



Advancing towards functional environmental flows for temperate floodplain rivers



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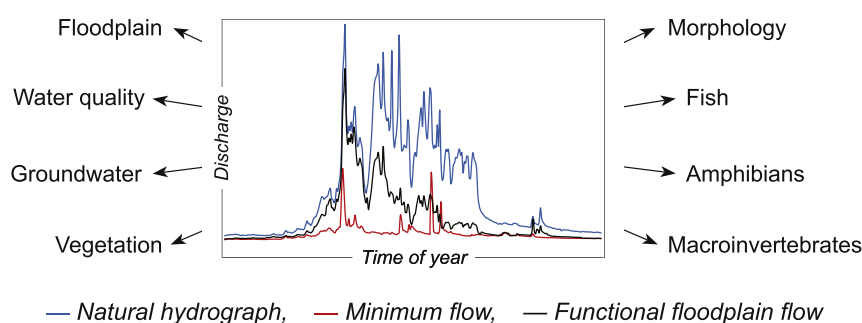
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HIGHLIGHTS

- E-flow assessment currently does not include the requirements of healthy floodplains.
- Based on literature, we pinpoint fundamental principles for viable e-flow management.
- Ecologically sustainable environmental flows must be function- and process-oriented.
- Key flow regime elements determining ecological functions/processes are identified.
- We establish a holistic conceptual framework for e-flows in floodplain rivers.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 12 September 2017

Received in revised form 15 March 2018

Accepted 19 March 2018

Available online 28 March 2018

Editor: R Ludwig

Keywords:

Dynamic flow
Process-oriented
Functional floodplain flow
River restoration
Water management
Dams

ABSTRACT

Abstraction, diversion, and storage of flow alter rivers worldwide. In this context, minimum flow regulations are applied to mitigate adverse impacts and to protect affected river reaches from environmental deterioration. Mostly, however, only selected instream criteria are considered, neglecting the floodplain as an indispensable part of the fluvial ecosystem. Based on essential functions and processes of unimpaired temperate floodplain rivers, we identify fundamental principles to which we must adhere to determine truly ecologically-relevant environmental flows. Literature reveals that the natural flow regime and its seasonal components are primary drivers for functions and processes of abiotic and biotic elements such as morphology, water quality, floodplain, groundwater, riparian vegetation, fish, macroinvertebrates, and amphibians, thus preserving the integrity of floodplain river ecosystems. Based on the relationship between key flow regime elements and associated environmental components within as well as adjacent to the river, we formulate a process-oriented *functional floodplain flow (ff-flow)* approach which offers a holistic conceptual framework for environmental flow assessment in temperate floodplain river systems. The *ff-flow* approach underlines the importance of emulating the natural flow regime with its seasonal variability, flow magnitude, frequency, event duration, and rise and fall of the hydrograph. We conclude that the ecological principles presented in the *ff-flow* approach ensure the protection of floodplain rivers impacted by flow regulation by establishing ecologically relevant environmental flows and guiding flow restoration measures.

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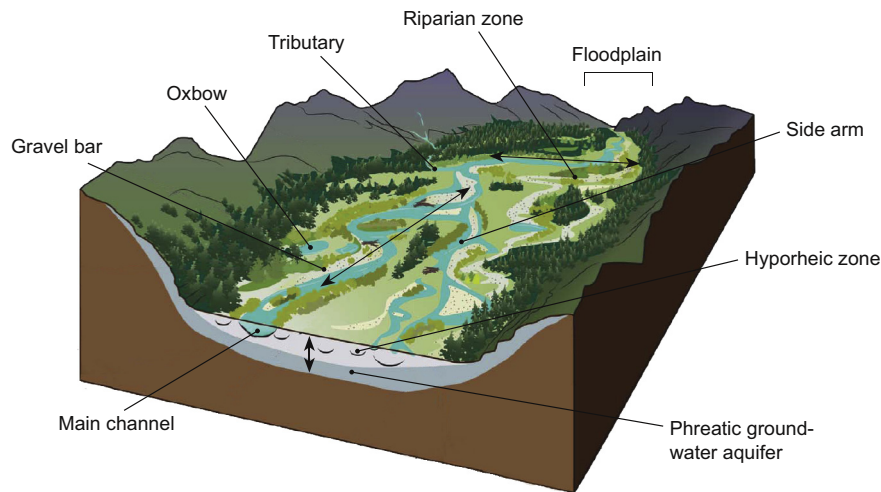


Fig. 1. A gravel-bed floodplain river with its main elements. The arrows show the river's three-dimensional structure, i.e., its longitudinal, vertical, and transversal floodplain gradients (adapted from Hauer et al., 2016).

1. Introduction

The natural hydrological flow regime is referred to as the river's master variable, arranging patterns and processes of the physical and biological environment (Power et al., 1995; Walker et al., 1995). River flows provide adequate habitat quality and quantity for riverine biota which are adapted to seasonally fluctuating flows (Lytle and Poff, 2004; Mims and Olden, 2012). The flow regime influences water quality, water temperature, nutrient cycles, and oxygen levels (Baldwin and Mitchell, 2000; Henriksen et al., 2008; Nilsson and Renöfält, 2008; Tockner et al., 2000), as well as geomorphological processes which shape the river and its floodplain (Egger et al., 2013, 2015; Opperman et al., 2010). The integrity, health, resilience, and productivity of riverine ecosystems depends upon the variability of flow with its constant changes between high and low flows (Naiman et al., 2008).

