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Scaling biodiversity responses to hydrological regimes

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ABSTRACT

Of all ecosystems, freshwaters support the most dynamic and highly concentrated biodiversity on Earth. These attributes of freshwater biodiversity along with increasing demand for water mean that these systems serve as significant models to understand drivers of global biodiversity change. Freshwater biodiversity changes are often attributed to hydrological alteration by water-resource development and climate change owing to the role of the hydrological regime of rivers, wetlands and floodplains affecting patterns of biodiversity. However, a major gap remains in conceptualising how the hydrological regime determines patterns in biodiversity's multiple spatial components and facets (taxonomic, functional and phylogenetic). We synthesised primary evidence of freshwater biodiversity responses to natural hydrological regimes to determine how distinct ecohydrological mechanisms affect freshwater biodiversity at local, landscape and regional spatial scales. Hydrological connectivity influences local and landscape biodiversity, yet responses vary depending on spatial scale. Biodiversity at local scales is generally positively associated with increasing connectivity whereas landscape-scale biodiversity is greater with increasing fragmentation among locations. The effects of hydrological disturbance on freshwater biodiversity are variable at separate spatial scales and depend on disturbance frequency and history and organism characteristics. The role of hydrology in determining habitat for freshwater biodiversity also depends on spatial scaling. At local scales, persistence, stability and size of habitat each contribute to patterns of freshwater biodiversity yet the responses are variable across the organism groups that constitute overall freshwater biodiversity. We present a conceptual model to unite the effects of different ecohydrological mechanisms on freshwater biodiversity across spatial scales, and develop four principles for applying a multi-scaled understanding of freshwater biodiversity responses to hydrological regimes. The protection and restoration of freshwater biodiversity is both a fundamental justification and a central goal of environmental water allocation worldwide. Clearer integration of concepts of spatial scaling in the context of understanding impacts of hydrological regimes on biodiversity will increase uptake of evidence into environmental flow implementation, identify suitable biodiversity targets responsive to hydrological change or restoration, and identify and manage risks of environmental flows contributing to biodiversity decline.

Key words: biotic homogenisation, climate change, community composition, diversity, drought, environmental flows, flow regulation, spatial scaling, species richness.

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I. INTRODUCTION

The hydrological regime plays a central role in the biophysical dynamics of freshwater environments, such as rivers, floodplains, and wetlands (Hart & Finelli, 1999; Sponseller, Heffernan & Fisher, 2013). Understanding the responses of freshwater biodiversity to hydrological variation is key to predicting the consequences of changing hydrology due to human water use and climate change. Specifically, these mechanistic relationships are key to informing the management of hydrological regimes to protect or restore freshwater biodiversity and ecosystem services (Davies *et al.*, 2014). However, ambiguous and inconsistent relationships between hydrology and freshwater biodiversity have been reported (Dewson, James & Death, 2007; Downes, 2010). In part, this inconsistency is likely because research has inadequately distinguished how effects of hydrology on freshwater biodiversity vary across spatial scales (Pegg & Taylor, 2007) or condense biodiversity to simple metrics with no reference to spatial scaling (e.g. Yang, Sun & Yang, 2016). Consequently, there remains a clear need to determine the mechanisms underlying effects of hydrology on freshwater biodiversity across spatial scales. A strengthened conceptual understanding of the relationships between hydrology and biodiversity across spatial scales would be of significant

value to global efforts to manage hydrological regimes for biodiversity outcomes.

Conceptual models of linkages between hydrology and freshwater biodiversity vary in the extent to which they incorporate the role of ecohydrological mechanisms across spatial scales (Lake, 2000; Ward & Tockner, 2001; Larned *et al.*, 2010). Existing models have a strong focus on the effects of distinct components of the hydrological regime. Both Lake (2000) and Lepori & Hjerdt (2006), for example, emphasise the role of hydrological disturbances (e.g. floods) as drivers of temporal variation in species diversity. By contrast, Ward, Tockner & Schiemer (1999) and Larned *et al.* (2010) focus on the role of aquatic habitat patch size and among-patch connectivity in response to water-level fluctuations influencing the number of taxa occupying patches and variation in assemblage composition among patches at the scale of individual rivers and their floodplains. These existing conceptualisations therefore focus on the role of individual ecohydrological mechanisms (*sensu* Sponseller *et al.*, 2013) in isolation and do not integrate how spatial dynamics of biodiversity vary in response to hydrological regimes. This limitation highlights that a significant gap remains in understanding how hydrological regimes influence freshwater biodiversity from individual patches to across multiple regions.

Table 1. Definition of terms used in this synthesis relevant to conceptualising the effects of hydrological regimes on multi-scale biodiversity patterns in freshwater ecosystems

Term	Definition
Biodiversity	The variability among living organisms from all sources, <i>inter alia</i> , terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes variation within species, among species and of ecosystems [Convention on Biological Diversity (Gaston, 1996)]
Taxonomic diversity (TD)	The variety and variation of organisms based on taxonomy measured at multiple spatial scales. Also known as species diversity (where species-level taxonomy is used to discriminate organisms)
Functional diversity (FD)	The breadth of biological or functional characteristics of organisms within a community, measured at multiple spatial scales (Petchey & Gaston, 2006). Often referred to as functional composition or trait diversity
Phylogenetic diversity (PD)	The breadth of evolutionary history among organisms in a community (Faith, 1992; Graham & Fine, 2008). Phylogenetic diversity emphasises the phylogenetic distinctness of organisms, and therefore future evolutionary potential
Alpha diversity	The number of taxa (TD), number of functional characteristics (FD), or the breadth of phylogenetic distinctness among taxa (PD) within a location. Forms part of 'inventory diversity' (Jurasinski, Retzer & Beierkuhnlein, 2009)
Gamma diversity	The number of taxa (TD), number of functional characteristics (FD), or the breadth of phylogenetic distinctness among taxa (PD) within a region. Forms part of 'inventory diversity' (Jurasinski <i>et al.</i> , 2009)
Beta diversity	Spatial variation in the composition of taxa, functional groups or phylogenies among locations within a region (Anderson <i>et al.</i> , 2011). Beta diversity is most commonly considered with respect to taxonomic diversity, yet is also applied to functional and phylogenetic diversity (e.g. Graham & Fine, 2008; Villéger, Grenouillet & Brosse, 2013). Beta diversity occurs <i>via</i> two processes: turnover (replacement) and nestedness (loss) (Baselga, 2010; Legendre, 2014). Described as 'differentiation diversity' (Jurasinski <i>et al.</i> , 2009)
Biotic homogenisation	The process of increasing similarity of communities (taxonomic, functional or phylogenetic) over time (Olden & Rooney, 2006). Quantified by declines in beta diversity and driven by species invasions, extinctions, and environmental changes
Spatial scale	Spatial scale has two core components: spatial grain and spatial extent. Spatial <i>grain</i> refers to the size of the individual sample unit considered in a study, whereas spatial <i>extent</i> is the overall area covered by a study, and hence contains all sampling units (Wiens, 1989; Whittaker, Willis & Field, 2001)
Location	A location refers to the study site and corresponds to spatial grain. In freshwaters, this is a wetland, riffle-pool sequence, or defined length of river (Heino, 2011)
Region	A region spans multiple locations within an ecologically or environmentally defined area. This could be a major tributary (sub-basin), drainage basin or ecoregion (Heino, 2011)
Hydrological regime	The temporal sequence (frequency, duration and timing) of wetting and drying (hydroperiod; water regime) and flow events (flow regime) experienced by a freshwater ecosystem (Poff <i>et al.</i> , 1997; Brock <i>et al.</i> , 2003; Gordon <i>et al.</i> , 2004; Boulton <i>et al.</i> , 2014). Hydrological regimes encompass hydrological variability across annual, monthly, daily, minutes and millisecond time scales (Biggs, Nikora & Snelder, 2005, see also Walker, Sheldon & Puckridge, 1995)
Hydrological disturbance	Temporal variation in the hydrological regime that applies a damaging force to an environment occupied by organisms (Lake, 2000; Cardinale <i>et al.</i> , 2005). Disturbances can be predictable or unpredictable (Resh <i>et al.</i> , 1988; Poff, 1992)
Environmental flows	The protection, allocation and delivery of hydrological regimes to sustain or restore aquatic ecosystems, thereby mitigating undesirable effects of human water use and hydrological alteration

Human exploitation of water and consequent hydrological impacts on rivers, floodplains, and wetlands are consistently attributed as causing changes in freshwater biodiversity worldwide (Poff *et al.*, 1997; Bunn & Arthington, 2002; Dewson *et al.*, 2007; Poff & Zimmerman, 2010; Strayer & Dudgeon, 2010). Empirical evidence of biodiversity responses to altered hydrological regimes has so far concentrated on relatively fine spatial scales, typically in terms of local species richness or average composition among sites (Bunn & Arthington, 2002; Dewson *et al.*, 2007; Poff & Zimmerman, 2010). Such an emphasis on local biodiversity responses further highlights the limited conceptual and empirical understanding of effects of hydrological alteration on freshwater biodiversity across

spatial scales. This gap is problematic because the protection, allocation, and delivery of water for the conservation and restoration of freshwater ecosystems and freshwater biodiversity (termed 'environmental flows'; Table 1) is based on evidence of the effects of hydrological alteration or hydrological gradients on river and floodplain ecosystems (Olden *et al.*, 2014).

The use of biodiversity as a framework for evaluating the performance of hydrological management is pertinent given that effects of hydrological change on freshwater biodiversity are used as justification for preserving and restoring hydrological regimes for environmental purposes (e.g. Bunn & Arthington, 2002; Dudgeon *et al.*, 2006; Poff & Zimmerman, 2010). Furthermore, biodiversity change

is central to global assessments of overall biodiversity condition over time (e.g. McGill *et al.*, 2015), including in freshwaters (Vörösmarty *et al.*, 2010; Turak *et al.*, 2017). Understanding effects of hydrological regimes on patterns of freshwater biodiversity across spatial scales therefore has benefits for conceptualising how the management of hydrological regimes contribute to overall global biodiversity.

We contend that the application of spatial scaling is essential for clarifying understanding of the effects of hydrology on biodiversity in the context of both freshwater conservation management and fundamental ecological theory of factors governing biodiversity. While environmental flows are targeted to preserve or restore freshwater biodiversity (Acreman *et al.*, 2014; Swirepik *et al.*, 2016), a deficient understanding of biodiversity responses to hydrology across spatial scales means that conceptual theory will continue to generate confusion and restrict application of evidence to informing how environmental flow programs can be applied across multiple spatial scales (Lepori & Hjerdt, 2006). Concepts central to conservation biology have not been effectively applied to freshwater conservation management, leading to a sustained gap between freshwater science and conservation (Strayer & Dudgeon, 2010). A unified conceptual understanding of the relationships and underlying ecohydrological mechanisms driving biodiversity across spatial scales will make a significant contribution to improving the relevance of freshwater science (*sensu* Swirepik *et al.*, 2016) to freshwater conservation management. Given that freshwaters support the greatest proportion of global biodiversity in relation to their small areal extent (Wiens, 2015), these environments serve as useful model systems to understand fundamental ecological mechanisms that affect biodiversity.

