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Legacies, lags and long-term trends: Effective flow restoration in a changed and changing world

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Abstract

1. Human impacts on natural ecosystems are pervasive and will play out more severely as human populations and per capita resource use increase. Freshwater ecosystems are critical for human well-being and experience a diverse range of human-induced pressures. Most river systems throughout the world have much-altered flow regimes.
2. The Murray–Darling Basin in southeastern Australian has been the focus of an extensive water reform process to address the over-allocation of water for human uses. This has included many scientific investigations, hydrological modelling and the development of institutional and market structures to reallocate water. Substantial recovery of water has been achieved, which has been used to restore aspects of the natural flow regime.
3. We reviewed recent papers on responses to flow restoration in the Murray–Darling Basin and complemented this with inferences from the global literature. Ecological responses to flow restoration are often inconsistent, site and taxon specific and difficult to detect.
4. By combining ideas from mainstream thinking in restoration ecology with the insights from our review, we propose a conceptual model for understanding responses to flow restoration. This model incorporates key factors that influence the size of ecological responses to restoration, including existing ecological condition, legacy impacts of past change, interactions with other variables, life-history traits of taxa and broad-scale and long-term trends due to climate or land-use change.

KEYWORDS
antecedent conditions, environmental flows, Murray–Darling Basin, river management

1 | INTRODUCTION

The ecological impacts of human actions are pervasive at a global scale, profoundly affecting freshwater ecosystems, which have lost and continue to lose, disproportionately more species than other ecosystems (Ormerod, Dobson, Hildrew, & Townsend, 2010; Strayer & Dudgeon, 2010). Increasing global demands for fresh water for human consumption, agriculture and energy production means that most of the world's large river basins are now substantially degraded ecologically (Nilsson, Reidy, Dynesius, & Revenga, 2005; Vörösmarty et al., 2010). Given the predominance of degraded ecosystems, there is an increasing emphasis on environmental restoration and management to protect and to restore freshwater ecosystems (Dudgeon et al., 2006). This has resulted in large-scale and resource-intensive restoration programmes in stream and river habitats throughout the world, for example, Colorado River Restoration Project (Follstad Shah, 2007), Murray–Darling Basin Plan (Kneebone & Wilson, 2017) and the Danube Restoration Project (Schiemer, Baumgartner, & Tockner, 1999). However, given the economic and social investment in these large programmes, there has been ongoing and increasing concern about a failure to detect some of the expected improvement in condition after restoration activities have been implemented. This is not only due partly to a lack of monitoring (Bernhardt et al., 2007), but also because of the major challenges involved in restoring natural patterns of biodiversity and ecosystem function in rivers and streams (Dufour & Piégay, 2009). Flow restoration can be particularly challenging because of ongoing human needs for water and the exploitation of riverine systems (e.g. floodplains) that need to be accommodated in restoration planning.

Globally, rivers are experiencing significantly altered patterns of flow from human activities (Vörösmarty et al., 2010). This has occurred through abstraction (harvesting) of water for irrigation, mining and domestic supply, and alterations of rivers for flood control and for the generation of hydroelectric power. Flow is a "master variable" of patterns of biodiversity and ecosystem function in rivers and streams, both in total volume of water and in terms of the size, timing and frequency of high- and low-flow events (Poff et al., 1997). The natural flow regime has been associated with roles in river ecosystems, including acting as a cue for species reproduction and movement, mobilising nutrients and energy, altering chemical conditions, creating physical habitat through disturbance and providing passage for organisms laterally and longitudinally (e.g. Bunn & Arthington, 2002). Modification of flow regimes by human activities can reduce average or base flows, remove mid-size flood events, reduce flow variability, impede longitudinal and lateral connectivity and alter seasonal flow patterns (e.g. Arthington, Bunn, Poff, & Naiman, 2006; Gehrke, Brown, Schiller, Moffatt, & Bruce, 1995; Toth, Obeysekera, Perkins, & Loftin, 1993). Flow management often decouples sediment dynamics and water quality from the flow regime, and is associated with engineering interventions, such as channelisation and levees, which further influence river flow dynamics (e.g. Poff et al., 2010; Wohl et al., 2015). Water releases to restore or to protect aspects of the natural flow regime are often referred to as "environmental flows" (eflows) or environmental watering (Arthington, Naiman, McClain, & Nilsson, 2010; Arthington et al., 2006). These include protection of flows to avoid loss of key components of the flow regime (King et al., 2015), and flows that are provided to restore the natural flow regime (sensu Poff et al., 1997), or that are "designed" to create a flow regime intended to deliver specific ecosystem outcomes (Acreman et al., 2014).

