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Beyond the natural flow regime? Broadening the hydro-ecological foundation to meet environmental flows challenges in a non-stationary world

N. LeRoy Poff[1,2]

[1]Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO, USA

[2]Institute for Applied Ecology, University of Canberra, Bruce, ACT, Australia

Correspondence
N. LeRoy Poff, Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO, USA.
Email: poff@lamar.colostate.edu

Abstract

1. The natural flow regime concept has contributed significantly to environmental flows (e-flows) science and applications over the last 20 years. Natural flow regimes reflect long-term, historical patterns of flow variability that have shaped riverine species' adaptations and continue to shape community and ecosystem structure and function. This scientific perspective, however, carries with it important assumptions about climatic and ecological stationarity in terms of "reference" conditions that provide a basis for comparing success or outcomes of e-flow interventions.
2. Non-stationarity in climate and other environmental conditions (temperature, sediment, nutrients) and in ecological features (non-native species spread) presents important challenges for environmental flows science. Reliance on the assumption of restoration to reference conditions for either hydrologic or ecological conditions is no longer tenable, and an expanded e-flows science foundation is needed to meet several challenges facing future e-flows implementations.
3. Currently recognised limitations of e-flows science contribute to the emergence of research frontiers that need further development. These are (1) shifting from static, regime-based flow metrics to dynamic, time-varying flow characterisations; (2) expanding the ecological metrics (and space–time scales) used in e-flows from primary reliance on ecosystem states to include process (population) rates and species traits; (3) incorporating other "non-flow" environmental features (e.g. temperature, sediment) to guide prioritisation of e-flows applications with a likelihood of success; and (4) broadening the ecological foundation of e-flows to incorporate more ecological theory that will contribute to a more predictive science.
4. The natural flow regime perspective of managing for historical variability will remain important to understand ecological response to hydrologic alterations and to inform e-flows management. However, under shifting hydro-climatic and ecological conditions, a new imperative of managing for resilience is emerging, that is, identifying and prescribing e-flows to sustain robust, persistent and socially valued ecological characteristics in a flexible and adaptive management framework.

KEYWORDS
environmental flows, hydroecology, hydrologic alteration, non-stationarity

1 | INTRODUCTION

Environmental flows (e-flows) science and practice have strong roots in the natural flow regime paradigm (Poff et al., 1997). This concept built on the growing understanding among riverine ecologists that temporal variability in streamflow provides a range of ecosystem processes and habitat needs that sustain high native diversity (e.g. Poff & Ward, 1989; Puckridge, Sheldon, Walker, & Boulton, 1998; Resh et al., 1988; Richter, Baumgartner, Powell, & Braun, 1996; Stanford et al., 1996; Walker, Sheldon, & Puckridge, 1995). River management via e-flows should thus aim to restore a range of flows, not simply some static flow condition such as minimum flow. The "natural" flow regime is effectively measured from the long-term instrumental time series of unimpaired flows and can be summarised in terms of ecologically relevant components, including magnitude, frequency, duration, timing, rate-of-change of flow conditions, interannual variability, and predictability of flow events. The pattern of flow variation over time depends on climatic regime (precipitation and temperature), along with the catchment's vegetation, soils, geology and topography, and flow regime "types" vary geographically (e.g. Archfield et al., 2013; Biggs et al., 1990; Kennard et al., 2010; McManamay, Bevelhimer, & Kao, 2014; Poff, 1996). Specific combinations of flow regime components can lead to species adaptation over evolutionary time (Lytle & Poff, 2004), and they shape contemporary community composition by defining a template that favours (or disadvantages) different species depending on how well those species' needs are met by (or inhibited by) the prevailing flow regime components (see Poff et al., 1997). It follows that human-caused changes in flow regime can modify time-varying habitat availability, life history cues for species, and habitat-specific species interactions, and thus cause declines in species performance and impairment of ecological processes and ecosystem functions (Bunn & Arthington, 2002). This has been shown empirically for many systems, including fish (Kiernan, Moyle, & Crain, 2012; Mims & Olden, 2012), riparian plants (Merritt & Poff, 2010), and invertebrates (Carlisle, Wolock, & Meador, 2011), among others (reviewed in Poff & Zimmerman, 2010; Olden et al., 2014). Therefore, a common aim of contemporary e-flows management is to reverse alteration of specific natural flow regime components in an effort to restore particular ecological target(s).