A river is more than the channel wherein it flows. A healthy river system encompasses diverse habitats along its longitudinal, vertical, and transversal floodplain gradients (Aarts et al., 2004; Ward, 1989; Fig. 1), nurturing diverse species assemblages along its aquatic-terrestrial transition zones (Junk et al., 1989; Ward and Stanford, 1995). Floodplain ecosystems rely on intact connectivity, ensuring the exchange of matter, energy, and biota between the floodplain and the river channel (Tockner et al., 2000; Junk et al., 1989). These landscapes are shaped by recurring cycles of flooding and drying, erosion and sedimentation, as well as complex exchanges between surface- and groundwater (Baldwin and Mitchell, 2000; Tockner et al., 2008).

Floodplains are the naturally accompanying ecosystem of many rivers and thus contribute positively to their ecological status (Grizzetti et al., 2017). They belong to the most productive landscapes worldwide and constitute hotspots of biodiversity (Hauer et al., 2016; Opperman et al., 2010; Ward et al., 1999). In Switzerland, 80% of the fauna are found in riverine floodplains which constitute <1% of the country's surface (Tockner and Stanford, 2002). Regardless, many floodplain rivers are subjected to abstraction and storage of flow. Changes in the hydrological regime and the de-coupling of river channel and floodplain have been identified as the primary reasons for the rapid loss of riverine floodplains (Hughes et al., 2012; Tockner and Stanford, 2002), which now belong to the most threatened ecosystems worldwide (Junk and Wantzen, 2004; Tockner and Stanford, 2002). In Europe, few naturally functioning floodplain rivers remain (Gurnell et al., 2016). Across the pan-Alpine river network, only 8% (4669 km) of rivers are still accompanied by floodplains (Litschauer, 2014). Since 1850, 90% of pristine floodplains in Switzerland have vanished, resulting in the endangerment of 153 vascular plant species (Müller-Wenk et al., 2004). Austria has also

lost 85% of its floodplains (Poppe et al., 2003), which is why >60% of the remaining floodplain areas are protected (Lazowski et al., 2011).

Environmental flow regulations are increasingly implemented to safeguard river reaches downstream of dams from environmental degradation and to maintain a defined ecological condition. However, assessments of environmental flows have mainly focused on determining minimum flows for chosen instream flow criteria (e.g., fish), while the rest of the ecosystem has usually been disregarded (Acreman et al., 2009; Petts, 2009). Although it is commonly known that a functioning floodplain is vital for the health of the entire ecosystem, its requirements have rarely been included in environmental flow assessments (Meitzen et al., 2013; Pusch and Hoffmann, 2000). For this reason, Thoms and Sheldon (2002) argue that environmental flow assessment must go beyond the consideration of only single elements. Instead, it must focus on central ecological processes and functions and their related pivotal hydrological drivers which are needed to sustain the whole ecosystem. While tropical floodplains and (semi-)arid rivers have received much attention in the past (Hughes and Rood, 2003; Junk et al., 1989; Yang et al., 2016), essential functions of temperate floodplains have been neglected in environmental flow assessment to date.

The objectives of this study are, therefore, to analyze the interplay between central abiotic and biotic elements (morphology including sediment transport, water quality, floodplain, groundwater, riparian vegetation, fish, macroinvertebrates, and amphibians) of temperate floodplain rivers and river flow, and to identify the key flow regime elements which determine their ecological functions and processes. We review studies linking ecosystem elements with the aspects of the natural flow regime as well as their responses to regime alterations. Understanding the relationship between flow and ecosystem components will enable us to establish truly ecologically-relevant environmental flows in temperate floodplain rivers. We will begin by highlighting elements and targets of environmental flow definitions. We will then discuss the relationship between river flow and the studied elements, describing natural and modified fluvial ecosystems. Finally, based on these connections, we will then formulate a *functional floodplain flow (ff-flow)* approach which offers a holistic conceptual framework for environmental flow restoration in temperate floodplain rivers impacted by flow regulation.

2. Environmental flow: objectives and definition

Dams are constructed for multiple purposes, including flood control, irrigation, water supply, recreation, or hydropower generation. Their operation entails a diversion or storage of water, whereby the natural

Table 1
Key flow elements, habitats, and targets contained in environmental flow definitions.

	Source
<i>Flow elements</i>	
Flow regime	1; 2; 3
Dynamic and variable flow	1; 4; (5)
Magnitude/quantity of water flow	1; 2; 5; 6; 7; 8; 9
Frequency	1; 6
Duration	1
Timing/temporal patterns of water flow	1; 4; 5; 6; 7; 8; 9
Rate of change	1
Quality of water flow	5; 7; 8
<i>Habitats (hydrologic systems)</i>	
River channel	1; 2; 3; 5; 10
Riparian zone/bank zone	5; 10
Floodplain/wetlands	1; 2; 3; 5; 10
Groundwater	1; (3); 5
Estuary/coastal zone	1; 3; 5; 7; 10
<i>E-flow targets</i>	
Integrity and health of the river ecosystem	(3); 5; 6; 9; 10; 11; 12
Maintenance of ecosystem functions and processes	1; 2; 8; 9
Ecosystem services (general)	3; 8; 11
Social and economic services (provided by diverse habitats of the ecosystem)	(3); 4; 5; 6; 7; 8
Achievement of legislated ecological objectives	13

¹Arthington and Pusey (2003); ²Tharme (2003); ³Dyson et al. (2003); ⁴Brown and King (2003); ⁵Hirji and Panella (2003); ⁶Gupta (2008); ⁷Brisbane Declaration (2007); ⁸Hirji and Davis (2009); ⁹Arthington (2012), in: Meitzen (2016); ¹⁰ISE (2002); ¹¹IWMI (2004), in: Moore (2004); ¹²Meitzen et al. (2013); ¹³EC (2015).

river flow downstream of the facility is fundamentally altered (Poff and Hart, 2002). In response to the degradation of aquatic ecosystems generated by the intensification of water resources infrastructure development and the accompanying overuse of water resources, the 'environmental flow' (hereafter *e-flow*) concept was developed (EC, 2015; Matthews et al., 2014). Although this concept has been in existence for many decades, a coherent definition is lacking (Moore, 2004). Multiple authors have attempted to provide adequate definitions. Nowadays, one of the most widely accepted and best-known is the Brisbane Declaration (2007) describing *e-flow* as, "the quantity, timing, and quality of water flows required to sustain freshwater and estuarine ecosystems and the human livelihoods and well-being that depend on these ecosystems." Although *e-flow* definitions may differ, they generally contain two key aspects: (1.) the flow regime elements to be considered; (2.) the targeted level of ecological protection.