The target readership for this synthesis is both ecologists who study the factors responsible for freshwater biodiversity and conservation managers who make decisions about the management of hydrological regimes to protect and enhance freshwater biodiversity. We present a synthesis for applying concepts of spatial scaling to the mechanistic relationships between biodiversity and hydrology in surface water ecosystems (spanning rivers, floodplains and wetlands). While our synthesis is based on a systematic review of the literature, our aim is not to attempt a quantitative review (e.g. Poff & Zimmerman, 2010; McMullen & Lytle, 2012) but rather to illustrate how multiple ecohydrological mechanisms might influence patterns of freshwater biodiversity across spatial scales. After briefly defining concepts of biodiversity and spatial scaling, we identify the key components of hydrological regimes applicable for conceptualising effects on biodiversity. We synthesise the primary evidence of the mechanistic roles of hydrology (*sensu* Sponseller *et al.*, 2013) on patterns of freshwater biodiversity across different spatial scales to develop a unified conceptualisation. We conclude with four principles for applying these concepts to hydrological management, and highlight six key themes to address gaps in evidence.

II. MULTI-SCALE BIODIVERSITY AS A CONCEPT FOR UNDERSTANDING ECOLOGICAL RESPONSES TO HYDROLOGY

(1) Definitions of biodiversity adopted in this synthesis

Biodiversity is defined as the variety of life forms, including diversity within species, between species, and among ecosystems (Gaston, 1996; Gaston & Spicer, 1998; Table 1). Biodiversity is therefore a multi-faceted and multi-scaled concept that spans variation in the taxonomic, functional and evolutionary attributes of species (Purvis & Hector, 2000; Pavoine & Bonsall, 2011; McGill *et al.*, 2015; Jarzyna & Jetz, 2016). The focus of this synthesis is on biodiversity at the community level (i.e. multi-species assemblages) because (i) this level of ecological organisation is the most widely adopted as representative of biodiversity (Magurran, 2004; McGill *et al.*, 2015) and (ii) much of the ecohydrological literature has focussed on this level of organisation (e.g. Lake, 2000; Ward & Tockner, 2001; Bunn & Arthington, 2002; Larned *et al.*, 2010; Chester & Robson, 2011). Therefore, we cover assemblages of multiple species that span a range of functional ecological roles and evolutionary histories.

(2) Spatial scaling of freshwater biodiversity

Despite being intuitively simple, biodiversity is conceptually complex (Hamilton, 2005; Chiarucci, Bacaro & Scheiner, 2011) and therefore it is necessary to decompose biodiversity into a set of measurable and related components (Reyers *et al.*, 2012). Species diversity, as the best-known subset of biodiversity (McGill *et al.*, 2015), is expressed as a series of components that describe different aspects of the spatial distribution of species across landscapes. The numbers of species at local and regional spatial extents are defined as alpha and gamma diversity, respectively (Whittaker, 1960; Anderson, Ellingsen & McArdle, 2006; Anderson *et al.*, 2011) whereas spatial variation in community composition across a landscape is defined as beta diversity (Anderson *et al.*, 2006). Alpha and gamma diversity share the same unit of measurement (e.g. number of taxa) differing only in terms of spatial extent, and can be described as ‘inventory’ diversity, whereas beta diversity represents the degree to which communities differ in space (i.e. ‘differentiation diversity’; Jurasinski *et al.*, 2009). Alpha, beta and gamma components of diversity can all be applied to each of the three facets of multi-species diversity (i.e. taxonomic, functional and phylogenetic) (Devictor *et al.*, 2010; Swenson, 2011; Table 1).

Beta diversity is the most complex of these spatial components of biodiversity (Legendre & De Cáceres, 2013) and this complexity warrants further description. There are two distinct forms of beta diversity: (i) change in composition along an environmental gradient (‘directional turnover’) and (ii) non-directional variation in composition among sample units within a defined spatial area (Anderson *et al.*, 2011). Variation in composition can be distinguished either in terms of variation among samples within a region, or as variation

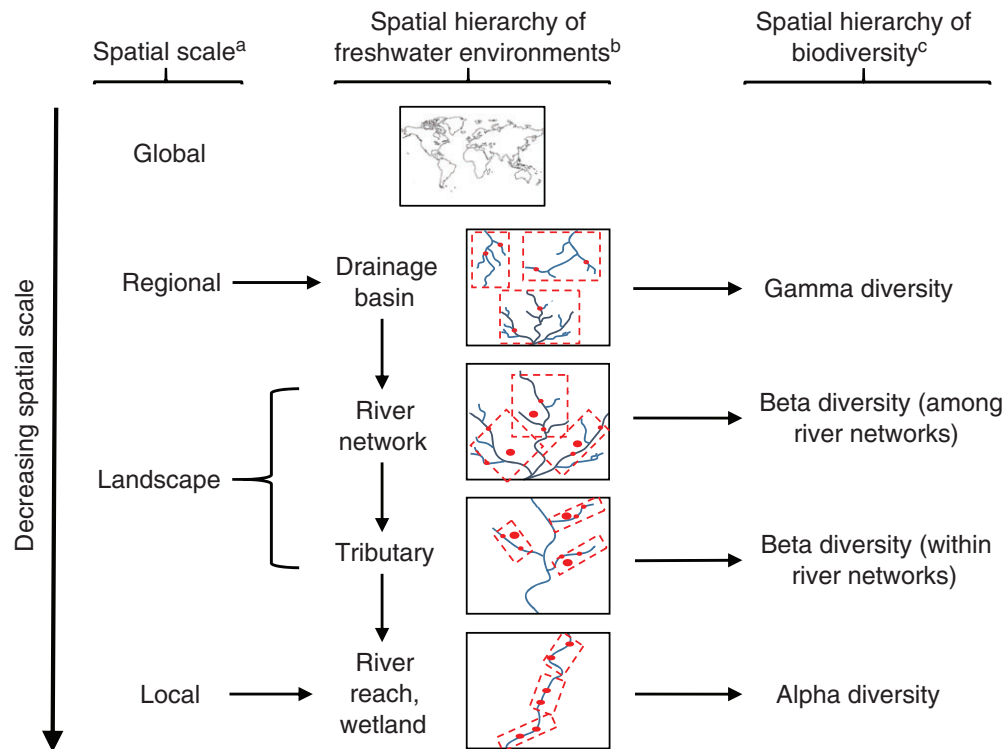


Fig. 1. Schematic diagram representing how riverine environments (including floodplains and wetlands) are arranged as a nested hierarchy of spatial scales and are integrated into analysing and understanding freshwater biodiversity across spatial scales. This schematic diagram integrates common terminology of spatial scales adopted in the general ecological literature (^aWhittaker *et al.*, 2001), conceptualisations of the hierarchical nature of river-floodplain systems (^bFrissell *et al.*, 1986) and applicable measures of biodiversity as relevant to each level within the river-floodplain systems (^cPavoine *et al.*, 2016).

among regions, reflecting the nested hierarchy of spatial scales and ecological processes structuring communities (see Pavoine, Marcon & Ricotta, 2016). Differences in composition (directional or non-directional) among samples or groups of samples are driven by replacement ('turnover') and/or loss of taxa, functional traits, or phylogenetic linkages ('nestedness') (Baselga, 2010; Carvalho, Cardoso & Gomes, 2012; Legendre, 2014). Beta diversity requires that the specific taxonomic, functional or phylogenetic identities of taxa are known (Olden & Rooney, 2006), as separate locations may have the same number of taxa (alpha diversity) but differ in species identity, for example (see Van Grunsven & Liefing, 2015).

Spatial scaling is fundamental to the measurement of all aspects of biodiversity (Wiens, 1989), and clear definitions of 'location', 'region', 'grain' and 'extent' are necessary for understanding biodiversity patterns (*sensu* Levin, 1992). While there is no consensus on the size applicable to each term (Whittaker *et al.*, 2001), spatial scaling is hierarchically nested (Ward & Tockner, 2001; Heino, Melo & Bini, 2015; Pavoine *et al.*, 2016; Fig. 1). For the purpose of this paper, a location (*sensu* Wiens, 1989) is a sampling site (e.g. riffle, stream reach, wetland) and sites are located within regions. A region can be an entire river drainage network (i.e. river basin) or major tributary system within a river basin (distinguished on the basis of geography or hydrology). Finally, spatial extent

spans the entire area included in a study, and therefore may cover multiple regions (Wiens, 1989). These definitions are consistent with the freshwater biodiversity literature (Heino, 2011; Tornwall *et al.*, 2015).

III. THE HYDROLOGICAL BASIS FOR FRESHWATER BIODIVERSITY

The hydrological regime of rivers and wetlands is the combination of the water regime and the flow regime (Table 1). Water regime refers to the temporal pattern of drying and wetting of aquatic habitats across the landscape (Boulton *et al.*, 2014, p. 7). The water regime is particularly relevant to systems where surface water is not permanent (e.g. floodplains, wetlands, temporary rivers and streams) (e.g. Brock *et al.*, 2003; Larned *et al.*, 2010). Water dynamics can be determined by methods that measure the temporal sequence of water presence, absence or depth (e.g. Ward *et al.*, 2013; Bhamjee, Lindsay & Cockburn, 2016). By contrast, the flow regime represents the temporal sequence in the movement and volume of water passing a point in space (e.g. water discharging from a tributary into a main channel) and is measured or estimated by streamflow gauges or modelling tools such as rainfall-runoff models. These two elements of the hydrological regime need to be

distinguished because discharge (i.e. flow) cannot occur in the absence of water, whereas the presence of water can occur independently of discharge. Each element of the hydrological regime underpins the primary ecohydrological mechanisms influencing river–floodplain systems and their biodiversity (disturbance, connectivity, habitat; Sponseller *et al.*, 2013). The water regime determines wetting–drying dynamics and aquatic habitat area (for example), whereas the flow regime determines variations in channel hydraulics that function as disturbances for aquatic organisms (Boulton *et al.*, 2014).

The interaction between temporal and spatial variation (*sensu* Ward, 1989) in hydrological regimes forms the hydrological template for freshwater biodiversity. Temporally, the hydrology of freshwaters describes the sequence of timing, duration, frequency, magnitude (or depth) and rate of change of events (Poff *et al.*, 1997; Casanova & Brock, 2000). Ecological effects of these hydrological events are a fundamental theme in freshwater research (Puckridge *et al.*, 1998; Bunn & Arthington, 2002; Biggs *et al.*, 2005; Leira & Cantonati, 2008). Temporal variation in hydrology occurs over all possible time scales (e.g. years, months, days, seconds; Biggs *et al.*, 2005), and is driven by the dynamics of rainfall, run-off, evaporation, surface–groundwater interactions, and the freezing and thawing of snow and ice (Euliss *et al.*, 2004; Gordon *et al.*, 2004). The temporal hierarchy concept (Puckridge *et al.*, 1998; Biggs *et al.*, 2005; Fig. 2) hypothesises that variation in hydrology occurs over multiple time scales and different ecohydrological processes and patterns are evident at distinct temporal scales (Biggs *et al.*, 2005). For example, rivers in boreal or tropical climates have seasonal and relatively predictable inter-annual hydrological variability, whereas hydrological variability of arid and subtropical rivers is most apparent across multiple years (Puckridge *et al.*, 1998; Fig. 3).