These basic hydro-ecological principles have helped provide a common structure to consolidate and guide development of e-flows, including methods to quantify hydrologic alteration (e.g. Richter et al., 1996) and flow–ecology relationships (Davies et al., 2014; King et al., 2016; Koster, Crook, Dawson, Gaskill, & Morrongiello, 2017; Taylor & Cooke, 2012; Webb, Arthington, & Olden, 2017) and to construct "holistic" frameworks for managing flow-altered rivers at regional scales (e.g. Arthington, Bunn, Poff, & Naiman, 2006; Poff et al., 2010). E-flows has grown in scope and impact over the past 25 years (Figure 1, see Arthington, 2012; Acreman, Overton, et al., 2014; Poff & Matthews, 2013), and it has now arguably achieved a position of recognition and influence on water resources policy from local to national scales in many places (see Poff, Tharme, & Arthington, 2017 for more discussion). With the increasing attention to the social dimension of e-flows (see Jackson, 2017), e-flows science and management in the future will increasingly include social-ecological considerations. Indeed, e-flows principles are now being proposed to refine estimates of global water availability for human consumption to account for ecosystem needs (Gerten et al., 2013) and to guide planning on water allocation to freshwater ecosystems and irrigated agriculture to meet United Nations' Sustainable Development Goals (Jägermeyr, Pastor, Biemans, & Gerten, 2017).

The success of e-flows over the last 25 or so years reflects an assimilation of new methods, modelling tools, and scientific understanding about freshwater ecosystems into a strong, theory-based scientific foundation (Figure 1). The continuing success of e-flows science over the next 25 years (and beyond) will rely critically on sustaining a rigorous scientific foundation. But new challenges are emerging and these require not only re-visiting those tenets of the natural flow regime that are fundamental to contemporary e-flows practices but also renewed efforts to develop a more robust ecological foundation to support a more predictive e-flows science. The purpose of this article is to evaluate these challenges emerging from climatic non-stationarity and to explore some avenues by which e-flows science can transition from relatively static, regime-based hydro-ecological characterisations to more dynamic, time-varying flow characterisations that can be linked mechanistically to a wide range of ecological performance metrics applicable over a range of spatial and temporal scales. E-flows science is comprised of many elements (Table 1), and several efforts towards more dynamic hydro-ecological characterisations are already evident in the literature. The aim here is to offer a framework that places these new developments in context of emerging challenges to continuing success of the e-flows enterprise.

2 | EMERGING CHALLENGES FOR E-FLOWS SCIENCE

2.1 | Non-stationarity

Water resources planning and management in the 20th century were largely founded on the assumption that the climate was stationary, that is, means and variances of hydro-climatic processes that drive hydrologic regimes were relatively stable over the period of the Holocene epoch (Milly et al., 2008) or the last 10–11 thousand years. This perspective allowed the assumption that precipitation and runoff processes in undisturbed catchments occur within some describable range of variation that can be characterised by long-term averages (or standard deviations) of ecologically relevant flow regime components of magnitude, frequency, duration, and timing (e.g. Richter, Baumgartner, Wigington, & Braun, 1997; Richter et al., 1996). Such catchments could be considered as "reference." But in the last decade, it has become clear that the global climate system is changing due to human activities and that we are entering the so-called Anthropocene epoch, where rapid global warming (coupled with global transformation of the land surface) is causing means and variances of temperature and precipitation to start changing (Milly et al.,