Table 1 summarizes the key aspects of well-known definitions and lays the foundation for the establishment of a holistic definition for the *functional floodplain flow* (*ff-flow*) approach presented in this paper. Many authors assert that the quantity, timing, and the quality of water flow are key elements of an *e-flow* regime. Arthington and Pusey (2003) refer to the five central components of the natural flow regime (i.e., magnitude, frequency, duration, timing, rate of change; Poff et al., 1997) and state that these aspects are necessary to "maintain or restore the biophysical components and ecological processes of in-stream and groundwater systems, floodplains and downstream receiving waters." Multiple other authors also explicitly mention habitats beyond the river channel, such as riparian and bank zones, floodplains, wetlands, or groundwater. Most *e-flow* definitions aim to protect or restore the integrity and health of river ecosystems. Some refer to ecosystem functions and processes as well. Frequent targets are also ecosystem services offered by free-flowing rivers and maintained through *e-flow* releases (Auerbach et al., 2014; Richter, 2010). An *e-flow* regime that restores the integrity and health of a river system will also facilitate the provisioning of social and economic services (e.g., Jorda-Capdevila and Rodríguez-Labajos, 2017) and assist in achieving ecological objectives such as those of the EU Water Framework Directive (EC, 2015).

Based on these considerations (Table 1), we define *e-flow* as 'a river flow capable of maintaining the natural functions and processes regarding quality, quantity, and temporal cycles, to retain the integrity and resilience of riverine ecosystems inclusive of all their related components (river, floodplain, groundwater) as well as associated ecosystem services'.

3. Ecological principles for the functional floodplain flow

3.1. Seasonality of hydrological flow regimes

The natural flow regime is the primary conductor of ecological processes in river ecosystems and guarantees the long-term preservation of their functionality, biodiversity, and ecological integrity (Junk et al., 1989; Karr, 1991; Poff et al., 1997; Richter et al., 1997). It can be described by the five flow regime components, as defined by Poff et al. (1997). Multiple hydrological regime types exist, which are differentiated by climatic, geological, and topographic factors (Mader et al., 1996; Rinaldi et al., 2016). Flow regimes of temperate rivers are characterized by spring/summer peak discharge due to melting snowcaps and glaciers. Low flows occur periodically in late summer, fall, or during winter while precipitation events throughout the year lead to quickly fluctuating river flows.

The interaction of river hydrology and morphology shapes riverine populations (Bunn and Arthington, 2002). Plants and animals are adapted to naturally recurring drought and flood events (Lytle and Poff, 2004). Among others, the life cycle of many riparian species, fish, macroinvertebrates or amphibians is synchronized with the occurrence of specific flow events (Lytle and Poff, 2004; Poff et al., 2010; Trush et al., 2000). Intra- and inter-annual flow variability sustains ecological processes in the river and the adjacent floodplain and maintains ecosystems of high abiotic and biotic diversity (Meitzen et al., 2013; Poff et al., 1997; Ward et al., 2002). Flood pulses are a central component of floodplain rivers (Junk et al., 1989) and support diverse ecological functions along the four-dimensional linkages of lotic systems (i.e., lateral, longitudinal, vertical, and temporal connectivity; Ward, 1989).

3.2. Effects of flow alteration

Changes in the hydrological regime can be identified depending on location and climatic condition and the type and management of dams. Storage dams homogenize the seasonal flow variability downstream by decreasing peak flow events and increasing minimum flows as well as the duration of near bankfull discharges (Poff et al., 2006). Diversion hydropower plants in temperate rivers drastically reduce the latter two as well (Fig. 2a), whereas peak-load operating facilities also exhibit a high sub-daily flow variability caused by low flow and high peak flow cycles (Greimel et al., 2016). Irrigation dams, especially in Mediterranean regions, create a significant shift in seasonality when irrigation water is distributed via the river channel (Fig. 2b; Magdaleno and Fernández, 2011). The extent of hydrological changes also depends on the reservoir's capacity to store flow (e.g., seasonal, weekly, run-of-river – Fig. 2c) and can result in non-natural flood events (Richter and Thomas, 2007). Diverted water is returned to the river at the tailrace, which is situated either a few meters or up to several kilometers downstream of the intake structure ('non-consumptive use'). Abstracted water used, for example, for irrigation or water supply, may not be returned at all ('consumptive use').