Spatial variation in hydrological regimes is also important in structuring freshwater biodiversity, and occurs both within and among river networks. Often, headwater streams (first to second order) drain small catchment areas, and therefore have rapid fluctuations in discharge (e.g. Baker *et al.*, 2004). By contrast, the presence and movement of water typically becomes more permanent as rivers increase in size (e.g. Svec, Kolka & Stringer, 2005), although there are exceptions (e.g. Lake, 2003; Larned *et al.*, 2011). For example, rivers can have permanent discharge in headwaters before becoming progressively intermittent (ceasing to flow and often losing surface water), and then return to permanent discharge in lowlands due to confined upwelling aquifers (e.g. Selwyn River, New Zealand; Larned *et al.*, 2010). Floodplains have high spatial variation in inundation dynamics as a function of inundation volume, geomorphology, and connection to the stream network (e.g. Benke *et al.*, 2000; Van Der Nat *et al.*, 2002). Spatial variation in hydrology is also evident among drainage networks because of differences in climate, geomorphology and land cover (Puckridge *et al.*, 1998; Detenbeck *et al.*, 2005; Poff, Bledsoe & Cuhaciyan, 2006, e.g. Fig. 3).

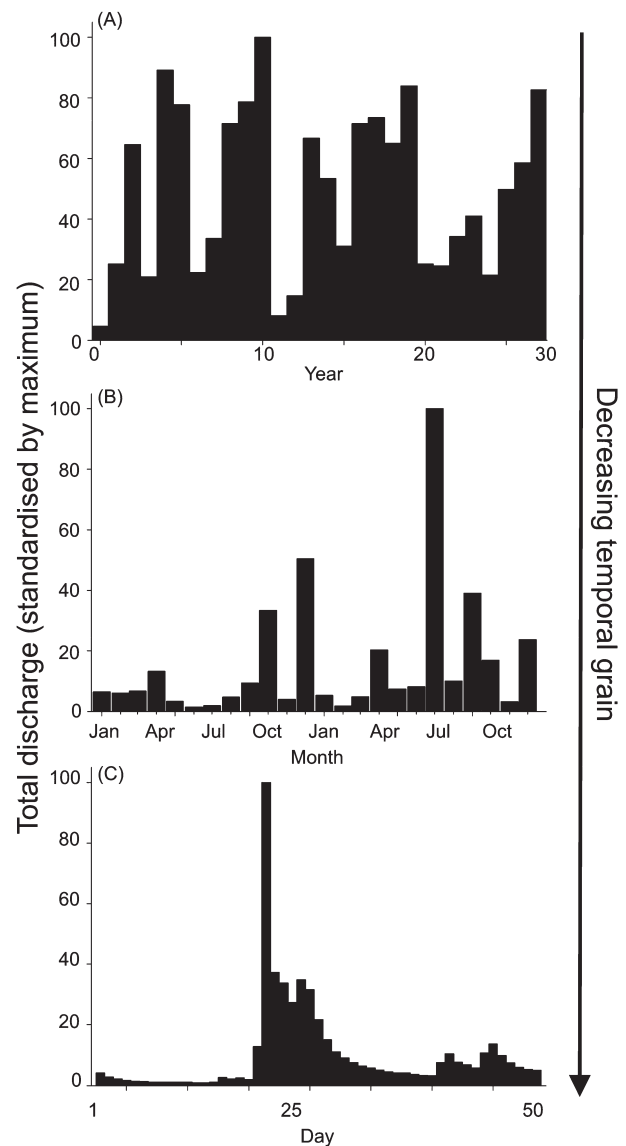


Fig. 2. Hydrological variability (as discharge variability) expressed across multiple temporal scales: annual (A), monthly (B) and daily (C). The y-axis is scaled by maximum discharge to emphasise temporal variability independent of differences in maximum discharge.

IV. BIODIVERSITY RESPONSES TO HYDROLOGICAL REGIMES ACROSS SPATIAL SCALES

We systematically reviewed primary evidence documenting responses of freshwater biodiversity to natural hydrological variation sourced from systematic literature searches using the *Web of Science* (see online Supporting Information: Appendix S1 and Table S1). We deliberately selected literature documenting responses to natural hydrological variation because the understanding of natural responses is necessary to predict effects of anthropogenic changes in hydrological regimes (Fukami & Wardle, 2005; Davies

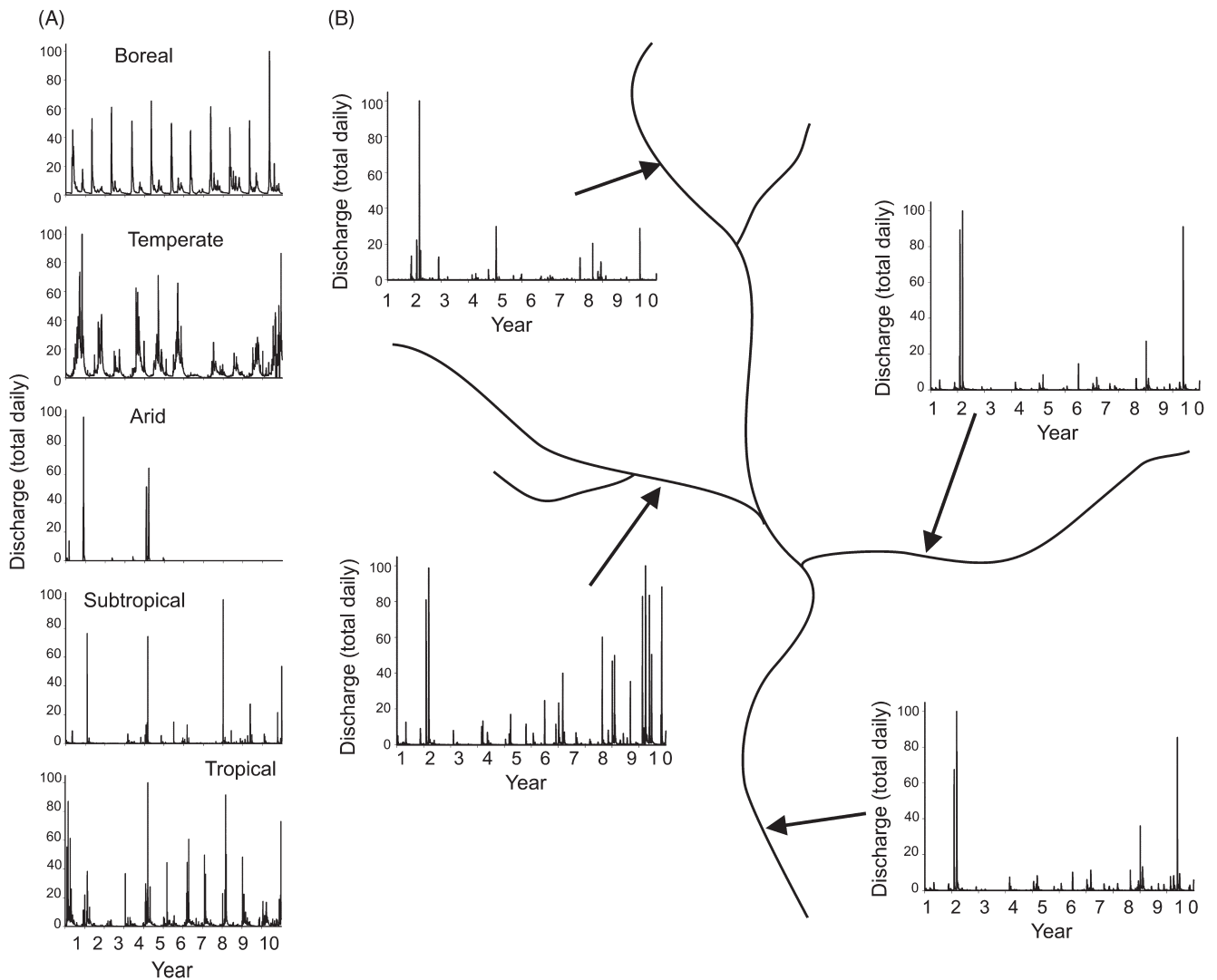


Fig. 3. Spatial variation in temporal hydrological discharge occurs (A) among and (B) within river basins as a function of differences in climate, drainage area, geomorphology and land cover. [Sourced from example streamflow gauging stations from the Finnish Environmental Institute (Finland), New South Wales Department of Primary Industries (Australia), and the Queensland Department of Natural Resources and Mines (Australia)].

et al., 2014). Our synthesis highlights the effects of hydrology on freshwater biodiversity across spatial scales *via* the three fundamental mechanistic roles of water (*sensu* Sponseller *et al.*, 2013; Table 2). First, water acts as a vector for connectivity and movement of energy, material and organisms. Second, water acts as a disturbance for ecosystems and contributes to geomorphic change. Third, water acts as a resource or habitat for biota.

(1) Effects of hydrological connectivity on freshwater biodiversity across spatial scales

Hydrological connectivity is a key driver of both local- and landscape-scale freshwater biodiversity. Increasing hydrological connectivity predominantly increases taxonomic alpha diversity yet the role of connectivity may depend on how

points in space are connected laterally or longitudinally to river–floodplain networks. For example, fish species richness is higher in floodplain pools or wetlands when hydrological connectivity is more prolonged, more frequent, or permanent (Lasne *et al.*, 2007; Uchida & Inoue, 2010). However, for other organism groups, effects of connectivity are less consistent. Taxonomic alpha diversity of macroinvertebrates and diatoms may peak at intermediate levels of hydrological connectivity (Van Den Brink *et al.*, 1996; Gallardo *et al.*, 2014). Effects of hydrological connectivity on macrophyte alpha diversity are variable, with higher numbers of taxa occurring in hydrologically connected (compared to fragmented sites; e.g. Akasaka & Takamura, 2012) or in fragmented or more frequently isolated sites *versus* permanently connected sites (e.g. Keruzoré *et al.*, 2013). Hydrological connectivity positively influenced alpha diversity of aquatic bacteria

Table 2. Responses of freshwater biodiversity to major ecohydrological mechanisms across different spatial scales. Additional examples are summarised in Table S1 (Supporting Information)