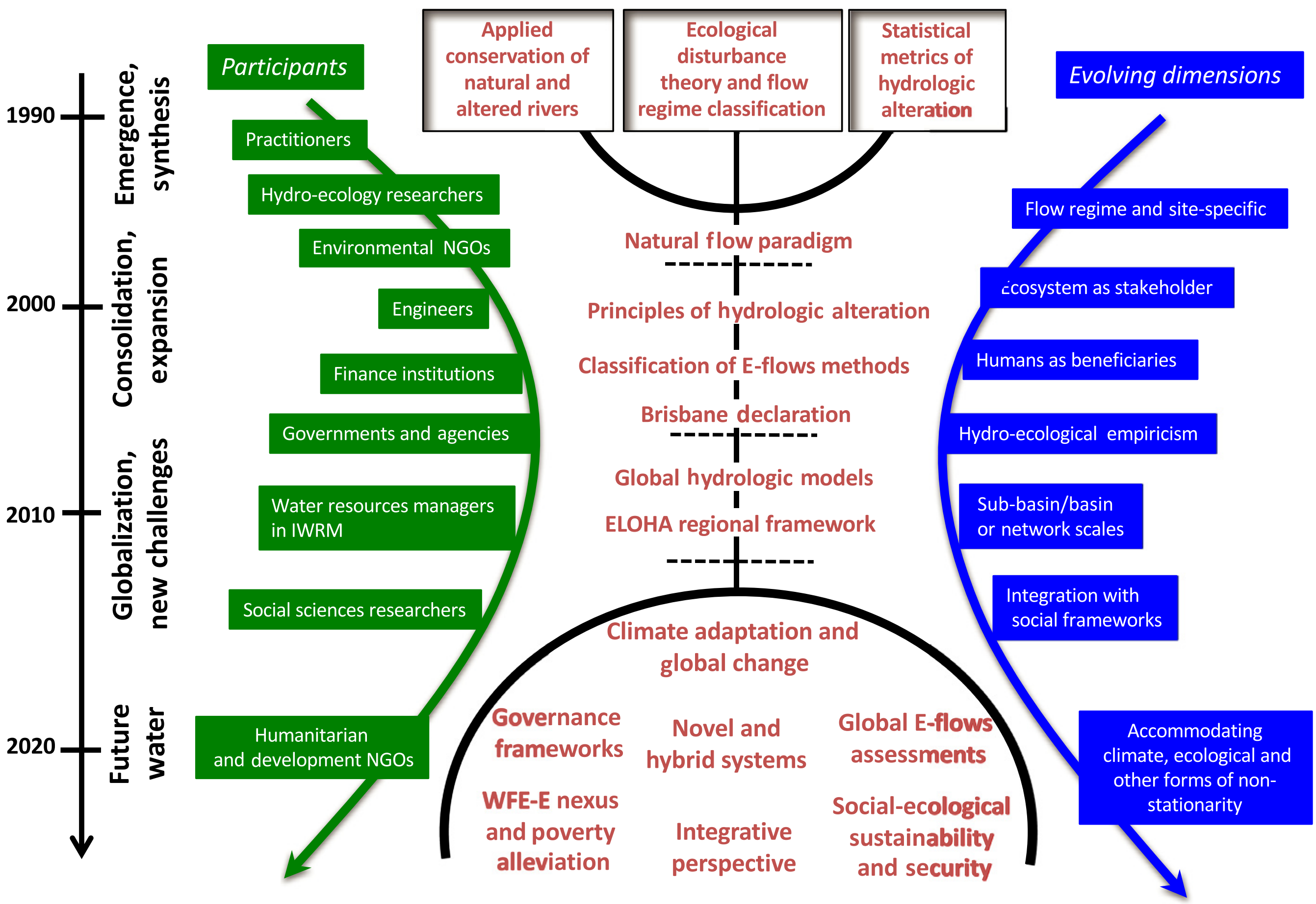

FIGURE 1 Time line of holistic e-flows. Originally published in Poff and Matthews (2013) and modified in Poff et al. (2017). Reproduced with permission by Elsevier [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Characteristic elements of the generally prevailing e-flows science perspective contrasted with an expanded e-flows science perspective required to meet non-stationarity and other challenges

	Generally prevailing	Needed in addition
Ecological targets	Static (fixed)	Dynamic (moving target)
Spatial scale	Local	Regional context
Temporal scale	Time averaged	Time varying
Hydrologic statistical foundation	Regime metrics	Antecedent flows, individual flow events
Management aim	Restoration of targets	Resilience of targets, prevent failure
Ecological response units	States	Rates, traits
Hydro-ecological modelling	Correlative	Mechanistic

2008). This non-stationarity creates challenges for e-flows science in that hydrologic baselines are shifting, leading to modified long-term regime averages and to probable transformations of regimes themselves in coming years (e.g. Laize et al., 2014; Reidy Liermann et al., 2012), perhaps to novel regimes compared to historical norms (Williams, Jackson, & Kutzbac, 2007). Thus, rapid climate change and other sources of hydrologic non-stationarity (population growth, changing landuse, etc.) make reliance on historical hydrologic time series highly questionable for use as a “reference” condition for e-flows practices (Acreman, Arthington, et al., 2014; Kopf, Finlayson, Humphries, Sims, & Hladyz, 2015; Poff et al., 2016).

A second and equally challenging feature of the Anthropocene is the recognition that ecological systems are also non-stationary. The theoretical assumption that local ecological disequilibrium is stabilised at larger landscape scales (DeAngelis & Waterhouse, 1987) and thus leads to a kind of regional-scale dynamic equilibrium is now undercut by the pervasive effects of human activities on ecosystems across all scales. Human modification of aquatic ecosystems has created non-stationarity in ecosystems processes through legacy effects (e.g. Thompson, King, Kingsford, Mac Nally, & Poff, 2017; Wohl, 2001) and through the spread of non-native species, which disrupt biotic interactions (Hobbs et al., 2006; Rahel & Olden, 2008) and diminish the relevance of “reference” conditions in freshwater systems globally (Humphries & Winemiller, 2009; Kopf et al., 2015). These ecological non-stationarities limit the use of historical conditions as a guide for restoration endpoints (Hobbs, Higgs, & Harris, 2009; Moyle, 2014).