Any modification of the natural hydrology may entail morphological and biological ecosystem transformations (Poff and Zimmerman, 2010), whereby floodplains are especially sensitive to hydrological changes (Fantin-Cruz et al., 2015). Any alteration of the flow regime and its five components (sensu Poff et al., 1997) modifies ecological processes and patterns, depending on the position within the river network

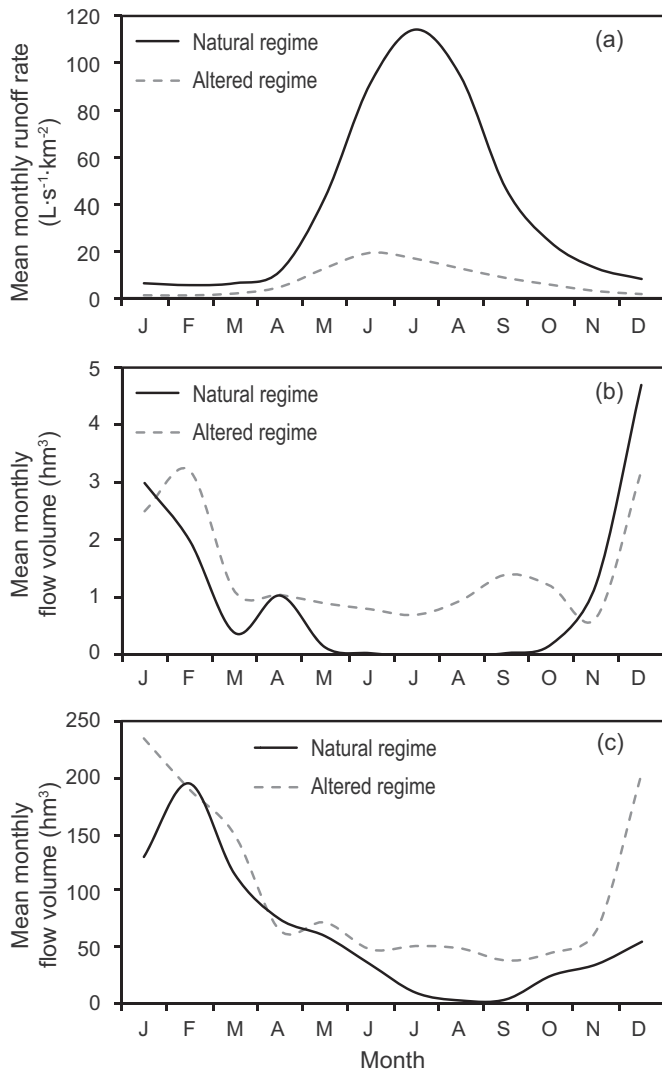


Fig. 2. Changes in the intra-annual variation of monthly runoff rate/streamflow volume caused by (a) a hydropower derivation dam of high storage capacity in an alpine river, (b) a water storage dam for summer irrigation in a Mediterranean river, and (c) a run-of-river hydropower scheme in a Mediterranean river. The dotted grey line represents the regulated river section where water is abstracted, while the black line represents the corresponding free-flowing river (data source: (a) Hydrographisches Zentralbüro, Austria, (b, c) Portuguese National Water Resources Information Service (<http://snirh.apambiente.pt/>)).

(Poff et al., 2006). E-flow assessment targeted at the maintenance of floodplain river functions and processes must, therefore, incorporate flow alteration-ecological and geomorphological response relationships (see e.g., García de Jalón et al., 2017; Poff and Zimmerman, 2010; Webb et al., 2013) so that the main hydrological drivers needed for flow restoration can be determined (Richter and Thomas, 2007). Most e-flow studies that incorporate the water demand of riverine floodplains and wetlands originate from Australia, South Africa, or North America and are primarily based on research in arid or semi-arid rivers (Hughes and Rood, 2003). Nevertheless, it is possible to draw conclusions from these studies that can contribute to the e-flow debate in temperate regions as well.

Based on previous flow classifications (Arthington et al., 1992; Caruso et al., 2013; King et al., 2003; Richter et al., 2006), we will describe five different kinds of river flows—low flow, mean flow, small flood, large flood, and flow variability—and their importance to functions and processes of floodplain river ecosystems. Each component is described separately, yet they are all interrelated (Poff et al., 1997), as depicted by ‘flow variability.’

3.3. Low flow

Low river flows occur in seasonal periods where there is no rainfall and where only the base flow remains in the river channel. In contrast to quickflows, which contain the direct response of the catchment to precipitation, low-level stream flows originate from either groundwater or delayed sources such as melting glaciers or subsurface storage. Low flows are often defined as flows occurring 70–99% of the time (Smakhtin, 2001). These flow magnitudes govern the availability of minimum aquatic habitat (Postel and Richter, 2003) as they determine the minimal wetted perimeter, available depths, and hydraulic conditions. Hence, they may regulate the carrying capacity of riverine ecosystems as they often present ecological bottlenecks (Behnke, 2007; Jowett et al., 2005; Rolls et al., 2012). Nevertheless, they are a central element of the natural flow regime and are of ecological importance (Humphries and Baldwin, 2003). Monthly low flows vary throughout the season and can be distinguished from extreme low flows (Caruso et al., 2013).

During periodic low flow conditions, the groundwater table in the floodplain sinks as water flows back into the main channel (Smakhtin, 2001; Stanford and Ward, 1988). During winter, low flow conditions exist when vegetation is dormant (Rood et al., 2007). In contrast, summer low flows occur during the growing season. When alluvial groundwater sources can be accessed, these periods promote the regeneration of native riparian and floodplain vegetation (Flanagan et al., 2017) and simultaneously remove invasive species (Postel and Richter, 2003). Plant seedlings can sprout and grow without being washed away (Johnson, 1994; Postel and Richter, 2003). Thus, these periods are essential for the progression of floodplain vegetation (Johnson, 1994), but also in preparation for the next flood pulse (Junk et al., 1989) as the drying of floodplain soils facilitates aerobic processes which increase the availability of nutrients at the next flooding (Baldwin and Mitchell, 2000; Richter and Thomas, 2007). Seasonal floodplain water bodies dry out, guaranteeing that they remain unoccupied by fish. The absence of such predators from ephemeral habitats supports the survival of aquatic life-stages of amphibians (Adams, 1999; Babbitt and Tanner, 2000; Hauer et al., 2016). When the floodplain is dry, amphibians, in their terrestrial life stages can utilize diverse habitats, especially large wood deposits, for resting and foraging (Indermaur et al., 2009a, 2009b).