Ecohydrological mechanism	Organism group	Biodiversity facet	Biodiversity response	Examples
<u>Connectivity</u>				
<u>Local</u>				
	Fish, macroinvertebrates, macrophytes	Taxonomic	Taxon richness increases with increasing hydrological connection	Lasne, Lek & Laffaille (2007), Algarte <i>et al.</i> (2009), Uchida & Inoue (2010), Akasaka & Takamura (2012), Fazi <i>et al.</i> (2013) and Paillex <i>et al.</i> (2013)
	Macroinvertebrates, waterbirds	Functional	Functional richness has a positive or hump-shaped association with increasing hydrological connectivity	Paillex <i>et al.</i> (2013) and Almeida, Gimenes & Dos Anjos (2017)
	Macroinvertebrates	Functional	Functional richness peaks at locations with intermediate hydrological connectivity	Gallardo <i>et al.</i> (2014)
	Fish, macroinvertebrates, macrophytes	Taxonomic	Spatial variation in composition increases with increasing hydrological fragmentation among locations	Sheldon, Boulton & Puckridge (2002), Thomaz, Bini & Bozelli (2007), Fernandes <i>et al.</i> (2009), Leigh & Sheldon (2009), Macedo-Soares <i>et al.</i> (2010), Akasaka & Takamura (2012), Fazi <i>et al.</i> (2013) and Starr, Benstead & Sponseller (2014)
<u>Disturbance</u>				
<u>Local</u>				
	Biofilm	Functional	Increasing duration of channel-drying disturbances reduces functional richness	Timoner <i>et al.</i> (2014)
	Macroinvertebrates	Taxonomic	Richness increases with time since flooding	Port <i>et al.</i> (2012) and Greenwood & Booker (2015)
	Macroinvertebrates, macrophytes	Taxonomic	Unimodal peak in richness with flood disturbance frequency and intensity	Townsend, Scarsbrook & Dolédec (1997), Riis <i>et al.</i> (2008), Death & Winterbourn (1995), Riis & Biggs (2003) and Death & Zimmermann (2005)
	Macroinvertebrates	Taxonomic	Channel drying reduces taxon richness	Bogan & Lytle (2011) and Fritz & Dodds (2005)
	Macrophytes	Functional	No effect of wetland drying frequency on functional richness	Arthaud <i>et al.</i> (2012)
	Macroinvertebrates	Taxonomic	Drying disturbances reduced spatial variation in composition among locations	Chase (2007)
	Waterbirds	Taxonomic	Spatial variation in community composition linked with differences in drying/ inundation frequency	Kingsford, Jenkins & Porter (2004)
	Fish	Taxonomic	Basin-scale richness decreases within increasing intra- and inter-annual discharge variability	Iwasaki <i>et al.</i> (2012), McGarvey (2014) and Jardine <i>et al.</i> (2015)
	Fish	Functional	Change in functional composition along gradients of hydrological variability, seasonality, and predictability	Tedesco <i>et al.</i> (2008), Mims & Olden (2012), Sternberg & Kennard (2013) and McManamay & Frimpong (2015)
<u>Habitat</u>				
<u>Local</u>				
	Macroinvertebrates, macrophytes, riparian plants	Taxonomic	Richness increases with increasing hydrological habitat persistence (hydroperiod)	Larimore, Childers & Heckrotte (1959), Feminella (1996), Della Bella, Bazzani & Chiarotti (2005), Fritz & Dodds (2005), Stromberg <i>et al.</i> (2005), Davey & Kelly (2007), Hassall, Hollinshead & Hull (2011), Keruzoré, Willby & Gilvear (2013) and Brendonck <i>et al.</i> (2015)
	Macroinvertebrates	Functional	Increasing functional richness with increasing duration of channel drying	Bogan, Boersma & Lytle (2013) and Garcia-Roger <i>et al.</i> (2013)

Table 2. Continued

Ecohydrological mechanism	Organism group	Biodiversity facet	Biodiversity response	Examples
	Macroinvertebrates	Taxonomic	Richness increases with duration of flowing water	Fritz & Dodds (2005), Stromberg <i>et al.</i> (2005), Chakona <i>et al.</i> (2008), Clarke <i>et al.</i> (2010) and Santos & Stevenson (2011)
	Fish, macroinvertebrates	Taxonomic	Richness positively associated with minimum or mean discharge	Konrad, Brasher & May (2008), Niu, Franczyk & Knouft (2012) and McHugh <i>et al.</i> (2015)
	Macroinvertebrates	Phylogenetic	Phylogenetic diversity increases with surface water permanence	Silver, Vamosi & Bayley (2012)
	Fish, macroinvertebrates	Taxonomic	Linear or stepped decline in richness during receding water levels due to loss of habitat	Boulton (2003), Bêche <i>et al.</i> (2009), Bogan & Lytle (2011), Procopio (2012), McHugh <i>et al.</i> (2015) and Stubbington <i>et al.</i> (2015)
	Macrophytes, waterbirds	Taxonomic	Richness increases with increasing water-level stability	Kingsford <i>et al.</i> (2004), Capon (2005) and Nielsen <i>et al.</i> (2013)
	Riparian plants	Taxonomic	Richness peaks at locations with intermediate surface water compared to locations with permanently or rarely inundated sites	Pettit, Froend & Davies (2001) and Katz, Denslow & Stromberg (2012)
	Waterbirds	Functional	Functional richness increases with floodplain water-level variation	Kingsford <i>et al.</i> (2004) and Lawson <i>et al.</i> (2015)
Landscape	Fish, phytoplankton	Functional	Increasing turnover of taxa with adaptations to flow (e.g. dispersal, body shape, spawning habitat) with increasing flow permanence	Poff & Allan (1995), Alexandre, Ferreira & Almeida (2013) and Fraissé, Bormans & Lagadeuc (2013)
	Macroinvertebrates	Functional	Replacement of taxa in locations that dry driven by desiccation-resistant taxa	Bogan <i>et al.</i> (2013)
	Benthic algae, macroinvertebrates, riparian plants	Taxonomic	Change in composition along spatial gradient of surface-water permanence, driven by both turnover and nestedness	Stromberg <i>et al.</i> (2005), Datry, Larned & Scarsbrook (2007), Ledger <i>et al.</i> (2008), Stromberg <i>et al.</i> (2009), Davidson <i>et al.</i> (2012) and Datry <i>et al.</i> (2014a)
	Benthic algae, benthic biofilms, macroinvertebrates, macrophytes	Taxonomic	Change in composition along gradient of increasing duration of flowing water	Robach, Eglin & Tremolieres (1997), Besemer <i>et al.</i> (2009), Leigh & Sheldon (2009), Garcia-Roger <i>et al.</i> (2013), Tormés & Ruhi (2013) and Warfe <i>et al.</i> (2014)
	Macroinvertebrates, riparian plants, zooplankton	Taxonomic	Decreased spatial variation in composition among locations with reduced surface-water permanence	Capon (2005) and Thomaz <i>et al.</i> (2007)
Regional	Fish	Taxonomic	Basin-scale species richness increases with discharge volume	Oberdorff, Guégan & Hugueny (1995), Xenopoulos <i>et al.</i> (2005), Xenopoulos & Lodge (2006), McGarvey (2014) and McGarvey & Terra (2016)

(e.g. Fazi *et al.*, 2013), periphyton (e.g. Algarte *et al.*, 2009) and macroinvertebrates (Starr *et al.*, 2014) and this effect is evident both in terms of connectivity between floodplain wetlands and their associated stream network, and also in site-to-site connectivity within stream channels.

Effects of hydrological connectivity on local-scale functional diversity are much more variable and less well understood than effects of taxonomic diversity. Hydrological connectivity was positively associated with functional alpha diversity of waterbirds in wetlands of lowland floodplain rivers in Brazil (Almeida *et al.*, 2017). By contrast, functional alpha diversity of floodplain macroinvertebrate assemblages peaked in periods of relatively intermediate hydrological connectivity and was lower for highly fragmented and highly connected sites (Paillex *et al.*, 2013; Gallardo *et al.*, 2014). These inconsistencies likely reflect the fact that different organism groups are used to test connectivity–diversity relationships, but may also reflect differences in the spatial (longitudinal *versus* lateral; Amoros & Bornette, 2002) and temporal (duration and frequency) aspects of hydrological connectivity. Inconsistencies may also result from comparisons between groups of sites that are hydrologically connected at the time of field surveys but are not permanently connected.

Empirical evidence shows that hydrological connectivity is an important determinant of compositional variability of assemblages across landscapes (beta diversity) for multiple organism groups, as predicted by conceptual models (Thomaz *et al.*, 2007; Larned *et al.*, 2010). Beta diversity of bacteria, fish, macroinvertebrates and macrophytes is generally lowest in river–floodplain or wetland complexes during periods of high hydrological connectivity mediated by flood inundation, and increases during water recession as sites within rivers or river–floodplain networks become progressively fragmented (e.g. Fernandes *et al.*, 2009; Gomes *et al.*, 2012; Fazi *et al.*, 2013; Starr *et al.*, 2014). However, when multiple organism groups are analysed simultaneously from one study system, the effect of temporal variation in hydrological connectivity on compositional variability varies with dispersal ability (Padial *et al.*, 2014). Differences in taxonomic composition along hydrological connectivity gradients (e.g. Algarte *et al.*, 2009) provide further evidence for the role of connectivity as a mechanism linking hydrology and freshwater beta diversity.

(2) Effects of hydrological disturbance on freshwater biodiversity across spatial scales

Environmental disturbances affect biological communities (Resh *et al.*, 1988; Poff, 1992; Lake, 2000). At local scales, hydrological disturbances impact freshwater organisms *via* the process of physical scouring (by flooding) and desiccation of organisms (by drying). The effects of hydrological disturbance on alpha diversity vary for flooding and drying disturbances. Unprecedented drying events reduced macroinvertebrate alpha diversity in arid-climate streams in the USA (Bogan & Lytle, 2011), and richness of macroinvertebrate assemblages is negatively associated

with increasing hydrological ‘harshness’ (including channel drying) (Fritz & Dodds, 2005). Effects of flooding disturbances are more complex, with the response of macroinvertebrate and macrophyte alpha diversity to flooding frequency or intensity ranging from hump-shaped (e.g. Townsend *et al.*, 1997; Riis *et al.*, 2008), supporting the intermediate disturbance hypothesis (Connell, 1978), to linear (either positive or negative; e.g. Death & Winterbourn, 1995; Bornette, Amoros & Lamouroux, 1998). The effect of flood disturbance frequency on alpha diversity of benthic algae appears to depend on the degree of substratum armouring (e.g. Biggs & Smith, 2002). This finding suggests that both physical characteristics of study sites and biological traits of study organisms influence the relationship between hydrological disturbances and local biodiversity. Additionally, discrepancies among studies may be due to differences in the severity of hydrological disturbances and the fact that a broad spectrum of disturbances is rarely included in individual studies (Riis *et al.*, 2008). However, patterns of recovery of local species richness with increasing time since flood disturbance are broadly consistent among studies (e.g. Greenwood & Booker, 2015).

Hydrological disturbances can also affect functional alpha diversity of freshwater organisms. Functional diversity of benthic biofilm assemblages was significantly reduced by stream-drying disturbances (Timoner *et al.*, 2014) yet macrophyte functional richness did not differ in floodplain lakes that varied in drying disturbance frequency (Arthaud *et al.*, 2012). The predictability and variability of discharge (as measures of disturbance) are also strongly associated with the prevalence of functional traits of riverine fish in sites across the USA (Mims & Olden, 2012; McManamay, Bevelhimer & Frimpong, 2015). Yet it is unknown whether this variation in trait prevalence translates into variation in local functional-trait richness in aquatic systems.

At landscape scales, spatial variation in hydrological disturbance regimes affects both taxonomic and functional beta diversity. In floodplain lakes, waterbird taxonomic composition differed significantly between hydrologically stable lakes and lakes that were more disturbed by water-level fluctuations (Kingsford *et al.*, 2004). Spatial variation in functional composition of fish assemblages can reflect spatial gradients of discharge variability (Poff & Allan, 1995). Hydrological disturbances also alter beta diversity between sites with similar hydrology. For example, spatial variation in macroinvertebrate composition among experimental ponds with drying disturbances was significantly lower than spatial variation among permanently wetted ponds (Chase, 2007).

Hydrological disturbances also strongly affect regional gamma diversity. Fish have been the primary organism group for researching differences in basin-scale biodiversity associated with hydrology (see Table S1, Supporting Information). Iwasaki *et al.* (2012), McGarvey (2014); Jardine *et al.* (2015) and McGarvey & Terra (2016) each compared regional gamma diversity of fish across different parts of the globe [e.g. Northern Hemisphere (Iwasaki *et al.*, 2012) and tropical regions (Jardine *et al.*, 2015)] and related the total

number of species to temporal discharge variability. Across all of these studies, there was a consistent and significant negative relationship between increasing hydrological variability (e.g. inter-annual variation in discharge) and fish gamma diversity, suggesting that hydrological disturbances constrain regional diversity (Iwasaki *et al.*, 2012; McGarvey, 2014; Jardine *et al.*, 2015; McGarvey & Terra, 2016). However, it is unknown whether this relationship applies to other organism groups.