Studies investigating the effects of restoring flow regimes downstream of dams commenced mainly in the early 2000s (e.g. King et al., 2010; Richter & Thomas, 2007; Sun, Yang, & Cui, 2008; see Olden et al., 2014 for a review). The increasing number of studies have generated empirical data on flow–ecology relationships and contributed to the development of conceptual or theoretical models that are now being used in water management and in policy decisions (e.g. King et al., 2010; Koster, Amtstaetter, Dawson, Reich, & Morrongiello, 2016; Shafroth et al., 2010). The provision of flows for environmental benefits has moved from providing minimum base flows (e.g. Acreman & Dunbar, 2004) to considering the importance of the timing, magnitude and frequency of flow events (e.g. Lytle & Poff, 2004). Biotic responses to flow modification are well known to be highly variable among systems and environmental conditions (Poff & Zimmerman, 2010), so that flow regimes may need to be tailored to particular environmental outcomes (Acreman et al., 2014). However, there is a concern about the robustness of experimental design and monitoring in many environmental flow studies (Davies et al., 2014; King et al., 2015; Konrad et al., 2011; Olden et al., 2014). Increasing competition for freshwater resources between consumptive and environmental users necessitates greater knowledge and certainty about the nature and magnitude of responses to water provided for environmental outcomes (Galat, 2008; Poff, 2017; Rosenfeld & Ptolemy, 2017).

Our focus is on the Murray–Darling Basin (MDB) in southeastern Australia, which in many respects is an exemplar system in which to embed our commentary. The MDB has been the focus of an extensive water reform process to address the over-allocation of water for human uses (Kneebone & Wilson, 2017). There has been an investment of >$AUD13B, which has involved a lengthy process of scientific investigation, hydrological modelling and the development of institutional and market structures to reallocate water (Hart, 2016). Key to this has been the development of sets of eco-hydrological relationships that have allowed the estimation of a "sustainable diversion limit" for the rivers of the MDB (Swirepik et al., 2016). The process of reform has been contested politically and scientifically (see Capon & Capon, 2017; Hart, 2016 for a review). Notwithstanding the multi-million dollar investments in monitoring, ecological responses to eflows in the Murray River have been inconsistent, site and taxon specific and sometimes difficult to detect (e.g. Campbell, Johns, & Nielsen, 2014; Vivian, Marshall, & Godfree, 2014; Zampatti & Leigh, 2013).

Water reform for improved ecological outcomes is achieved through a broad understanding of the potential benefits of eflows and the likely impediments to observing ecological responses on specific time scales. Understanding the likely time scale of the targeted ecological response is important for developing a narrative for decision makers and the general public alike (King et al., 2015). Here, we conceptualise a set of generic response curves to the provision of eflows, incorporating factors that may influence the nature of the ecological response: antecedent conditions and their legacies, natural history and changing underlying conditions. Building on the review by Davies et al. (2014), we describe studies of the outcomes of eflows in the Murray–Darling Basin to our proposed mechanisms affecting responses and place them in the context of key international studies. We assess the potential role of species traits in predicting responses. Finally, we discuss the challenges of predicting whole-of-ecosystem responses to eflows.

2 | FACTORS LIMITING ECOLOGICAL RESPONSES TO FLOW RESTORATION

The provision of eflows is intended to either protect or to restore the ecological condition of an “asset” (a population, an ecological process or an aquatic ecosystem) (Arthington et al., 2010). Improving condition may mean triggering a fish-breeding event, restoring geomorphological processes to enhance habitat, enhancing waterbird breeding or watering riparian plants to improve vegetation condition. We define ecological condition as the deviation from an agreed-upon ecological state (e.g. a pre-impact reference condition or a predetermined improved environmental condition). We conceptualise an eflow as a single pulse event that generates a positive response in condition, although eflows more typically are a complex set of actions that include prolonged flows, series of flow peaks and “piggyback flows,” which are designed to mimic or to prolong natural flow events.