2.2 | Shifting from static to dynamic modelling

Hydro-climatic transience requires a more dynamic hydro-ecological modelling approach. E-flows science has relied heavily on regime-based thinking, that is, developing metrics that capture long-term regime averages such as average peak and low flow magnitudes or average timing of such events (e.g. Olden & Poff, 2003; Richter et al., 1996). Such metrics are typically correlated with relatively static measures of ecological condition, such as ecosystem states (Poff & Zimmerman, 2010; Wheeler, Wenger, & Freeman, 2018). These flow–ecology relationships reflect a kind of "evolutionary" time scale, that is, the temporal pattern of flow variation that establishes the template on which some adaptations of species have been set (Lytle & Poff, 2004; Poff et al., 1997); this evolutionary history perspective provides theoretical expectations likely species' responses to particular kinds of flow alterations. Regime-based metrics also inform us about what type of general ecological patterns we should expect through species sorting, that is, particular patterns of flow variation act as a "filter" to favour species having attributes that match the temporal dynamics of that habitat, and disfavour those that do not, as has been shown for riparian vegetation (Merritt, Scott, Poff, Auble, & Lytle, 2010), fish (Mims & Olden, 2012; Poff & Allan, 1995) and invertebrates (Chadd et al., 2017; Kakouei, Kiese, Kails, Pusch, & Jänig, 2017; Monk et al., 2006; Zuellig & Schmidt, 2012).

What has not been sufficiently appreciated in the practice of e-flows is the importance of short-term flow variation that occurs in "ecological time." Individual flow events, while contributing to the long-term average regime, often act as important mortality agents and thus can shape local dynamics over shorter, management-relevant time scales. For example, individual hydrologic extremes (e.g. high magnitude flows or prolonged droughts) can have direct ecological consequences that are not expected under the long-term average for those flow components. Populations may be vulnerable to being locally extirpated by individual events or sequences of extreme events (see Bogan & Lytle, 2011; Bond et al., 2015; McCarthy et al., 2014; Ruhí, Olden, & Sabo, 2016; Wang et al., 2017; Yen, Bond, Shenton, Spring, & Mac Nally, 2013). Non-stationarity imposes not only shifting baselines but increasing variance that will expose species to more frequent or intense extreme hydrologic events that can also have strong effects of species performance and persistence (e.g. Bogan, Boersma, & Lytle, 2014).

Given the transience of hydro-climatic conditions, reliance on regime-averaged metrics (i.e. static metrics) and ecological responses will be inadequate to predict ecological responses in many instances. A more process-based understanding of ecological responses to individual hydrologic events or sequences of events becomes critical. This implies a need for e-flows science to broaden its widely held perspective on a largely static, regime-averaged approach that generates correlations between flow variables and ecological responses to a more dynamic, "mechanistic" understanding of flow–ecology relationships, that is, how individuals, populations, or communities respond to a specific hydrologic event of any given magnitude. This kind of understanding arises from linking changes in species performance directly to short-term hydrologic variation and antecedent flow conditions that can influence ecological response to a particular hydrologic event (e.g. Beesley et al., 2014; King et al., 2015; Leigh, 2013).

2.3 | Scaling hydro-ecological relationships in space and time

E-flows studies and applications have mostly used regime-averaged metrics to explain changes in ecosystem state variables (e.g. number and abundance of species). Wheeler et al. (2018) report that measurement of ecological states, including their repeated measurement over time, comprise 72% of reviewed approaches for characterising flow–ecology relationships. Against this trend, some have argued that ecological processes, rather than habitat limitation per se, are a more appropriate focus for e-flows (e.g. Anderson et al., 2006; Lancaster & Downes, 2010; Shenton, Bond, Yen, & Mac Nally, 2012; Thompson et al., 2018) and there is a need to "put ecology back" into e-flows (Shenton et al., 2012). These differences in perspective are not unexpected given the multi-faceted and multi-scaled nature of the e-flows enterprise, which is loosely united under the broad and vaguely circumscribed banner of understanding and quantifying "flow-ecology relationships." What is largely missing from this discussion is explicit recognition that hydro-ecological relationships can be characterised at many space–time scales of hydrological and ecological grain, and these different perspectives carry with them implicit scaling features that constrain how well they can be used for different e-flows applications, ranging from individual localities to collections of local sites across geographic regions.

E-flows science and implementation are applicable to a variety of space–time scales using a variety of tools and ecological response types (Figure 2). The spatial extent of e-flows ranges (*X*-axis) from local sites to multiples of sites (basin) to broad-scale comparisons where species turnover due to biogeographic differences occurs among distant sites. As spatial extent increases, different tools are available to characterise hydrologic, hydraulic, and ecological features, generally progressing from fine-grained, intensive at-a-site measurement and modelling to more statistical characterisations. Different kinds of methods (*Y*-axis) are used in e-flows applications (observations, models, experiments), and these are often associated with particular spatial scales. A range of temporal scales are also applied (*Z*-axis), from daily (or sub-daily) to seasonal to annual or multiannual ("regime").