(3) Effects of hydrological habitat gradients on freshwater biodiversity across spatial scales

Hydrology strongly affects freshwater biodiversity as water presence and discharge determine habitat spatial extent, temporal persistence and hydraulics. Two major hydrological gradients are evident in the primary literature as being determinants of freshwater biodiversity. First, there is a strong effect of the duration of surface water (termed 'hydroperiod') on local biodiversity. For example, taxonomic alpha diversity of fish and macroinvertebrates is positively associated with hydroperiod duration (e.g. Chakona *et al.*, 2008; Beesley & Prince, 2010; Datry, 2012; Datry, Corti & Philippe, 2012; Bogan *et al.*, 2013; Datry *et al.*, 2014b). In addition to taxonomic alpha diversity, hydroperiod also affects functional alpha diversity through the prevalence of traits favoured by drying (Bogan *et al.*, 2013). Second, a decline in local species richness is linked with loss of specific in-stream habitats that are necessary for the persistence of specialised taxa. For example, inundation of riffles strongly depends on stream discharge, and therefore the loss of riffles is linked with removal of taxa that require flowing water for habitat or feeding [as found in studies of the effects of reductions in water discharge or differences between perennially and non-perennially flowing streams (e.g. Feminella, 1996; Boulton, 2003; Rose, Metzeling & Catzirikis, 2008; Santos & Stevenson, 2011; Warfe *et al.*, 2014)]. However, effects of habitat permanence on local taxonomic richness are strongly determined by seasonality. Clarke *et al.* (2010), for example, found that differences in local macroinvertebrate richness among permanently, intermittently and ephemeral flowing sites occurred during periods where hydrological differences were greatest among sites. Rapid recovery of local assemblages took place as discharge returned, particularly in ephemeral and intermittent streams (Clarke *et al.*, 2010).

Beyond in-stream sites, hydroperiod strongly affects local floodplain, riparian, and wetland biodiversity, yet there is variation in the shape of the response to hydroperiod gradients. Increasing taxonomic alpha diversity of floodplain or riparian vegetation assemblages is positively linked with frequency or duration of flooding and streamflow permanence (e.g. Capon, 2005; Stromberg *et al.*, 2005). By contrast, taxonomic alpha diversity of either wetland macrophytes or riparian vegetation was greatest at intermediate (Katz *et al.*, 2012; Nielsen *et al.*, 2013) or low (Pettit *et al.*, 2001) inundation frequency or duration. Functional alpha diversity of riparian vegetation was positively affected by inundation variability (Lawson *et al.*,

2015). These findings suggest that aspects of floodplain inundation (frequency, duration, and therefore temporal variability) affect taxonomic and functional alpha diversity of floodplain plant communities although evidence remains limited to determine if both taxonomic and functional facets of biodiversity respond in similar ways to individual hydrological gradients.

Water permanence in wetlands or floodplain lakes positively affects alpha diversity of diatoms, fish and macroinvertebrates (Table 2). Across tropical, temperate and arid environments, fish species richness in floodplain wetlands increases with increasing persistence and depth of sites (e.g. Puckridge, Costelloe & Reid, 2010; Penha *et al.*, 2017). A similar relationship is evident for wetland diatoms and macroinvertebrates with local species richness increasing with increasing duration of wetland inundation (e.g. Silver *et al.*, 2012; Chessman & Hardwick, 2014). Importantly, one of the few studies that test relationships between hydrology and phylogenetic diversity found a positive effect of water permanence on local phylogenetic diversity (Silver *et al.*, 2012).

Stream discharge magnitude and duration affects taxonomic alpha diversity but responses vary among organism groups. Reduced discharge during hydrological droughts lower alpha diversity of fish and macroinvertebrates in rivers (e.g. Clarke *et al.*, 2010; McCargo & Peterson, 2010), and spatial comparisons have found a positive effect of stream-discharge permanence on local taxonomic richness (e.g. Leigh & Datry, 2017). Taxonomic alpha diversity can be more strongly associated with minimum than with mean flow magnitude (Konrad *et al.*, 2008) or can be associated with stream cross-sectional area (McHugh *et al.*, 2015). Relationships between discharge permanence and the number of macroinvertebrate families vary in terms of phylogeny. For example, the number of macroinvertebrate families within each of the orders Ephemeroptera, Plecoptera and Trichoptera increased with discharge permanence and magnitude whereas the opposite response was found for the number of families of Odonata, Coleoptera, Heteroptera and Diptera (Belmar *et al.*, 2013). This may reflect broad differences in preferences for fast-flowing water by Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa and slow-flowing (or no-flow) water by Odonata, Coleoptera, Heteroptera and Diptera (OCHD) taxa. Similar family-based taxonomic diversity relationships occur for fish, suggesting that hydrology–biodiversity relationships are influenced by evolutionary history. For example, alpha diversity of species in the families Centrachidae and Cyprinidae was positively associated with temporal discharge variability, whereas discharge magnitude was positively linked with richness of species in the families Catostomidae and Percidae in the USA (Niu *et al.*, 2012).

Spatial variation in the hydrology of river and floodplain environments is an important determinant of biodiversity at landscape scales, and many of the hydrological gradients influencing aquatic habitat or aquatic resource dynamics identified above strongly influence patterns of beta diversity but in different ways from local-scale patterns. Spatial

variation in the duration or frequency of surface-water presence strongly affects spatial variation in taxonomic and functional composition of fish, macroinvertebrate, riparian plant and waterbird assemblages (Table 2). For example, spatial differences in taxonomic composition within river–floodplain systems are consistently reported in association with differences in surface-water permanence in both stream networks [e.g. USA, New Zealand, Europe, Australia (Stromberg *et al.*, 2005; Datry *et al.*, 2007, 2014a; Beesley & Prince, 2010; Bogan *et al.*, 2013; Tornés & Ruhí, 2013)] and floodplain wetland or riparian communities (e.g. Kingsford *et al.*, 2004; Davidson *et al.*, 2012; Nielsen *et al.*, 2013; Chessman & Hardwick, 2014). Where reported in the literature, nestedness is the dominant driver of compositional change along hydroperiod gradients (e.g. Datry *et al.*, 2014a). Compositional turnover (i.e. replacement) occurs in some systems or organism groups whereby taxa lost from permanently inundated sites are replaced by taxa adapted to desiccation or recolonisation in temporarily inundated sites (e.g. Bogan *et al.*, 2013).

Spatial variation in streamflow hydraulics is also an important determinant of taxonomic beta diversity, both within and among landscapes. Studies of biodiversity responses to spatial heterogeneity of discharge have focused heavily on macroinvertebrates, with differences in the assemblage composition among reaches or whole rivers associated with differences in discharge patterns (e.g. Feminella, 1996; Leigh & Sheldon, 2009; Clarke *et al.*, 2010; Warfe *et al.*, 2014; Leigh & Datry, 2017). Significant changes in composition along discharge gradients also occur for other organism groups, such as aquatic bacteria (Besemer *et al.*, 2009). Within-group compositional variability is often different for different hydrology (i.e. the magnitude of variation in composition among samples can be greater for particular hydrological conditions). For example, spatial variation in macroinvertebrate composition within ephemeral flowing headwaters was greater than that of perennially flowing streams, especially during dry seasons (Clarke *et al.*, 2010), whereas the macroinvertebrate communities were more variable in perennially flowing than in intermittently flowing streams (Warfe *et al.*, 2014).

Analyses based on data sets spanning multiple continents consistently show positive effects of annual discharge at the scale of entire river basins on taxonomic gamma diversity (Oberdorff *et al.*, 1995; Xenopoulos *et al.*, 2005; Xenopoulos & Lodge, 2006; Iwasaki *et al.*, 2012; McGarvey, 2014). In this context, discharge magnitude is viewed as analogous to geographical area in terrestrial species–area relationships, because an increasing volume of water creates greater space. Such relationships have been queried because regional species richness is not necessarily in equilibrium with contemporary hydrology (Olden *et al.*, 2010). Similar to responses of local biodiversity to discharge, mean-annual-low flow discharge was a stronger predictor of drainage basin-scale fish species richness in the Americas (McGarvey & Terra, 2016), suggesting that minimum habitat volumes constrain gamma diversity.

V. A CONCEPTUAL MODEL OF THE HYDROLOGICAL DRIVERS OF MULTI-SCALED FRESHWATER BIODIVERSITY

Evidence from empirical studies indicates that different ecohydrological mechanisms vary in how they influence biodiversity at different spatial scales (Table 2). In an attempt to unify these mechanisms, we present a conceptual model to summarise how different facets of biodiversity across different spatial scales vary in response to hydrology of river–floodplain systems (Fig. 4). In spatial terms, the model is structured around the mechanisms that influence biodiversity at regional scales, among landscapes, within landscapes, and at local scales (*sensu* Pavoine *et al.*, 2016). In the context of the hierarchical nature of river networks, the model is based on identifying mechanisms structuring biodiversity among rivers basins (as regions), among major tributaries within basins (as landscapes), among reaches within major tributaries, and at the reach scale.

At the scale of river basins, disturbance and habitat are primary ecohydrological drivers of freshwater biodiversity (Fig. 4). Regional biodiversity is positively influenced by aquatic habitat size (indicated by discharge volume), and constrained by disturbance history (e.g. temporal discharge variability). Disturbance constraints likely explain why drainage basins with high inter-annual variation in discharge support fewer fish species than other comparably sized river basins with more predictable hydrology (e.g. Puckridge *et al.*, 1998; Jardine *et al.*, 2015). In contrast to biodiversity at smaller spatial scales (i.e. within regions), current connectivity has little effect on regional biodiversity (although historical hydrological fragmentation may be important for gamma diversity because of vicariance leading to speciation events) (e.g. Griffiths, 2010). A gap in evidence of the effects of hydrological regimes on phylogenetic and functional diversity restricts the ability to make explicit predictions of these facets of biodiversity at regional scales. However, evidence of the roles of habitat persistence and disturbance at finer spatial scales suggests that phylogenetic and functional diversity are positively influenced by habitat size and negatively influenced by hydrological disturbance.

Spatial variation in taxonomic and functional composition among landscapes is influenced by habitat and disturbance (Fig. 4). In contrast to regional-scale biodiversity, the emphasis at landscape scales is on how assemblages vary taxonomically, functionally and phylogenetically in response to ecohydrological mechanisms. Spatial variation in habitat related to hydrological variables such as hydroperiod or discharge duration, and in hydrological disturbance regimes is linked positively with spatial variation in freshwater biodiversity among landscapes (e.g. Leigh & Sheldon, 2009; Warfe *et al.*, 2014).