We combined ideas from mainstream thinking in restoration ecology (Hobbs & Harris, 2001; Perring et al., 2015; Suding, 2011) with recent papers on responses to environmental watering in the Murray–Darling Basin (after 2012, see Davies et al., 2014 for previous work), complemented by some key international studies. Studies were restricted to those that described responses to the managed delivery of eflows rather than responses to natural flow events. We focused on measures that responded to the provision of flows and to interpretations for why responses may not have been seen, and commentaries on factors that may have affected responses (Table 1). We did not intend to provide a detailed meta-review, but rather, we assessed the degree to which the proposed conceptualisations of limitations to response to eflows may occur.

2.1 | Legacies and antecedent (prior) conditions

The potential for an environmental asset to respond to an eflow can be strongly influenced by antecedent conditions on a range of temporal scales (Table 1). The effects of historical disturbances in rivers and streams can affect outcomes of eflows long after the original disturbance (Humphries & Winemiller, 2009; Stanley, Powers, & Lottig, 2010; Wohl et al., 2005). Responses to restoration in urban streams can be modulated by legacy effects of the original clearance of catchments for agriculture (e.g. Utz et al., 2016), effects of channel works such as levees and bank stabilisation or pollution events. Legacy impacts affect responses to eflows in numerous riverine systems around the world. Ecological responses to flow restoration in the Upper Delaware River (U.S.A.) have been hindered by legacy effects of industrial pollution in the catchment (Parasiewicz, Castelli, Rogers, Vezza, & Kaupsta, 2017). Altered sediment dynamics from upstream impoundments have a substantial impact on the magnitude of ecological responses to the provision of eflows in the Colorado and Upper Mississippi Rivers, U.S.A. (Ladson & Argent, 2002; Shafroth et al., 2010). Eflows to restore salmonid populations in the Columbia River (U.S.A.) may have been hindered by the legacy effects of catchment logging (Ladson & Argent, 2002).

The removal of in-channel woody debris in the Murray River, largely for navigation, and the removal of trees and carbon from floodplains limit the degree to which the main river channel responds to eflows (Baldwin & Mitchell, 2000; Erskine & Webb, 2003). Sediment composition in the Murray River and its tributaries may continue to respond to the legacy of land clearance over the last century (Gell & Reid, 2016). Some of the relatively large site-to-site variability in responses to provision of flows may be due to the historical variability in intensity of management in the surrounding landscapes (Campbell et al., 2014). Understanding the degree to which historical disturbance events affect system response to eflows is important for developing realistic targets and for understanding smaller than anticipated ecological responses to eflows.

Over time scales of years to decades, the condition of an ecosystem as a consequence of more recent conditions can affect the potential for the system to respond to an eflow event (Table 1) (Horne et al., 2017). Between 1997 and 2010, southeastern Australia experienced the longest drought in the instrumental record. The relatively poor condition of the dominant canopy tree (river red gum *Eucalyptus camaldulensis*; Cunningham et al., 2009) and the degradation of understorey vegetation due to the prolonged drought meant that flowering and seeding responses to eflows were small initially, as trees first regained condition and vegetation regenerated from seed banks (Glenn, Nagler, Shafroth, & Jarchow, 2017). Similar effects were seen in the Platte River (U.S.A.), where low flows allowed the invasion of the channel by woody plants, which meant that in-river ecosystems did not recover even when flows were restored (Smith, 2011).