In this space–time-methods space, different types of ecological resolution are possible. Measures of ecological states are relatively "slow" variables that respond over periods of months (seasons) to years. For example, recruitment failure by insects (Kennedy et al., 2016) or riparian trees (Lytle & Merritt, 2004; Rood et al., 2003) does not manifest in species abundances for many months, and shifts in community structure under flow regulation (Mims & Olden, 2012) is a relatively slow process that can be measured across many sites simultaneously using monitoring data. The repeated measurement of snapshot state variables over time constitutes a kind of temporally varying ecological properties and is a predominant form

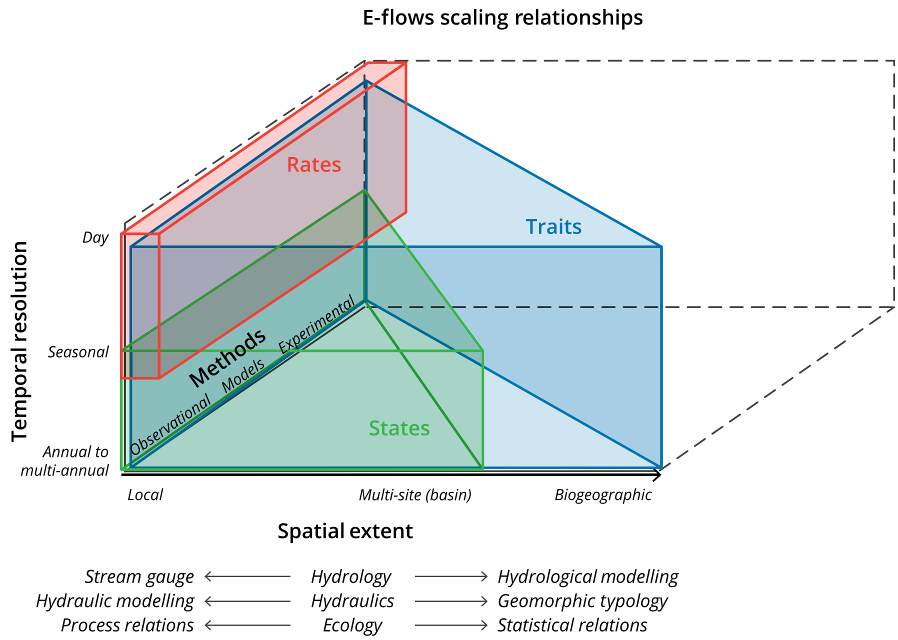

FIGURE 2 E-flows scaling relationships, showing grains of ecological response (states, rates, traits) in terms of spatial extent, temporal resolution, and methods of flow–ecology inference. Tools of hydrologic, hydraulic, and ecological analysis are arrayed on the spatial axis. Adapted from Poff et al. (2017). Reproduced with permission by Elsevier [Colour figure can be viewed at wileyonlinelibrary.com]

of flow–ecology relationship reported in the literature (Wheeler et al., 2018).

By contrast, rapid ecological responses can be captured by focusing on process rates. For example, population growth rate or mortality rate can be measured over days to weeks and provides insight into species performance under some hydrologic conditions, including dynamically varying ones (McMullen, DeLeenheer, & Lytle, 2017). Population demographic data are likely to be available for a limited number of species and usually at few sites, although efforts to generalise such data across "guilds" of functionally similar species could broaden the generality of this rate-based approach (e.g. see Baumgartner et al., 2014; Lytle, Merritt, Tonkin, Olden, & Reynolds, 2017; Shenton et al., 2012). A third type of ecological response variable would be species traits, attributes of species that can reflect a wide range of temporal response to hydrologic alteration, ranging from behavioural response to a specific hydrologic event (e.g. ability to move to avoid sudden flow changes) to a life history feature appropriate for regime-averaged metrics (e.g. generation time). Under more dynamic hydrologic conditions associated with non-stationarity, increasing emphasis is likely to be placed on process-based ("mechanistic") understanding of flow–ecology relationships, leading to more e-flows applications emphasising population-level rates for species or guilds of concern (e.g. Lytle et al., 2017) and traits-based approaches to attain broader spatial transferability (see Chen & Olden, 2018).