In contrast to among-landscape variation, biodiversity within landscapes depends on each of the major ecohydrological variables and connectivity is important at this spatial scale of biodiversity (Fig. 4). Hydrological connectivity negatively affects taxonomic and functional

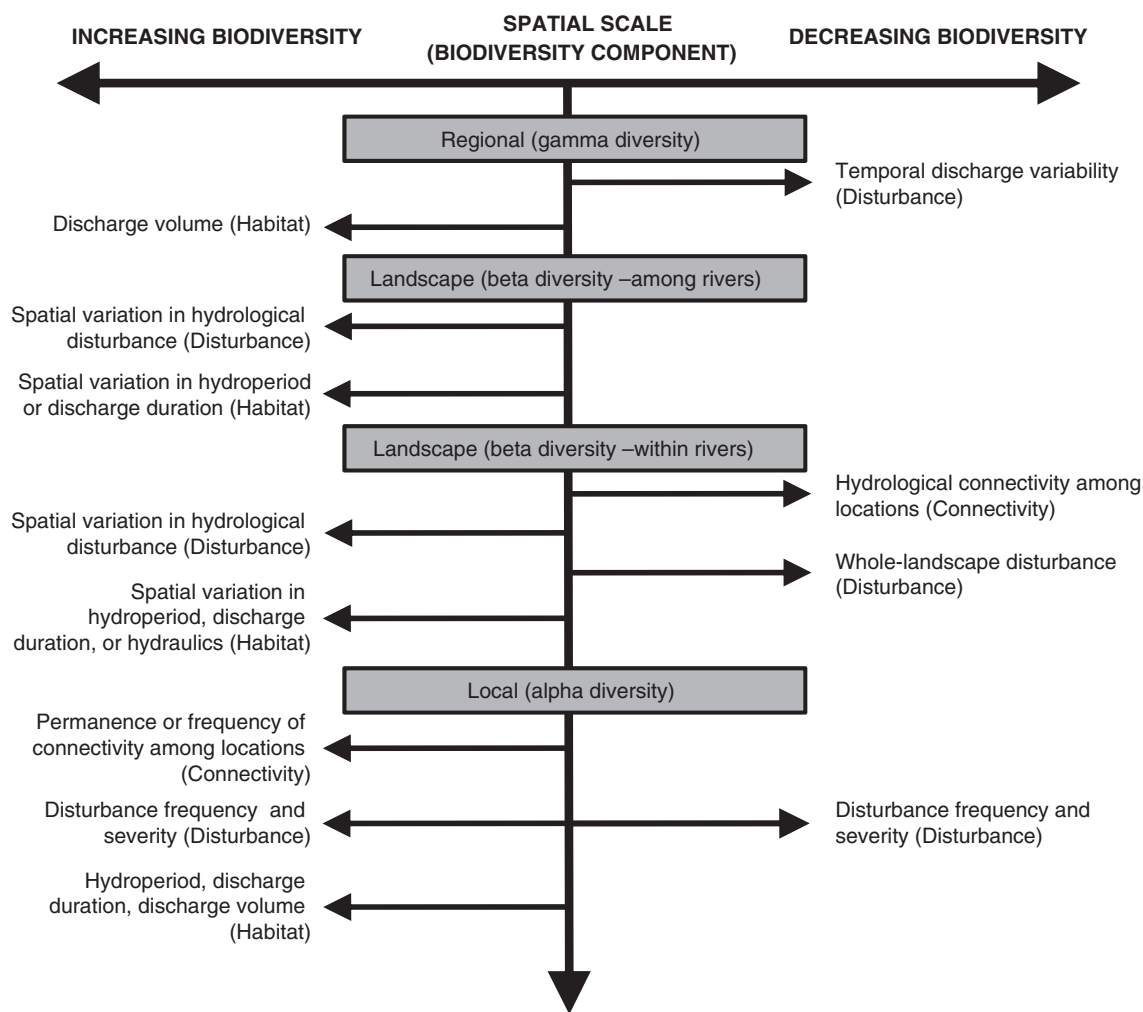


Fig. 4. A conceptual model summarising patterns of biodiversity across multiple spatial scales along distinct ecohydrological gradients in surface water and floodplain environments. The direction of each arrow along the gradient of increasing–decreasing biodiversity represents the shape of the effect of each ecohydrological mechanism, for each spatial scale of biodiversity. For example, increasing temporal discharge variability leads to decreasing regional biodiversity. Other variables unrelated (or only indirectly related) to hydrology (e.g. latitude, geomorphology, surrounding catchment characteristics) are not included but recognised as relevant to structuring freshwater biodiversity across spatial scales. The positive and negative effects of hydrological disturbance regime and local-scale biodiversity reflect contradictory and hump-shaped responses reported in the literature (see text for further details).

biodiversity because of greater opportunities for dispersal (Akasaka & Takamura, 2012). Spatial heterogeneity in physical habitat persistence and hydraulic habitat conditions, both mediated by the hydrological regime, positively affect landscape-scale biodiversity (e.g. Lamouroux, Poff & Angermeier, 2002; Horrigan & Baird, 2008; Sim *et al.*, 2013). Hydrological disturbance has multiple effects on landscape biodiversity; disturbances that affect entire landscapes (e.g. droughts) lead to reduced spatial variation in composition by removing organisms with patchy distributions or specialised ecological niches that are unable to resist the disturbances (e.g. Chase, 2007). However, where the timing and magnitude of hydrological disturbances are spatially variable within the landscape, taxonomic and functional beta diversity increase (e.g. Bogan *et al.*, 2013). This

matches the heterogeneous disturbance hypothesis originally proposed for terrestrial landscapes (Warren *et al.*, 2007) and has substantial application to hydrological disturbances in freshwaters.

At local spatial scales, freshwater biodiversity is influenced by a broader combination of ecohydrological mechanisms (Fig. 4). Here, hydrological connectivity often positively influences local functional and taxonomic richness, at least up to a point (e.g. Lasne *et al.*, 2007; Paillex *et al.*, 2013). Disturbance impacts depend primarily on the breadth of the disturbance gradient; increasing flood disturbance impacts on local taxonomic diversity by progressively removing taxa *via* scour processes (e.g. Biggs & Smith, 2002), yet hydrological disturbance frequency or intensity can produce a unimodal response of alpha diversity (e.g. Riis *et al.*, 2008),

Table 3. Principles for developing a multi-scaled understanding of biodiversity responses to hydrological regimes

Principle	Premise
1. Understanding biodiversity responses to hydrological regimes across spatial scales is essential for quantifying the true impacts of hydrological regime change on freshwater biodiversity	Empirical research and conceptual understanding of the effects of anthropogenic changes to hydrological regimes has inadequately considered how responses of biodiversity vary across different spatial scales
2. Effects of hydrological regime change on freshwater biodiversity are best addressed when the specific spatial scale(s) of impact and underlying ecohydrological mechanisms are identified	Application and delivery of environmental flow programs will best achieve desired biodiversity targets when the spatial scales of biodiversity responses to hydrological regimes are understood and linked to specific ecohydrological mechanisms
3. Risks of environmental flows as a driver of further biodiversity decline can be addressed and managed when links between hydrological regimes and freshwater biodiversity are tied to spatial scaling	Poor consideration of how hydrological regimes influence freshwater biodiversity across spatial scales means that there is a risk that environmental flow programs may contribute to biodiversity loss at specific spatial scales
4. Biodiversity responses to hydrological regimes across spatial scales depend on the biological and ecological characteristics of organisms used for assessment	Effects of hydrological regimes on patterns of biodiversity across spatial scales are variable among different organism groups

supporting the intermediate disturbance hypothesis. Aquatic habitat persistence, volume, and within-habitat hydraulic variability each positively drive functional and taxonomic richness (e.g. Clarke *et al.*, 2010; Timoner *et al.*, 2014; McHugh *et al.*, 2015).

VI. PRINCIPLES AND APPLICATIONS OF A MULTI-SCALED CONCEPTUAL UNDERSTANDING OF FRESHWATER BIODIVERSITY RESPONSES TO HYDROLOGICAL REGIMES

An overarching goal of freshwater conservation policies globally is to sustain and restore the biodiversity of freshwater ecosystems [e.g. National Principles for the Provision of Water for Ecosystems (ARMCANZ & ANZECC, 1996; Arthington & Pusey, 2003); European Water Framework Directive (Acreman & Ferguson, 2010)]. However, the lack of general theory of the multi-scalar and multi-faceted responses of biodiversity to hydrological alterations is likely a barrier to the success of water policies and environmental flows in meeting biodiversity targets. We detail four principles to enhance a conceptual understanding of how hydrological regimes affect freshwater biodiversity across spatial scales (Table 3). In so doing, we highlight how the restoration of hydrology *via* environmental flows can benefit freshwater biodiversity from an explicit consideration of spatial scaling.

(1) Principle 1: understanding biodiversity responses to hydrological regimes across spatial scales is essential for quantifying the true impacts of hydrological change on freshwater biodiversity

Empirical evidence of the impacts of hydrological alteration on freshwater biodiversity is used widely to justify the provision of hydrological regimes to sustain or

restore freshwater biodiversity (e.g. Bunn & Arthington, 2002; Poff & Zimmerman, 2010). However, the true extent of the consequences of anthropogenic hydrological change for freshwater biodiversity are almost certainly underestimated, because freshwater biodiversity research has inadequately dealt with issues of spatial scaling when quantifying impacts of hydrological change on specific spatial components of freshwater biodiversity. In addition, the effects of hydrological change on phylogenetic diversity of communities across spatial scales are simply not represented in the hydrological alteration literature (e.g. Poff & Zimmerman, 2010), and evidence of functional biodiversity responses to hydrological change remains extremely limited.

Inventories of taxa at local scales (i.e. alpha diversity) are used extensively as biodiversity indicators for freshwater biomonitoring programmes (e.g. Davies *et al.*, 2010; Carlisle, Wolock & Meador, 2011), studying the effects of hydrological alteration (e.g. Kingsford *et al.*, 2004; Nielsen *et al.*, 2013), and evaluating the performance of restoration of freshwater ecosystems (e.g. Palmer, Menninger & Bernhardt, 2010; Yang *et al.*, 2016). However, as the simplest attribute, alpha diversity reflects only a single aspect of biodiversity (Angermeier, 2010; McGill *et al.*, 2015). Use of local-scale biodiversity responses to hydrological regimes may be insensitive to change when compared to other spatial components of biodiversity. For example, taxonomic alpha diversity of macroinvertebrates did not differ between regulated (sustained low-flow) and unregulated reaches (variable intra-annual discharge) in California (USA), yet within-reach beta diversity was significantly lower in the regulated reach (Marchetti *et al.*, 2011), and higher fish beta diversity was evident in unregulated *versus* regulated reaches in the eastern USA (Freedman *et al.*, 2014). Beyond the context of hydrological change, measures of biodiversity that assess spatial variation in assemblage composition are more responsive to anthropogenic disturbances and conservation management actions (e.g. Passy & Blanchet, 2007).

Further compounding the issue is that few studies examining biodiversity responses to hydrological change simultaneously assess effects across the full range of spatial scales that occur in the spatial hierarchy of freshwater systems (i.e. are impacts of hydrological alteration more evident at specific spatial components of biodiversity?). Assessing the responses of biodiversity to hydrological alteration at single spatial scales constrains understanding to focus only on that specific spatial scale (*sensu* Levin, 1992), while ignoring potential and more-severe responses at other spatial scales. A critical point here is that some studies quantify the number of taxa present at multiple spatial extents within rivers (e.g. samples, sites, reaches) in association with differences in hydrology (e.g. Robson, Hogan & Forrester, 2005). Such studies make comparisons of taxon richness across differing areas (*sensu* Wiens, 1989; Jurasinski *et al.*, 2009), yet do not address other important aspects of biodiversity (e.g. spatial variation in composition) across the spatial hierarchy of freshwater networks. By contrast, simultaneous assessment of biodiversity across the multiple hierarchical levels of freshwater systems (*sensu* Pavoine *et al.*, 2016) is hypothesised to give a much stronger and more practical understanding of how hydrological regimes influence biodiversity across spatial scales.