Low river flows also govern natural changes in the water quality, i.e., extended summer base flows cause an increase in water temperature and a decrease in dissolved oxygen levels (Nilsson and Renöfält, 2008). Native species can cope with such circumstances, especially if habitat diversity is high (Dunbar et al., 2010a). Macroinvertebrates may avoid desiccation by seeking shelter in the hyporheic interstitial (Hynes, 1970; Stubbington, 2012). Stable summer low-flows support rearing of juvenile fish (Freeman et al., 2001). Upwelling of cool, oxygenated hyporheic groundwater sustains aquatic organisms during summer low flows, while hyporheic flow in winter provides suitable, warm instream winter habitats, even though icing can occur (Hauer et al., 2016; Power et al., 1999).

Prolonged or extreme low flows or droughts, however, can have detrimental effects on the ecosystem (Table 2; Dewson et al., 2007; Humphries and Baldwin, 2003; Poff and Zimmerman, 2010). Such situations can arise if an e-flow assessment is based solely on static minimum flow considerations and does not match natural low flow patterns. Many countries use exceedance percentiles of the flow duration curve in the range of Q_{75} – Q_{95} for minimum flow recommendations (Smakhtin, 2001; Tharme, 2003), however, such artificial extensions of low flow situations may result in the system's loss of resilience (Colloff & Baldwin, 2010). Riparian plants whose roots do not reach lowered groundwater tables will experience drought stress and will likely die if these situations prevail (Egger, 1997; Johnson, 1994; Postel and Richter, 2003; Rood et al., 2013; Stromberg et al., 2007; Webb et al., 2013). If floods are absent for too long, vegetation can follow the

Table 2

Typical flow alterations caused by dams and flow abstraction, and related morphological, floodplain/floral and faunal responses of floodplain river ecosystems. Management options for flow restoration measures are proposed.

Flow characteristic	Alteration	Morphological response	Floodplain/floral response	Faunal response	Flow management recommendation
Magnitude	Flow stabilization (loss of high flow events and reduction of flow variability)	Reduced habitat creation processes via sediment redistribution mechanisms ^a , diminished habitat diversity ^a	Reduced water and nutrients directed towards floodplain plant species, leading to altered recruitment and failing of seedling establishment (ineffective seed dispersal, loss of scoured habitat patches needed for plant establishment, seedling desiccation) ^{b,c} , reduced productivity and decomposition rate ^a Lower species richness, altered assemblages ^{a,c} , successful invasion of non-native species ^{a,c} Vegetation encroachment into channels ^b , terrestrialization of flora ^c , increased riparian cover ^c Excessive growth of aquatic macrophytes ^d	Competitive species dominate while poor competitors/sensitive species are lost, altered assemblages and dominant taxa ^{a,c} Invasion and establishment of exotic species, causing local extinction, threat to locally adapted species, altered communities ^{a,b,c,d} Reduced diversity and abundance ^{a,c} Reduction in fish populations ^d Increased standing crop and reduced diversity of macroinvertebrates ^d	Increase seasonal variation of flow/reintroduce aspects of the natural flow regime ^{a,d,e} Provide flushing flows to clear channels of encroaching vegetation and alien species and to mobilize sediments acting as diversity-enhancing disturbances ^a Promote longer periods of inundation through floods ^d Vary flow during wet season, but with removal of some floods ^f Incorporate interannual flow variability (i.e., wet, normal, and dry years) ^e
	Decreased water level in main channel/reduced mean daily flow	Alteration of size and pattern of the active channel and its geomorphic complexity ^g Deposition of fine sediments in gravel ^b (esp. in pools ^l), increased sedimentation and riparian vegetation encroachment into the active channel may change channel and floodplain morphology, e.g., decreased depth/width or creation of new floodplain terraces from drying channel sections ^{h,j}	Reduced soil moisture availability for riparian vegetation ^g , reduced groundwater depth negatively affects riparian organisms, higher mortality ^k Shifts in density, productivity and species composition ^h Alterations in amount and availability of habitat space and patch size ^g	Changes in amount and availability of habitat space, patch size, amount of water, food and cover available for organisms ^g Smaller refuges for fish, greater mortality in the main channel through competition and predation ^l Increased risk of anoxia ^l (e.g., through rise of summer water temperature and aggravation of water pollution effects ^h) Interruption of migration pathways ^l Changes in fish and macroinvertebrate assemblage structure, abundance, and diversity ^k	Maintain (monthly varying) minimum flow to sustain aquatic habitat (in dry season) ^{f,m,n} to limit stressful habitat conditions ^e , inundate riffle zones ^m , provide adequate water levels over in-channel spawning habitats ^l Provide higher minimum flows to ensure connectivity for in-channel migration (to/from feeding, resting or spawning areas) ^{a,f,l,m} , and to keep fish and amphibian eggs suspended ^f Release river flows to maintain water table levels in the floodplain, soil moisture for plants ^f , nutrient delivery ^m Maintain adequate water quality ^l , e.g., suitable water temperature, dissolved oxygen, and water chemistry ^{f,m} Support hyporheic organisms (living in saturated sediments) ^f
	Decrease of high flow pulses	Change in spatial range of processes and size of functional surfaces ^g , e.g. stabilization and narrowing of river channel ^{b,j} , reduction of active floodplain surface ^g Change in dominant particle size of bed material ^g , bed armoring ⁱ , deposition of fine sediments in gravel ^{b,j}	Floodplain aquifers are not adequately recharged ^o , causing long-term dehydration of riparian habitats ^g Terrestrialization of riparian species ^c , vegetation encroachment into channel ^f	Changes in amount and types of habitats for aquatic, semiaquatic, and terrestrial biota ^{b,g} Adverse effects for fish ^k , e.g., less space for reproduction, refuge, and feeding of young and adult fish during flood ^l , reduction of lateral connectivity ^a Clogging of the riverbed disconnects surface and groundwater and reduces reproductive success of fish and lowers numbers of aquatic species generally ^a	Provide habitat maintenance flows (incl. sediment load) that perform specific functions, e.g., clean spawning gravels, enable longitudinal and lateral connectivity or serve as migration cues ^{g,l} , move bed sediments ^p , shape physical character of river channel including pools, riffles ^{f,m} , determine substrate composition by transporting and sorting sediments ^{f,m,q} , prevent riparian vegetation from encroaching into channel ^{f,m} , replenish and maintain floodplain water table ^p , restore normal water quality conditions after prolonged low flows ^f , flush away waste products and pollutants ^f , increase water exchange between surface and hyporheic habitats ^a Release wet-season 'initiation flows' to kick-start ecological processes and provide ecological cues ^e
	Decrease of peak flows/overbank	Reduced channel migration and development of secondary	Failure of flooding of all or part of the floodplain ^l , reduced	Changes in number and types of habitats for aquatic,	Provide flushing flows and continuity of sediment transport