2.4 | Incorporating non-flow environmental factors in e-flows science and assessment

A simplifying assumption of e-flows applications has been that flow is the "master variable" and other environmental drivers (e.g. temperature, sediment, hydraulics) can be considered as having lesser importance. Scientifically, it is well accepted that flow is a necessary, but not necessarily sufficient, environmental control on aquatic and riparian species and ecosystems (e.g. Arthington, 2012; Dudgeon et al., 2006; Dunbar et al., 2010; Lamouroux, Hauer, Stewardson, & Poff, 2017; Olden & Naiman, 2010; Poff et al., 1997; Walker et al., 1995; Wohl et al., 2015), and the embrace of flow alteration at the expense of other key environmental drivers has largely been a pragmatic choice. However, quantitative ecological responses to hydrologic alteration alone tend to be "noisy" and may have low general transferability (Poff & Zimmerman, 2010), although stratification by river type and careful selection of ecological metrics can enhance transferability (e.g. Chen & Olden, 2018). Other factors can themselves limit ecological response potential; therefore, including those factors more actively into e-flows applications is needed and can improve hydro-ecological predictions (Kennard, Olden, Arthington, Pusey, & Poff, 2007; King et al., 2016; McManamay, Orth, Dolloff, & Mathews, 2013). Indeed, there are many examples of where flow restoration fails to have a benefit in habitats that are impaired by sediment depletion (see Wohl et al., 2015; Yarnell et al., 2015) or by temperature alteration (e.g. McManamay et al., 2013), indicating the necessity of restoring some normative habitat conditions before e-flows can be successfully applied.

A significant challenge for e-flows science and practice is to develop the capacity to more confidently state under what environmental circumstances flow interventions will be successful in sustaining robust and persistent socially valued ecological characteristics under changing conditions. Specifying when flows are limiting and how specific interventions can lead to well-defined ecological outcomes is needed to build trust with managers and social support for providing water to ecosystems. Clearly, where environmental changes have been very extensive, such as below large hypolimnetic-release dams and hydropeaking dams, the prospect of ecological restoration is limited (Acreman, Arthington, et al., 2014) but can nonetheless achieve desirable ecological outcomes where mechanistic flow–ecology relationships can be specified (e.g. Kennedy et al., 2016; Rood et al., 2003). But many e-flows applications occur in less severely flow-modified settings where the alteration of other, non-flow, environmental factors potentially limit the effectiveness of e-flows interventions. In some cases, it may be less expensive and more socially desirable to pursue other restoration approaches if flow is not the limiting factor (e.g. riparian restoration, Stewart-Koster et al., 2010). These considerations suggest that re-thinking and expanding of the hydro-ecological foundation of e-flows science and application is needed, in order to consider ecological responses to hydrologic alteration in the context of multiple limiting factors and across a range of spatial, temporal, and ecological scales.

2.5 | Broadening the ecological foundation towards a more predictive e-flows science

As e-flows science moves into the challenging new era of hydro-ecological non-stationarity, a more sophisticated ecological foundation is needed, one that incorporates key ecological principles into a more dynamic framework in support of a more predictive e-flows science. Figure 3 is a conceptual representation of a species-centric ecological foundation that focuses primarily at the population and community levels, where much of e-flows work is done, and that makes explicit linkages between local and regional spatial scales. Communities of species are composed of individual species populations, so factors that limit population success translate into measured community-level responses. A local population of a species persists when conditions for all life stages of that species are met. Successful completion of the species' life cycle depends on a number of environmental variables being within a range of tolerance (flow regime, temperature regime, sediment regime, and nutrient/chemistry conditions over the lifespan of the organism). If enough individuals complete their life cycles to maintain a viable population, then the species persists at the site, and the more favourable conditions are for growth and survival, the more abundant the species should be at that site.

For many species, successful life cycle completion also has a spatial context beyond simply the local habitat. Many fish, for example,