(2) Principle 2: effects of hydrological change on freshwater biodiversity are best addressed when the specific spatial scale(s) of impact and underlying ecohydrological mechanisms are identified

The failure to consider explicitly how different facets of biodiversity respond to environmental gradients across spatial scales has been identified as a fundamental impediment to addressing anthropogenic impacts to protect biodiversity (McGill *et al.*, 2015). Following from Principle 1, it is essential that efforts to preserve or restore hydrological regimes are delivered at the spatial scale at which impacts of anthropogenic hydrological regime change are most evident. Despite hydrological regime alteration being typically apparent at spatial extents covering $>10^1$ km of river networks, most studies examining the responses of freshwater biodiversity are based on data from study sites spanning $<10^{-1}$ km (Table 2; Poff & Zimmerman, 2010), concordant with the spatial scale of freshwater biodiversity research more generally (Tornwall *et al.*, 2015). If the impacts of hydrological change on freshwater biodiversity are greater at spatial scales larger than individual study sites, but these impacts are not quantified, then there is an increased risk that restoration of elements of natural hydrological regimes will not meet targeted levels of biodiversity response. This situation reflects the need to match the spatial scales of research to (i) questions of ecological interest, and (ii) test hypotheses at scales that are relevant to conservation actions (*sensu* Fausch *et al.*, 2002). If hydrological change differentially alters biodiversity across spatial scales (e.g. Pegg & Taylor, 2007) then we hypothesise that maintaining or restoring aspects of hydrological regimes across the spatial scales where impacts are most evident is likely to produce the most apparent recovery of freshwater biodiversity. For example, a minor

effect of hydrological alteration on local biodiversity but more substantial impact on landscape-scale biodiversity would suggest a need to coordinate the delivery of environmental flows within and between river basins (potentially achieved by spatially desynchronising the delivery of environmental flow programs among river basins).

The success of implementing environmental flows to achieve the goal of protecting and enhancing freshwater biodiversity across spatial scales is likely to be improved if the underlying causal mechanisms linking hydrological change and biodiversity responses across spatial scales are known. If a specific mechanism is identified as linking hydrological alteration to biodiversity responses at particular spatial scales, then the restoration of hydrological regimes by environmental flows can be tailored around the frequency, timing, duration and magnitude of hydrological events (*sensu* Poff *et al.*, 1997) that confer the environmental conditions to restore biodiversity at the spatial scale of interest. Clearly, ecohydrological mechanisms are unlikely to produce consistent responses for different organism groups (due to differences in biology and ecology; see Principle 4). However, linking hydrology to biodiversity responses across spatial scales *via* specific ecohydrological mechanisms will almost certainly better equip water-management policies with the evidence to preserve freshwater biodiversity at scales of interest.

(3) Principle 3: risks of environmental flows as a driver of further biodiversity decline can be addressed and managed when links between hydrological regimes and freshwater biodiversity are tied to spatial scaling

Environmental flows are widely advocated and used as a tool for freshwater biodiversity conservation (Poff & Matthews, 2013; Acreman *et al.*, 2014). However, a poor consideration of how hydrology influences freshwater biodiversity across spatial scales creates the paradoxical situation where environmental flows may inadvertently contribute to further losses of biodiversity. These risks are critical to recognise because environmental flows often come at a cost to other water users (e.g. economic consequences of reduced water availability for human uses) or because of public investment in water intended for biodiversity benefits.

One potential risk of an inadequate understanding of the relationships between hydrological regimes and freshwater biodiversity across spatial scales is loss of spatial variation in assemblage composition. Termed 'biotic homogenisation', declines in spatial variation in biodiversity is one aspect of global biodiversity decline (McKinney & Lockwood, 1999; McGill *et al.*, 2015) that can be identified only when spatial variation in community composition (taxonomic, functional, or phylogenetic) is tied explicitly to spatial scale (Rooney *et al.*, 2007). Homogenisation of freshwater communities is often examined in the context of the spread and establishment of non-native fauna (e.g. Vileger *et al.*, 2011), but biotic homogenisation can also occur independently of non-native species (e.g. Loughheed *et al.*, 2008; McCune & Vellend, 2013; Trentanovi *et al.*, 2013; Li & Waller, 2015;

Perkin *et al.*, 2015). However, because spatial variation in functional and taxonomic composition within and among river networks is tied to spatial variation in hydrology (Table 2), environmental flow programs that fail to account for spatial variability across larger spatial extents may lead to biodiversity loss at landscape scales but preservation of biodiversity at local scales. This possibly creates a paradox for conservation management whereby actions designed to preserve or enhance biodiversity may inadvertently contribute to biodiversity loss due to inadequate consideration of how biodiversity responses vary across spatial scales.

Our emphasis on beta diversity and risks to biodiversity *via* environmental flows here is important because this component of biodiversity is often overlooked when planning and communicating outcomes of hydrological regime change. For example, changes to future hydrology and consequences for freshwater biodiversity focus heavily on aspects of 'inventory' diversity (*sensu* Jurasinski *et al.*, 2009; e.g. Palmer *et al.*, 2008). However, water resource development has reduced spatial variation in hydrological regimes at multiple spatial scales (within rivers, e.g. Thoms & Parsons, 2003; among rivers, e.g. Poff *et al.*, 2007). Alternatively, there is also evidence that dams have caused hydrological regimes to become more spatially variable (McManamay, Orth & Dolloff, 2012). Evidence of the effects of hydrological change on spatial variation in biodiversity remains a key knowledge gap (Poff *et al.*, 2007; Rahel, 2010), yet such evidence is essential to ensuring that environmental flows do not contribute further to biodiversity loss *via* biotic homogenisation.

(4) Principle 4: biodiversity responses to hydrology across spatial scales depend on the biological and ecological characteristics of organisms used for assessment

Inconsistencies in the relationships between hydrology and freshwater biodiversity across spatial scales among different organism groups can create further uncertainty for freshwater conservation managers for managing hydrology. The ecological and biological characteristics of different organism groups (e.g. riparian plants, riparian fauna, fish and waterbirds) have a major role in determining the effect of hydrological regimes on freshwater biodiversity. Importantly, aspects of hydrology can simultaneously affect the biodiversity of different organism groups in contrasting ways *via* different ecohydrological mechanisms. For example, alpha diversity of riparian macroinvertebrates increases with time since inundation (Datry *et al.*, 2012), indicating that inundation of riparian zones by flooding acts as a disturbance for riparian invertebrates, whereas alpha diversity of riparian vegetation communities increases with water permanence, highlighting the importance of water as a resource for plants (Stromberg *et al.*, 2005).

Differences in the responses of biodiversity to hydrology across spatial scales among organism groups underscores the need to understand the effects of hydrology on specific organism groups. Few studies compare responses of different

organism groups to environmental gradients in aquatic ecosystems (Johnson *et al.*, 2014), and this deficiency is evident in our review of the literature (Table S1, Supporting Information). In a study comparing ecological characteristics of intermittently and permanently flowing rivers in Tasmania, Australia, Warfe *et al.* (2014) found that while differences in assemblage composition between flow regimes were clear for riparian vegetation, biofilms, and macroinvertebrates (i.e. beta diversity), responses of alpha diversity to differences in flow regime were inconsistent among organism groups. This finding highlights that biological and ecological attributes (e.g. life-history, trophic ecology and habitat preference) of the specific organism group need to be evaluated when conceptualising the role of hydrology in freshwater biodiversity and making recommendations for environmental flows to protect or enhance it.

VII. FUTURE RESEARCH OPPORTUNITIES FOR ADVANCING A CONCEPTUAL UNDERSTANDING OF HYDROLOGY – BIODIVERSITY LINKAGES

Synthesising evidence of the effects of hydrological regimes on freshwater biodiversity across its multiple facets and spatial components highlights that important gaps in knowledge still remain within the topic of ecohydrology. Here, we emphasise six key topics for refocussing research to strengthen our ability explicitly to understand and predict biodiversity responses to hydrological regimes (Table 4).

(1) Simultaneous multi-scaled assessment of biodiversity responses to hydrology

Most research of the effects of hydrology on biodiversity has examined the responses of a single spatial component of biodiversity (Bunn & Arthington, 2002; Poff & Zimmerman, 2010; Table S1, Supporting Information). Focussing on single aspects of biodiversity (e.g. inventory, differentiation; Jurasinski *et al.*, 2009), leads to conclusions being applicable only to that specific spatial component and facet of biodiversity and therefore neglecting the influence of hydrology on biodiversity at other scales. For example, numerous studies show that increasing the duration of surface water persistence increases local taxonomic and functional richness (Section IV). However, increasing surface water persistence often occurs in conjunction with greater hydrological connectivity, which decreases spatial variation in composition among sites. While comparisons among geographically disparate studies help disentangle the effects of different ecohydrological mechanisms on patterns of freshwater biodiversity, few studies assess effects of hydrology on biodiversity responses across different spatial components of biodiversity simultaneously across the spatial extent of analysis.

The benefit of adopting a multi-scaled approach to quantifying biodiversity responses to hydrological regimes is that the mechanism(s) influencing each spatial component of biodiversity can be identified (e.g. Edge *et al.*, 2017)

Table 4. Research opportunities and relevance to improving understanding of hydrology–biodiversity linkages across spatial scales

Research gap	Approach	Relevance
Simultaneous multi-scaled assessment of biodiversity responses to hydrological regimes	Test how separate spatial components of biodiversity vary in response to hydrological gradients within specified spatial extents	Ecohydrological mechanisms responsible for variation in each spatial component of biodiversity are identified
Concordance of biodiversity responses to hydrological mechanisms among multiple organism groups	Sample multiple organism groups across the spatial hierarchy of river–floodplain networks and compare how biodiversity responses to hydrological regimes vary among organism groups	Informative to developing monitoring programs to evaluate outcomes of environmental flow programs on freshwater biodiversity
Multi-faceted biodiversity responses to hydrological regimes across spatial scales	Analyse patterns of taxonomic, functional, and phylogenetic biodiversity across spatial scales and test how variation in spatial components of biodiversity is associated with ecohydrological gradients	Addresses major gaps in understanding the effects of hydrological regimes (or hydrological regime change) on functional and phylogenetic facets of biodiversity across spatial scales
Combined use of natural and anthropogenic hydrological gradients to improve confidence of biodiversity responses to hydrological regimes	Compare how patterns of biodiversity are linked with ecohydrological mechanisms along separate natural and anthropogenic hydrological gradients	Inferences of the effects of hydrological regimes on biodiversity are strengthened when natural and anthropogenic gradients are used in combination
Temporal change in spatial biodiversity patterns	Test how different spatial components of biodiversity vary over time in response to ecohydrological events (e.g. flooding disturbance, inundation that enhances connectivity or prolongs habitat persistence)	Spatial components of biodiversity that respond more rapidly and consistently to hydrological events can be targeted during the design and evaluation of environmental flow programs
Cross-climate comparison of hydrology–biodiversity relationships	Replicate designed studies of biodiversity patterns across regions that have distinct climate and hydrological characteristics (e.g. differences in hydrological regime predictability)	Increases ability to develop broad generalisations of biodiversity responses to hydrological regimes and identify how the effects of hydrological regimes are dependent on other environmental variables

and therefore addressed more precisely by environmental flows. Multi-scaled assessment of biodiversity responses to hydrology could be analysed in ways that reflect the nested hierarchy of riverine environments. Pavoine *et al.* (2016) propose a framework for assessing variation in a facet (or facets) of biodiversity (taxonomic, functional, or phylogenetic) across four spatial levels: whole river basin (gamma), among regions (beta among), among sites within regions (beta within), and within sites (alpha). Such a framework brings together the inventory and differentiation aspects of spatial biodiversity (Jurasinski *et al.*, 2009) and existing data sets sourced from biodiversity monitoring or ‘river health’ programs could be readily analysed by existing community-level methods (e.g. those described by Anderson *et al.*, 2011).