Pre-existing ecological condition of vegetation has been widely shown to affect responses to flows (e.g. Capon, Balcombe, & McBroom, 2017; Nagler et al., 2015; Smith, 2011), and there are similar findings for fish, in which the abundance and individual condition of the stock influence the magnitude of the responses (King et al., 2010; Koster et al., 2017). Lagged responses to eflows due to existing poor ecological condition have been identified as an important issue in many parts of the world (e.g. Hughes & Rood, 2003; Richardson et al., 2007). Good ecological condition can constrain the degree to which a system can respond to eflows (Figure 1a). Delivery of eflows to systems that already are responding to water in the landscape, either through local rainfall or from upstream flooding, may lead to marginal improvement from any eflows provisions. Juvenile native fish in wetlands of the Murray River responded positively to frequent inundation of wetlands, but non-native species responded positively to long dry periods followed by short-term inundation events (Beesley et al., 2014). Understanding the interaction between existing ecological condition and the potential magnitude of responses will inform more realistic expectations for the amount of ecological improvement that is likely to be seen following eflows (Figure 1a).

TABLE 1 Recent (2014–2017) examples of studies of ecological responses to environmental flows in the Murray–Darling Basin. Shading shows where antecedent conditions ("legacies"), lag responses ("lags") and long-term trends in overall condition ("trends") may have altered responses based on review by the authors of this paper

Reference	Type of study	Outcome	General finding	Legacies	Lags	Trends
Capon et al. (2017)	Green house expt. (multiple sites sampled)	Vegetation recruitment responses to watering depend on canopy condition	Antecedent conditions that influence canopy condition affect watering outcomes			
Howard et al. (2017)	Field study (single site/flow)	Turtle body condition improved after eflow delivery. Abundance decreased	Individuals of long-lived species show immediate, but population responses lag			
Koster et al. (2017)	Field study (multiple sites and flow events)	Movement and spawning induced in golden perch by environmental watering. Magnitude of response variable between watering events	Likely role of antecedent conditions in determining magnitude of response			
King et al. (2016)	Field study (1 river, 10 years, 3 sites)	Temperature and flow influence the timing and strength of fish spawning	Short-term antecedent flow conditions influence spawning intensity			
Stocks et al. (2016)	Field study (1 river, 1 year, 20 sites)	Fish recruitment observed for species with opportunistic/equilibrium life histories including native fish and a significant pest species (carp)	Life-history traits of species influence potential to respond to flows. Presence of a significant pest may limit potential response of native fish species			
Doody et al. (2015)	Field study (1 system, space for time design)	Native tree show immediate physiological response to watering, but full response takes several years. Climate change may limit potential response	Individuals of long-lived species show immediate, but population level responses lag. Long-term trends in climate may affect responses to environmental flows			
Nagler et al. (2015)	Large-scale field study (remote sensing study of tree condition)	Immediate physiological response to watering, lasting 2 years. Response size affected by previous drought. Climate change likely to limit potential response	Individuals of long-lived species show immediate, but population level responses lag. Antecedent conditions/climate change affect watering outcomes			
Beesley et al. (2014)	Field study (6 wetlands, 1 river, 5 years	Native fish respond positively to frequent inundation of wetlands, while non-native fish responded positively to long/medium dry periods and short wet periods	Short-term (up to 5 years) antecedent flow conditions affect native and non-native fishes differently, potential opportunity for water management to favour native fish			
Campbell et al. (2014)	Field study (18 wetlands)	Changes in plant community composition when environmental watering is applied. High wetland-to-wetland variation	Variation in historical management of wetlands may affect outcomes			
Conallin et al. (2014)	Field study (single site/flow)	Movement of native turtles and bony herring and invasive carp and goldfish into wetlands with environmental flows	Presence of an invasive species may limit potential response of native fish species			

Invasive species can modulate the potential benefits of eflows. The legacy and ongoing effects of invasive species on ecosystems can be profound and can limit restoration improvements (e.g. D'Antonio & Meyerson, 2002; Richardson et al., 2007; Smith, 2011). The presence of invasive species can reduce positive ecological responses to eflows (Stocks et al., 2016). Eflows may favour invasive species over native species (Bond et al., 2014). Eflows can increase the spawning and recruitment of common carp (*Cyprinus carpio*) in the Murray River and its tributaries (Brown, Sivakumaran, Stoessel, & Giles, 2005; Conallin, Smith, Thwaites, Walker, & Gillanders, 2014; but also see King et al., 2016), while eflows can favour the invasion of exotic plants in riparian wetlands (Catford, Downes, Gippel, & Vesk, 2011; Richardson et al., 2007). The delivery of eflows needs to be conducted with concurrent management of invasive species.