(continued on next page)

Table 2 (continued)

Flow characteristic	Alteration	Morphological response	Floodplain/floral response	Faunal response	Flow management recommendation
	flows	channels, point bars, oxbows ^b , changes in channel planform (e.g., narrowing, downcutting) ^b Prevention of floodplain deposition and erosion ^b , reduction of active floodplain surface ^g Change in available space for river forms, sediments, and processes, floodplain size ^g , decrease in river's capability to transport tributary sediment inputs ^l Missing habitats for pioneer vegetation ^l	connectivity Alteration of amount and types of patches for riparian organisms ^g Terrestrialization of riparian species ^c , vegetation encroachment into channel ^f	semiaquatic, and terrestrial biota ^{b,g} May prevent fish from accessing the floodplain ^l , reduced floodplain spawning areas ^d entails abundance decline ^b	to modify/maintain channel structure ^{e,l,p} by retaining flood magnitude to scour channel and (encroaching) vegetation and purge alien species from aquatic and riparian communities ^{a,e,f,m} , mobilize sediments acting as diversity-enhancing disturbances ^{a,m} , create sites for recruitment of colonizing plants ^{l,r} , recharge river banks and floodplain water table ^{l,q,r} , disburse seeds and fruits of riparian plants ^l Reconnect floodplain and channel habitats by reintroducing overbank floods ^{a,q} , enable fish to spawn on floodplain, provide nursery area for juvenile fish ^f , provide new feeding opportunities for fish and waterfowl ^l , deposit nutrients on floodplain ^l , flush organic materials (food) and woody debris (habitat structures) into channel ^{f,m} Enable large floods to shape physical floodplain habitats ^f and to drive lateral movement of river channel ^{q,r} , forming new habitats (secondary channels, oxbow lakes) ^f
Frequency	Decreased variation		Competitive species will dominate while poor competitors might be lost ^a	Competitive species will dominate while weak competitors might be lost ^a , negative impacts on fish ^k	Increase seasonal flow variation ^a Coincide frequency of hydrograph components with life-history requirements ^{e,q}
	Increased frequency of low flow periods	Increased frequency of in-channel sediment deposition ^g and stability of channel and banks ^g (i.e., no sediment turnover)	Drought stress ^{g,s} , growth limitation ^s Reduced food web complexity ^f	Greater frequency of limiting hydraulic/habitat conditions ^t Altered availability of floodplain habitats for (semi-) aquatic species ^g Reduced food web complexity ^t	Restrict unnatural frequency of low flow periods by increasing minimum flow ^u
	Decreased frequency of high flow pulses	Alteration of frequency of mobility of channel bed and bank materials, frequency of changes in functional surfaces ^g Reduced flushing of sediments ^a	Long-term dehydration of riparian habitats leads to terrestrialization of riparian biota ^c	Less frequent rejuvenation of riverine and floodplain habitats ^v Adverse effects on fish ^k	Provide regular high flow pulses, preferably every year and correctly timed ^{e,l,q} Vary flow during wet season, but with removal of some floods ^f , to recharge groundwater aquifers ^q
	Decreased frequency of peak flows/overbank flows	Change in spatial range of frequency of functional surfaces ^g Less frequent resetting of the river/pioneer habitat creation	Shift in community composition ^c Reduction in species richness ^c Increase in wood production ^c	Aseasonal/reduced reproduction ^c Decreased abundance or extirpation of native fishes, decreased richness of endemic and sensitive fish ^c Reduced habitat for young fish ^c	Frequently inundate floodplains every 1–3 years ^{e,q} , adjust floods to connect floodplain waterbodies that are further away every 3–5 years ^l Establish large scouring floods ^q to control distribution and abundance of riparian and floodplain plants, and to maintain balance of species in aquatic and riparian communities ^f Reset floodplain vegetation succession every 10–20 years with large magnitude peak flows ^e Reduce frequency of flow variation ^a
	Increased variation (e.g., hydropedaling)	Increased erosion ^a	Impairment of germination, establishment, growth, and reproduction ^w Most riparian species disappear—easily dispersed, flexible, flood-tolerant and amphibious plants are favored ^w	Increased erosion leading to stress and loss of organisms ^{a,x} Reduced habitat availability ^a , diminished spawning and rearing success of fish ^x Lowered species richness and biomass of macroinvertebrates ^d	
Duration	Prolonged low flows	Change in magnitude of in-channel deposition processes ^g , limited sediment	Physiological stress leading to reduced plant growth rate, morphological change, or	Limits for aquatic organisms ^g or physiological stress ^a due to reduced river water quality	Prohibit unnatural prolongation of low flows by increasing minimum flow, but maintain