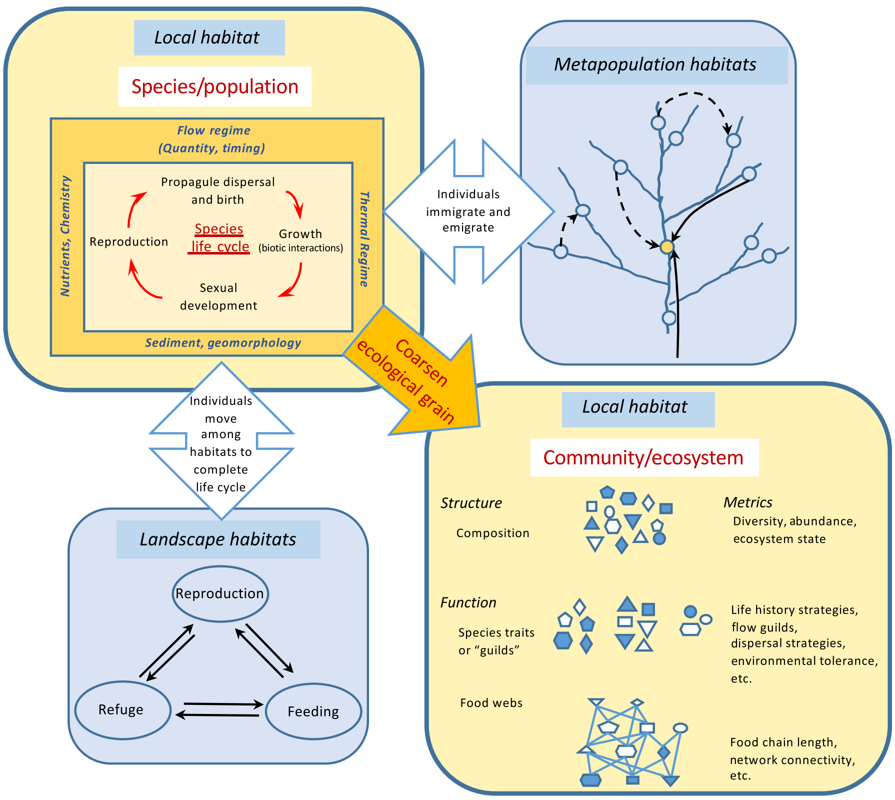

FIGURE 3 Integrative ecological foundation for e-flows applications illustrating population and community metrics at the local habitat scale and showing landscape dimensions of movement and dispersal needed for successful persistence of species populations at the local scale. Population-community linkages. Metrics used to characterise ecological responses to flow and other variables. Environmental variables at the local scale provide a habitat template (flow, temperature, sediment, nutrients/chemistry) that must be suitable for completion of species' life stages. Demographic rates can be measured for local populations. Communities of species (represented by symbols of differing shape and colour) comprise persistent populations, and transient migratory species and dispersing species. Community metrics can be measured in terms of taxonomic structure or of functional composition and organisation of species present. Landscape habitats are those required for different life cycle stages of species and these can range widely spatially depending on species mobility and lifetime habitat needs. Metapopulation habitats show localities ("sites") in a stream network and movement between them, either via instream movement or via dispersal along stream corridors (solid arrows) or aerially overland (dashed arrows). The yellow dot represents the "local habitat" showing the detailed species/population and community/ecosystem features. See text for further discussion [Colour figure can be viewed at wileyonlinelibrary.com]

require qualitatively different habitats for growth, reproduction, and refugia from unfavourable conditions such as disturbance or other stressors (Fausch, Torgersen, Baxter, & Li, 2002; Schlosser & Angermeier, 1995; see Figure 3). Accessing these habitats requires physical connectivity among them. For migratory species (e.g. some fishes and freshwater crustacea), connectivity between the ocean and upland spawning and rearing habitats allows life cycle completion. Aquatic insects also require multiple habitats to complete their life cycles, but within a much more spatially constrained area such as a single stream reach. Adult insects emerge into a suitable terrestrial environment where they can survive and reproduce. Oviposition occurs in specific habitats and juveniles disperse to growth habitats and may require stable refuge from extreme flow conditions. Elimination of viable oviposition habitats can lead to reduction or elimination of insect populations (e.g. Encalada & Peckarsky, 2012; Kennedy et al., 2016).

Another ecologically relevant spatial context is defined by organismal dispersal. To find habitats of suitable character, organisms disperse as propagules or move as juveniles or adults and colonise new localities. This creates a flux of individuals into and out of a local habitat via immigration and emigration. Thus, local populations are linked together in a metapopulation via dispersal (Fagan, 2002) and species' differences in dispersal characteristics can influence community structure across a metacommunity (Brown et al., 2011).

Ecological resolution is associated with varying space–time constraints (see Figure 2). Populations can be studied in terms of process rates (growth, mortality, immigration, emigration) that require a different scale of measurement than community-level states (e.g. species presence/absence). Although the mechanisms of presence/absence of a species in a community are embedded in finer grained population processes, the latter are typically not measured in community-level e-flows studies, due to logistical, time, and fiscal constraints. Community-level metrics are expressed either in terms of taxonomic structure (e.g. diversity) or community-wide function. Functional metrics (e.g. species traits) are more "mechanistic" in that they can be related to environmental conditions, and this is currently feasible for many taxa, including fish (Frimpong & Angermeier, 2009; Mims, Olden, Shattuck, & Poff, 2010), riparian vegetation (Merritt et al., 2010), and aquatic insects (Poff et al., 2006). Grouping species by similarities in species traits can be used to assess changes in communities across hydrologic gradients (Kakouei et al., 2017; Mims & Olden, 2012; Poff & Allan, 1995). Similarly, species may also be organised into "guilds" of different hydrologic requirements (e.g. Lytle et al., 2017; Merritt et al., 2010; Monk et al., 2006). A more structured trait approach is to organise species by trophic function into a food web and associated metrics, which can be related to hydrologic alteration (e.g. McHugh, McIntosh, & Jellyman, 2010; Sabo, Finlay, Kennedy, & Post, 2010; Thompson et al., 2018).