(2) Concordance of biodiversity responses to hydrological mechanisms among multiple organism groups

Ecohydrological research across spatial scales has disproportionately targeted particular organism groups overall (e.g. macroinvertebrates, fish) or particular organism groups at specific spatial components of biodiversity (e.g. a bias for macroinvertebrate biodiversity studies to focus on alpha and beta biodiversity components at the expense of regional-scale diversity responses; Table S1, Supporting Information). There remains a significant gap in research quantifying how

patterns of freshwater biodiversity vary across spatial scales in response to hydrology, particularly for amphibians, birds, microorganisms, and algae; Table S1, Supporting Information). Such knowledge gaps impede the ability to determine robust generalisations or theory of biodiversity responses to hydrological regimes by way of formal meta-analyses that are necessary for predicting broader biodiversity responses to hydrological alterations.

Inevitably, biodiversity assessments are based on a subset of organisms intended to serve as proxies (surrogates) for overall biodiversity, or on organisms of concern or significance. Cross-taxon congruency of biodiversity variables is generally low (Westgate *et al.*, 2014), suggesting that a range of organism groups is necessary for quantifying true biodiversity condition and responses to environmental gradients (Heino, 2010). However, few studies compare the effects of environmental gradients (particularly hydrological gradients) on different organism groups (e.g. invertebrates *versus* macrophytes *versus* fish) in freshwater ecosystems (e.g. Johnson *et al.*, 2014). It is therefore not yet understood how well spatial biodiversity patterns of particular organism groups (e.g. macroinvertebrates) reflect gradients in broader multi-organism-group biodiversity patterns. This gap could be addressed by first investigating relationships of hydrological gradients to different organism groups at the same spatial scales to test assumptions of concordance across organism groups, or if responses vary on the basis of organism

(e.g. dispersal) characteristics (e.g. Padial *et al.*, 2014). Issues of taxonomic surrogacy are important because monitoring programs evaluating the performance of environmental flows in biodiversity conservation across spatial scales are costly to implement. Therefore, if a subset of organism groups is a reliable surrogate for broader biodiversity across different spatial scales, this subset could be used to allocate monitoring resources to sampling more sites (or more frequently) rather than sampling multiple organism groups that show the same hydrological responses. Such evidence would be of significant value to conservation managers when designing cost-effective monitoring programs to assess the performance of environmental flow programs and understanding how impacts of hydrological alteration persist or vary over time.

(3) Multi-faceted biodiversity responses to hydrological regimes across spatial scales

Knowledge of the effects of hydrological regimes on functional and phylogenetic facets of biodiversity is respectively limited and almost non-existent, thereby hindering our ability to predict effects of hydrological changes on ecosystem functioning and evolutionary potential. Furthermore, there is inconsistent evidence that alpha, beta and gamma components of taxonomic, functional and phylogenetic diversity respond in the same way to environmental gradients in terrestrial systems (e.g. Meynard *et al.*, 2011; Tobias & Monika, 2012; Arnan, Cerdá & Retana, 2017). Studies from terrestrial or marine systems suggest that changes in taxonomic diversity may underestimate declines in functional and phylogenetic diversity (Baiser & Lockwood, 2011; D'agata *et al.*, 2014). An improved understanding of phylogenetic and functional responses to hydrology across spatial scales should begin with preliminary studies examining how the different facets of biodiversity respond to hydrological gradients across spatial scales for specific organism groups. Numerous advances exist in analytical methods and developments in frameworks for analysing taxonomic, functional and phylogenetic diversity patterns across spatial scales (e.g. Cardoso *et al.*, 2014; Hui & McGeoch, 2014; Pavoine & Ricotta, 2014; Pavoine *et al.*, 2016; Tucker *et al.*, 2017) and these should be applied to suitable new or existing freshwater biodiversity data sets where complementary hydrological data are available and as details of organism traits become better understood (Chessman, 2015). Some studies have explored patterns of phylogenetic and functional biodiversity in freshwater systems (e.g. Strecker *et al.*, 2011; Blanchet *et al.*, 2014; Heino & Tolonen, 2017), but none has explicitly tested how these facets vary in response to hydrology across spatial scales.

(4) Combined use of natural and anthropogenic hydrological gradients to improve confidence in biodiversity responses to hydrology

Outcomes of research examining biodiversity responses to gradients in natural hydrology are frequently applied to predicting consequences of anthropogenic changes in hydrology.

Dams alter hydrological regimes (e.g. Magilligan & Nislow, 2005) thereby creating spatial anthropogenic gradients in hydrology (Mackay, Arthington & James, 2014), and an extensive literature focusses on the ecological consequences of these changes (e.g. Poff & Zimmerman, 2010). Studies of these ecological responses to hydrological regime changes include a strong emphasis on multi-species biodiversity, yet the consequences for biodiversity are inadequately synthesised with frameworks of spatial scaling that have been adopted by ecology and conservation biology in general. At least two potential approaches can address this deficiency. First, existing literature could be synthesised (or re-synthesised) to explore how different components of biodiversity respond to anthropogenic hydrological gradients. Second, gaps in the existing literature could be filled by new studies designed to assess effects of anthropogenic alteration of hydrological regimes across spatial scales. The combined use of both natural and anthropogenic hydrological gradients can both strengthen the ability to predict impacts of anthropogenic changes and identify underlying causal ecological mechanisms responsible for biodiversity patterns (Fukami & Wardle, 2005).

(5) Temporal change in spatial biodiversity patterns

A consistent justification for research on the effects of hydrology on freshwater biodiversity is that more evidence is needed to predict future biodiversity condition in response to direct (e.g. water-resource development) and indirect (e.g. climate change) effects of humans on hydrology. While such predictions are adopted by monitoring programs to assess the consequences of such changes, they are also increasingly adopted when designing field monitoring to assess the performance of environmental flow programs in achieving their desired targets of biodiversity conservation or restoration. However, it is still unclear whether particular spatial components of biodiversity are more responsive (i.e. respond more rapidly or clearly) to hydrological events or hydrological regime change than others. If particular spatial components of biodiversity respond rapidly to hydrological events (e.g. managed floodplain inundation), their identification would be beneficial to designing monitoring programs with the most appropriate spatial grain and extent, and temporal frequency and duration of sampling (*sensu* Downes, 2010).

(6) Cross-climate comparison of hydrology–biodiversity relationships

Most studies of freshwater biodiversity responses to hydrology (and ecohydrological mechanisms) are based on data from single geographic regions representing specific climates, which in turn determine regional hydrological predictability. However, there is increasing combination or reuse of data sets from multiple climatic regions testing the effects of hydrological events on freshwater biodiversity (e.g. Datry *et al.*, 2014a) or comparing the effect of hydrology on freshwater biodiversity at single spatial scales (e.g. Leigh *et al.*, 2016).

Despite such broad-scale evidence, there remains a gap in understanding if effects of hydrological regimes and ecohydrological mechanisms on spatial components of biodiversity are generalisable across regions with contrasting hydrological predictability driven by climate (Fig. 3). For example, climatic variation may partly explain inconsistencies in the degree to which spatial variation in the taxonomic composition of assemblages is driven by turnover or nestedness along gradients of habitat persistence. Increasing emphasis on cross-climate studies would be of considerable benefit to determining the extent to which hydrology–biodiversity relationships can be generalised and adopted in environmental flow planning (*sensu* Poff *et al.*, 2010).

VIII. CONCLUSIONS

(1) The highly dynamic and concentrated nature of freshwater biodiversity, combined with sustained demands for fresh water to satisfy human demands, means that freshwaters provide a unique and essential model system for understanding the mechanisms that determine how patterns of biodiversity vary across spatial scales.

(2) The hydrological regime of rivers, wetlands and floodplains has long been viewed as the primary determinant of their biodiversity. Previous conceptualisations of the role of hydrology and syntheses of empirical evidence of the responses of biodiversity to hydrological change have not adequately addressed the dependency of biodiversity on spatial scaling, or only focussed on the role of single ecohydrological mechanisms.

(3) Scale-dependent biodiversity responses to hydrology are driven by different combinations of ecohydrological mechanisms operating at different spatial scales. Both habitat and disturbance mechanisms are major hydrological drivers of regional (basin)-scale freshwater biodiversity (gamma diversity) and variation in biodiversity among landscapes. At smaller spatial scales, hydrological connectivity becomes increasingly important as a driver of biodiversity, in terms of both spatial variation in composition (beta diversity within river networks) and local taxa richness (alpha diversity). Disturbance and habitat mechanisms linking hydrology and biodiversity remain important from regional to local spatial scales.

(4) Importantly, hydrology has contrasting effects on different spatial components of freshwater biodiversity. Recognising this contrast is critical because biodiversity at fine spatial scales may be positively influenced by hydrological gradients, whereas biodiversity at other spatial scales may decline along the same hydrological gradient. This difference emphasises that studies of responses of freshwater biodiversity to hydrological regimes must adopt a multi-scaled approach. However, simply increasing the spatial extent of biodiversity analysis does not address this issue.

(5) An overarching goal of freshwater conservation policies worldwide is to sustain and restore freshwater biodiversity. Quantifying the true effects on freshwater biodiversity of

hydrological change by anthropogenic impacts and climate change can be achieved only by integrating the responses of different spatial components of biodiversity to hydrology. Studies or monitoring programs that evaluate the effects of environmental flows on freshwater biodiversity but do not analyse responses in a multi-scaled context may miss detecting responses of biodiversity at specific spatial scales.

(6) We conclude that maximising the success and avoiding potential risks of environmental flow programs for freshwater biodiversity are best addressed by identifying how ecohydrological mechanisms influence biodiversity at separate spatial scales. In addition, the responses of biodiversity to hydrological regimes across spatial scales depend on the biological and ecological characteristics of focal organism groups because there is a substantial degree of inconsistency in hydrology–biodiversity relationships across different organism groups.

(7) There is a major need to determine how functional and phylogenetic facets of community-level biodiversity are influenced by hydrology to gain a stronger conceptual understanding of how hydrological change affects ecosystem functioning and the evolutionary capacity of biodiversity to adapt to further environmental changes.

(8) Our synthesis highlights significant gaps in the literature of freshwater biodiversity responses to hydrology. These gaps stem from a poor uptake of concepts of spatial scaling in freshwater ecology that have been adopted by conservation ecology more generally. Future research that addresses these knowledge gaps will provide a stronger basis for the management of hydrological regimes to achieving tangible benefits for freshwater biodiversity.

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XI. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Details of literature searches.

Table S1. Summary of studies reporting relationships between ecohydrological mechanisms and river–floodplain biodiversity across spatial scales sourced from *Web of Science*.

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