Table 2 (continued)

Flow characteristic	Alteration	Morphological response	Floodplain/floral response	Faunal response	Flow management recommendation
		transport fostering sediment deposition ^g , increased siltation ^h	mortality ^b Reduction or elimination of plant cover ^b Diminished plant species diversity ^b	(e.g., oxygen deficits), and temperature variation ^{a,h} , concentration in small areas ^b Long-term alteration in species distribution, abundance ^h , and diversity ^a	natural river characteristics ^e Increase seasonal high flows ^a
	Shortened flood peaks/interruption of flood	Alterations of magnitude of erosion on banks and in channels, bedload transport, channel sediment texture ^g	Encroachment of terrestrial organisms ^a	Exposure of floodplain spawning substrates, stranding and desiccation of eggs ^l , stranding of fish in temporary pools ^l Failure of eggs and larvae to colonize floodplain ^l	Increase duration of seasonal flood peaks ^a to allow ecological processes ^e
	Shortened duration of floodplain inundation		Less time for development of floodplain vegetation ^l , reduced growth rate or mortality ^c Altered assemblages, terrestrialization of species composition, increase in abundance of non-natives ^c , decline in wetland vegetation ^d , reduced area of riparian plant or forest cover ^c	Less time for growth of fish and to remain in floodplain refugia ^l Decreased abundance of young fish, change in juvenile fish assemblage ^c Loss of floodplain specialists in mollusk assemblages ^c	Alternate high short floods with lower but longer ones to favor all groups of species ^l Maintain diversity in floodplain forest types through prolonged inundation ^f , e.g., min. of three weeks and periodic connectivity between river and floodplain ^e , provide plant seedlings with continued access to soil moisture ^f , inundation for vegetation germination, fish recruitment, waterbird breeding ^m
Timing	Loss of seasonal flow or flood peaks/shifts in seasonality	Reduced habitat availability ^a , loss of seasonal floodplain waterbodies ^q Change in interactions between erosive flows and stabilizing vegetation ^g	Reduction or elimination of riparian plant recruitment, reduced plant growth rates, increased mortality, and changed succession patterns ^{a,b,c,k,r} Invasion of exotic riparian plant species ^{b,c} , reduction in species richness and plant cover ^c	Disrupted synchrony of life-cycle cues for fish (spawning, egg hatching, migration) ^{b,c,d,e,g} , reduced growth rate ^a Loss of fish access to floodplain ^b , decreased reproduction and recruitment ^c Change in assemblage structure ^c , invasion of exotic species ^a	Reintroduce seasonal flow peaks ^{a,e,p} to trigger flows for migration ^{a,m,p} and spawning (of floodplain species) ^l , and to deposit gravel or cobble in spawning areas ⁿ Retain spring flushing flow as cue to life cycle ^e Provide well-timed flows which allow delivery of seeds and establishment of seedlings ^{q,r} Provide adequate recession flows, allowing eggs to emerge ^e , fish larvae to develop ^l and to use nursery areas ⁿ
	Delay in arrival of seasonal flood peaks		Desynchronization of photoperiod, temperature, and hydrology inhibits successful flowering and seed dispersal of cottonwoods ^y	Changes in thermal coupling between flood and temperature influences physical readiness of fish to mature, migrate, and spawn ^l , e.g., delayed spawning ^d Desynchronization of fish larvae drift and movement to floodplains and backwaters ^l Washing-out of organisms ^{a,b} Submergence of nests and spawning sites at too great depths ^l	Ensure the correct timing of seasonal flood peaks so they can act as triggers for life-cycle cues (e.g., migration, spawning) ^{e,l}
Rate of change	Overly rapid rise in river stage	Weakening of banks and loss of vegetation ^a	Quick immersion of floodplain ^l , failed establishment and recruitment of riparian vegetation ^{a,j}		Reduce rates of change ^a , flood curves should be as smooth as possible ^l Flows shall ensure connectivity to the floodplain and induce lateral migration ^l
	Overly rapid fall in river stage/accelerated flood recession	Weakening of banks and loss of vegetation ^a	Fast drying of floodplain surface ^l Failure of seedling establishment and recruitment of riparian vegetation ^{a,b}	Increased stranding mortalities (in temporary water bodies) ^{a,b,l}	Reduce rates of change ^a , flood curves should be as smooth as possible ^l , esp. spring recession flows ^e , do not exceed threshold limits ^p Flows shall ensure connectivity and safe return of fish to the river and floodplain waterbodies ^l Gradual recession of water tables to expose moist sediment for seed germination after floods ^{m,r}