2.2 | Lags in ecological responses

Ecological responses to eflows usually are not immediate, requiring decisions about monitoring or reporting on ecological outcomes to

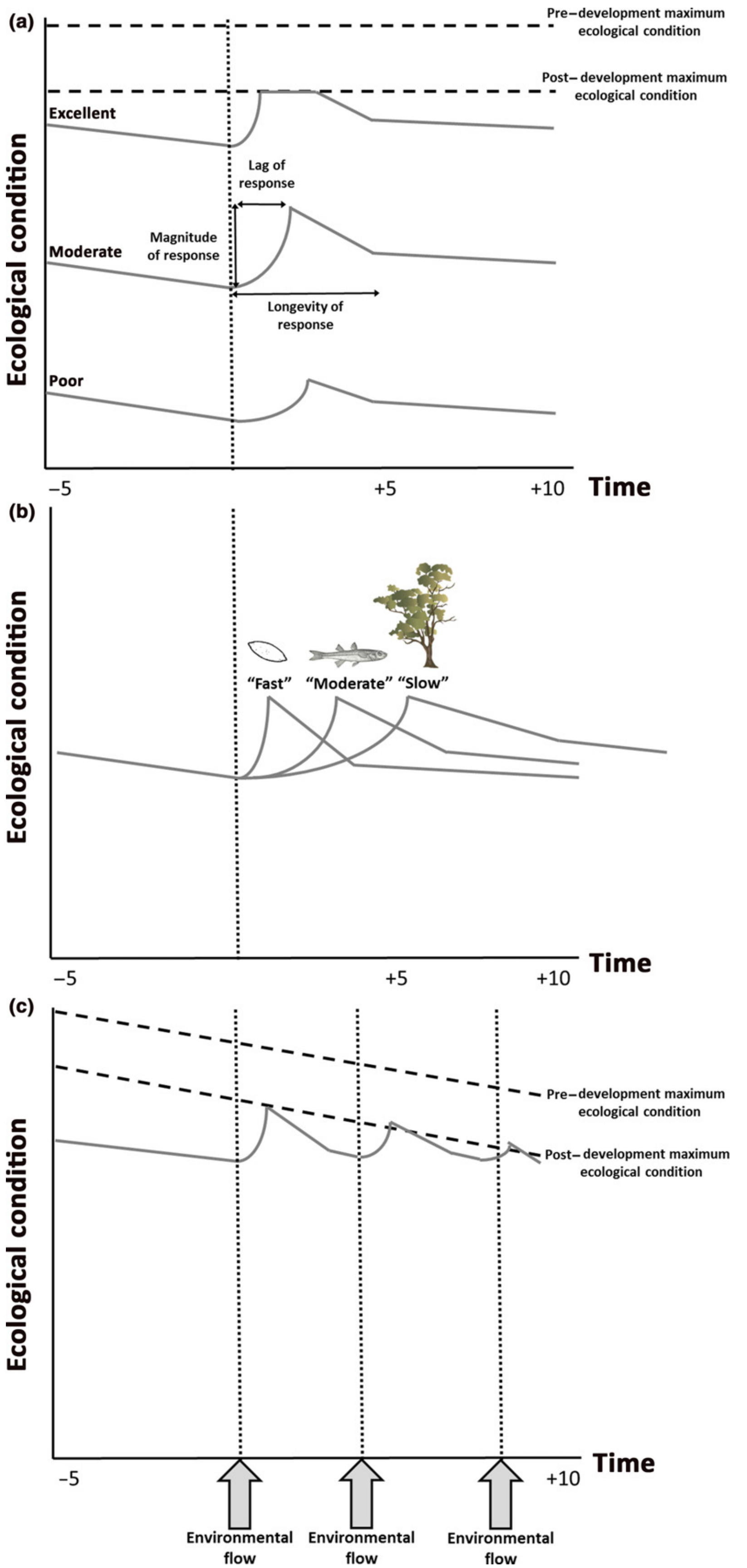

FIGURE 1 Conceptual framework for responses in improved ecological condition with provision of an environmental flow peak: (a) initial poor ecological condition reduces the magnitude of the response observed; (b) potential role of life-history traits ("fast" algae, "moderate" small bodied fish and "slow" riparian trees) in determining the time until responses are observed and (c) underlying long-term downward trend in condition reduces potential magnitude of responses to eflows through time [Colour figure can be viewed at wileyonlinelibrary.com]