The conceptualisation in Figure 3 aims to focus attention on the importance of understanding the influence of multiple environmental factors (i.e. not just flow) and spatial scale needed for species to complete their life cycles and thus persist as members of a community. It is certainly not the only way that a more predictive ecological foundation for e-flows could be framed, but it does afford a consistent way of formulating flow–ecology relationships and of guiding transferability of e-flows results.

3 | SHIFTING FROM FIXED TO MOVING ECOLOGICAL TARGETS—MANAGING FOR RESILIENCE

Hydro-ecological non-stationarity and the pervasive degradation of aquatic ecosystems by multiple environmental stressors create new challenges for freshwater conservation and sustainability. E-flows has largely been practiced with the intent of restoring a system to some level of historical condition, an approach that is now recognized as generally unobtainable. As systems continue to degrade, ongoing decision making about when and how to allocate e-flows in order to achieve the best possible outcomes will be required. Such "active management" (e.g. Doolan, Ashworth, & Swirepik, 2017; Horne et al., 2017) will require that e-flows science be able to inform managers on responses of species and ecosystems to water allocations as "baseline" hydrologic and ecological conditions change due to global warming and non-native species spread. In other words, e-flows management will have to contend with moving ecological targets in an adaptation mode, that is, using approaches that are flexible and robust and that accommodate uncertainty due to changing conditions (Poff & Matthews, 2013; Schindler & Hilborn, 2015).

A key tenet of natural flows thinking that carries forward into the Anthropocene is that managing for variability is central to ecological restoration because environmental heterogeneity is maintained, allowing for broad ecological response to changing conditions (e.g. Hiers, Jackson, Hobbs, Bernhardt, & Valentine, 2016; Schindler & Hilborn, 2015). An additional dimension from a conservation perspective is to manage for resilience, that is, to focus on maintaining key processes and relationships that are robust and able to persist with functional integrity under anticipated changes in social and environmental conditions (Allen, Cumming, Garmestani, Taylor, & Walker, 2011; Folke et al., 2010). Projecting ecological transitions under non-stationarity to guide successful management interventions will require a robust and flexible scientific framework that is squarely grounded in ecological principles and process-based understanding of flow–ecology relationships.

Projecting future changes in hydrology and ecology is fraught with uncertainty and generally not considered a quantitatively precise modelling exercise (e.g. Schindler & Hilborn, 2015). Therefore, risk-based approaches that assess vulnerability of ecological conditions against a range of possible future hydrologic states are needed. Decision scaling (Brown, Ghile, Laverty, & Li, 2012) is one such approach that has been used in an e-flows context to quantitatively project how dams might be operated under climate uncertainty to meet stakeholder-defined engineering and ecological performance targets (Poff et al., 2016). Explicit identification of ecological performance metrics and thresholds of failure allows tradeoffs among desired outcomes to be assessed relative to different management interventions. For example, species persistence is a simple ecological metric for ecological resilience. Several examples of modelling of species persistence under future hydrologic variability already exist (Bond et al., 2015; Ruhí, Holmes, Rinne, & Sabo, 2015; Shenton et al., 2012; Wang et al., 2017; Yen et al., 2013). The decision scaling approach would allow such risk-based models to be combined with a range of plausible future hydrologic conditions (modelled or scenario-based) arising from a number of non-stationary drivers (climate change, water demand, etc.) to evaluate how water infrastructure might be managed to attain both engineering (or economic) and ecological benefits. This kind of long-range vulnerability analysis could inform ongoing, annual, active, decision making on water allocations in order to increase the chances of achieving sustainable, resilient systems over longer time scales.

4 | CONCLUSION

Non-stationarity crystallises several challenges that e-flows science already faces and has begun to tackle. These include the need for a stronger ecological foundation that spans local to regional scales, for more process-based ("mechanistic") understanding of flow–ecology relationships and for inclusion of non-flow limiting factors into e-flows analyses and prescriptions. The dominant characteristics of e-flows as currently practiced are changing as the science adjusts to the necessities imposed by the non-stationary worldview (Table 1). E-flows science and application are moving into a new realm, one where expectations will be raised for efficient e-flows interventions that can produce measurable ecological outcomes (Poff & Schmidt, 2016). Increasingly, e-flows science will blend conservation and restoration objectives (see Wiens & Hobbs, 2015) across a range of hydro-ecological alteration, and it will incorporate principles of "ecosystems by design" (*sensu* Palmer et al., 2004; see Acreman, Arthington, et al., 2014). In this sense, non-stationarity presents an opportunity for e-flows science to evolve and develop a more robust and nuanced foundation in ecological science. Continued efforts in this direction will not only advance the science but expand opportunities for river scientists to pursue meaningful and achievable conservation objectives.

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ORCID

N. LeRoy Poff http://orcid.org/0000-0002-1390-8742

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