental flood pulses downstream of the release point in 2006 and 2007 led to considerable variation in system responses, such as riparian tree seedling mortality and benthic macroinvertebrate dynamics (Figs 7 & 9). Key feedbacks include the effects of beaver activity on channel morphology, local hydraulics and habitat for other aquatic organisms (Butler & Malanson, 2005). Further, interactions between riparian vegetation growth, bar and bank stability, and drag effects of vegetation generate feedbacks (Bennett & Simon, 2004; Corenblit *et al.*, 2007; Sandercock *et al.*, 2007) that influence the effects of a given environmental flow release over space and time.

The environmental flow experiments on the BWR have been facilitated by some of the unique characteristics of the system described above, including the close collaboration between water managers and scientists and the relative lack of constraints on environmental flow releases. The commitment of time and expertise by government and academic scientists has contributed a level of expertise and depth to the BWR studies that, on the one hand may not be typical or feasible for all environmental flow programs, but on the other hand has fostered efforts to develop models and insights about hydrology–ecology linkages that are generalisable beyond the BWR. At the regional scale, findings from the BWR will contribute to creation of a regional 'library' of hydrology–ecology response curves, which will facilitate knowledge transfer, aid identification of regional research needs and priorities, and help to create a foundation for efforts such as developing regional environmental flow standards (Poff *et al.*, 2010). More broadly, lessons from the BWR will help advance environmental flow science beyond qualitative understanding of how flows affect biota toward development of quantitative relationships between specific features of flow regimes and ecosystems.

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