consider likely response times for the chosen environmental asset (King et al., 2015). Failure to incorporate delays or "lags" into monitoring and communication strategies poses significant challenges to evaluating and articulating the benefits of flow restoration (Bernhardt & Palmer, 2011; Gutrich & Hitzhusen, 2004). Lags in responses may arise from basic biochemical processes that require time to be initiated, such as for sediment or litter dynamics (e.g. Baldwin & Mitchell, 2000; Hamilton, 2012). Lags may arise from hydrological processes in which eflows must first replenish shallow groundwater systems before surface water can trigger ecological outcomes (Wilby, Fenn, Wood, Timlett, & LeQuesne, 2011).

Life-history attributes can induce different degrees of lag in responses (Table 1). Taxa with short life cycles, short lived and often small bodied, often have rapid responses. Phytoplankton, some macroinvertebrates and bacteria respond very rapidly (within hours) to alterations in flow conditions (e.g. Watts et al., 2013; Whitworth, Baldwin, & Kerr, 2012). However, longer lived taxa may respond relatively slowly (potentially over several years) to eflows. Fish have a wide range of life-history traits, with species with "faster" life histories more likely to respond more rapidly to eflows (e.g. Arthington & Balcombe, 2011; Mims & Olden, 2013; Stocks et al., 2016). While eflows may improve individual body condition in some long-lived species (e.g. turtles; Howard, Beesley, Ward, & Stokeld, 2017; riparian trees; Doody et al., 2015), population responses for long-lived taxa are likely to take much longer, such as for platypus (*Ornithorhynchus anatinus*, Klamt, Davis, Thompson, Marchant, & Grant, 2016) and flood-dependent eucalypts (Mac Nally, Cunningham, Baker, Horner, & Thomson, 2011). The lengths of lags probably depend on pre-existing ecological condition, with degraded systems having longer lags than more natural systems (Bond, Lake, & Arthington, 2008) (Figure 1b). Eflows can affect differentially life-history stages, such as waterbird breeding events, so that population responses would be lagged. Demographic lags should be considered in ecological response modelling (Shenton, Bond, Yen, & Mac Nally, 2012) and predictions and expectations for eflow outcomes.

Differences in the life-history traits of taxa and the consequent disparities in responses to eflows may affect community assembly. "Foundation" species are structurally and functionally significant taxa that provide critical resources for the community (Ellison et al., 2005). These taxa are often long lived, with "slow" life histories. In the Murray River system, the river red gum is a foundation species (Kominoski et al. 2013), with response lags of several years to eflows likely needed to achieve canopy condition and flowering (Doody et al., 2015; Nagler et al., 2015). Lags in the red gum response may profoundly affect responses in other taxa, such as floodplain woodland birds and mammals (Mac Nally, Lada, Cunningham, Thomson, & Fleishman, 2014). Differences in life-history traits of species in communities may induce complex and potentially unpredictable community changes. Soon after an eflow event, there is likely to be a dominance of primary producers, favouring bottom-up dynamics, followed by primary consumers, favouring top-down dynamics, and eventually top predators, potentially generating trophic cascades. The role of species' traits in driving differences in responses to flow restoration has been described for vegetation (Merritt, Scott, Poff, Auble, & Lytle, 2010), fish (Mims & Olden, 2013) and macroinvertebrates (e.g. Bonada, Rieradevall, & Prat, 2007).

2.3 | Long-term trends

Successful local scale restoration needs to account for large-scale trends in ecological condition, such as climate change (Pachauri, Meyer, Plattner, & Stocker, 2015) and catchment scale, land-use change (Mac Nally et al., 2011). Riparian restoration may not result in biodiversity responses because of long-term drying and heating at regional scales (e.g. Perry, Andersen, Reynolds, Nelson, & Shafroth, 2012; Richardson et al., 2007). Aquatic systems are vulnerable because of projected changes in both temperature and rainfall due to climate change (Davies, 2010; Humphries & Winemiller, 2009; Timbal, 2015). The potential for the impacts of climate change to hinder the restoration of rivers is now well recognised (e.g. Dutta, Sharma, & Kumar, 2017; Palmer et al., 2008). Building longer term trends in stressors into management frameworks has been attempted for a number of systems globally (e.g. Ekblom, Gillson, & Notelid, 2017; Wang et al., 2017; Yan, Ludwig, Huang, & Werners, 2017). Interactions with other long-term trends, such as changes in riparian vegetation, are important (e.g. Mango, Melesse, McClain, Gann, & Setegn, 2011; Palmer et al., 2008).

Changes in the vegetation of riparian zones throughout the Murray–Darling Basin have been profound over the last century, initially from land clearance and more recently from restoration activities. The biota of streams with restored vegetation in their catchments may be more resistant to the impacts of changing climate than unrestored or degraded catchments (Thomson et al., 2012). However, much of southeastern Australia has experienced long-term drying and heating (Leblanc, Tweed, Van Dijk, & Timbal, 2012), upon which high-amplitude, short-term climate variation has been superimposed (Mac Nally, Horrocks, & Lada, 2017). Several important riparian tree species may be at the limits of their physiological tolerances in parts of the Murray River Basin, making them vulnerable to the effects of climate change (Mac Nally et al., 2011). Climate change may be a major impediment to achieving improvements in ecological condition from eflows (Table 1) (Doody et al., 2015; Nagler et al., 2015). Other long-term trends arising from native-vegetation clearance, agricultural intensification, altered rates of sediment supply or changes in water quality are likely to influence responses to eflows.

There are two important issues to consider vis-à-vis the effects of long-term trends in baseline conditions on responses to eflows. The first is the trend in the maximum achievable response to environmental watering given long-term change (Kingsford et al., 2015). If there is a decreasing trend in the maximum achievable condition, then ecological improvements from eflows may decline through time (Figure 1c). Second, the downward trend in baseline condition may be so substantial that even eflows cannot promote the persistence of many taxa. There is the potential for this to occur in some parts of the Murray–Darling Basin for taxa at the limits of their physiological tolerances, which is similar to predictions for salmonids in much of North America, where climate-change effects will hinder recovery of populations even when with eflows (Wenger et al., 2011). Conceptually and quantitatively, incorporating these into processes into expectations for eflow responses is an important part of understanding how benefits and costs might change against a background of overall decline in environmental suitability.

3 | TOWARDS PREDICTION FOR EFLOW ECOLOGY

Allocating water to the environment can be a contested action with diverse and opposing social, political and economic viewpoints. There is ever-increasing demand for fresh water around the world, which will require defensible justifications for the allocation of flows for improving ecological condition. We propose that future thinking on eflow objectives and outcomes should consider the following five factors:

1. Conceptual frameworks for predicting ecological responses to restoration actions need to take into account legacies, lags and long-term trends. Along with improved understanding of cause–effect relationships, this will lead to the development of more quantitative models and guide key data collection to inform those models and lead to better understanding. Such frameworks are important for communication and managing expectations of investors and the general public.
2. Responses to eflows differ in landscapes due to the legacies of previous disturbances and interactions with invasive species and land-use change. Understanding spatial patterns of responses to eflows and the contingencies that drive these is an important component of flow management.
3. Data and knowledge describing which ecosystem components will respond to restoration actions, and over what time scales (lags) and mechanisms, are urgently required. Improved understanding of how species' life-history traits determine the magnitude and timing of responses to eflows is a key research and management need.
4. Ecological responses to eflows are influenced by non-flow-related factors, through mechanisms and relationships that are often incompletely understood. These include sediment regime and dynamics, water quality, channel form (including engineering of channels), biotic demographic rates and ecological processes.
5. Understanding community-level responses to environmental flows requires a framework that accounts for interacting effects of antecedent conditions, lag responses, species traits' and species' interactions.

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