^a Renöfält et al. (2010); ^b Poff et al. (1997); ^c Poff and Zimmerman (2010); ^d Bunn and Arthington (2002); ^e Yarnell et al. (2015); ^f Postel and Richter (2003); ^g Graf (2006); ^h Heicher (1993), in: Smakhtin (2001); ⁱ Brandt (2000); ^j Ryan (1997); ^k Webb et al. (2013); ^l Welcomme (2008); ^m Davies et al. (2014); ⁿ Richter and Thomas (2007); ^o Smakhtin (2001); ^p Acreman et al. (2009); ^q Trush et al. (2000); ^r Hughes et al. (2012); ^s Rood et al. (2013); ^t Rolls et al. (2012); ^u Petts (2009); ^v Ward and Stanford (1995); ^w Bejarano et al. (2017); ^x Young et al. (2011); ^y Mahoney and Rood (1998);

water and move into the river channel, giving rise to morphological alterations (e.g., [Bejarano and Sordo-Ward, 2011](#); [Ligon et al., 1995](#); [Trush et al., 2000](#)). Flow abstraction generally has an adverse effect on fish abundance, assemblage, composition, and diversity ([Webb et al., 2013](#)). Native species may be suppressed by alien species ([Caiola et al., 2014](#)). Macroinvertebrates respond through declining species richness, diversity, abundance, and density ([Dewson et al., 2007](#); [Webb et al., 2013](#)). Prolonged low flows enhance in-channel deposition processes by limiting sediment transport ([Graf, 2006](#)). The shortage of pools and sedimentation thereof create great difficulty for adult trout in residual flow reaches ([Petts, 1996](#)), and loss of connectivity restricts escape into more favorable reaches ([Welcomme et al., 2006](#)). Evapotranspiration in summer may even exacerbate the minimum flow situation through additional streamflow losses ([Smakhtin, 2001](#)). Along with hydraulic changes, extended low flows entail water quality reductions, including oxygen deficits or enhanced water temperature variation due to reduced water volume of residual flow reaches ([Dewson et al., 2007](#); [Nilsson and Renöfält, 2008](#); [Smakhtin, 2001](#); [Welcomme, 2008](#)). A temperature model for the braided Hurunui River in New Zealand showed that every $1 \text{ m}^3 \cdot \text{s}^{-1}$ streamflow reduction resulted in a maximum temperature increase of $0.1 \text{ }^\circ\text{C}$ ([Hockey et al., 1982](#), in: [Mosley, 1983](#)). In residual flow reaches summer temperatures can, therefore, exceed critical temperatures, especially for stenothermic coldwater species ([Caissie, 2006](#)). Adverse consequences of changed thermal regimes have been documented, for example, with salmonid fish, stoneflies, or mayflies ([Caissie, 2006](#); [Cazaubon and Giudicelli, 1999](#); [Webb and Walling, 1993](#)).

Since low flows naturally lead to increased sedimentation rates, the combination of prolonged base flows and missing erosive high flows leads to clogging of the hyporheic interstitial, impeding important ecological functions such as fish spawning ([Kemp et al., 2011](#); [Milhous, 1998](#)). It is evident, therefore, that the protection of minimum flows is important but that other aspects of the flow regime are also significant for an ecologically-relevant e-flow allocation.

3.4. Mean flow

Discharges ranging from low flows to high flow pulses ([Section 3.5.1](#)) fulfill a series of ecological functions as they are sustained over extended time periods. According to [Leopold et al. \(1964\)](#), the mean annual flow is reached or exceeded about 25% of the time and fills the main channel to one-third of its bankfull depth. The magnitude is, in most cases, directly related to the size of the drainage area ([Leopold, 1994](#)) and is (along with the hydraulic parameters average river depth, width, and flow velocity) one of the key indicators which describe the longitudinal situation of the reach. These components are decisive for characteristic habitat forms and spacing ([Leopold et al., 1964](#)).

Discharges in the mean flow range allow for longitudinal connectivity between aquatic habitats, for example diurnal and seasonal habitat shifts of fish, including fall or spring spawning migration which can total many kilometers ([Jungwirth et al., 2000](#); [Lucas and Baras, 2001](#)). In general, adult fish profit from habitat conditions created by flows higher than low flows, as they predominantly occupy deep runs and pools of depths up to 0.8–2.4 m ([Jungwirth et al., 2000](#); [Nykänen et al., 2004](#)). The hydraulic conditions provided during such flows are particularly important for rheophilic fish species. The spawning habitat requirements of the European grayling, *Thymallus thymallus*, include flow velocities between 0.4 and $0.7 \text{ m} \cdot \text{s}^{-1}$ ([Jungwirth et al., 2000](#)). For the potamodromous nase, *Chondrostoma nasus*, flow velocity requirements are as high as 1.0 – $1.1 \text{ m} \cdot \text{s}^{-1}$ ([Melcher and Schmutz, 2010](#)). Many macroinvertebrates, e.g., rheophilic species or passive filter feeders such as *Hydropsychidae* or *Rheotanytarsus*, also rely on the presence of areas with stronger flow velocities. Passive filter-feeders aggregate in mean flow range areas as food delivery rates are high, and they exhibit faster feeding rates than in slow-flowing river sections ([Dewson et al., 2007](#); [King et al., 2008](#)).

The growth and survival of riparian and floodplain vegetation is primarily determined by the groundwater level and soil moisture availability during non-flood periods ([Stromberg et al., 1996](#)). Variable flows within the channel promote plant growth through lateral water seepage into the floodplain ([Hughes and Rood, 2003](#)). The level of the hyporheic groundwater table within the floodplain varies seasonally with the river flow ([Rood et al., 2013](#); [Stromberg, 1993](#)), whereby the average elevation can be linked with the mean water level in the river channel ([Fig. 3](#)). Therefore, mean flow ranges are the primary hydraulic and hydrological regulator of floodplain vegetation, determining where which species will thrive. Water availability is especially important during the recruitment phase and growing season where the water demand for plants is the highest of the year ([Egger et al., 2013](#); [Foster and Rood, 2017](#); [Karrenberg et al., 2002](#); [Ye et al., 2010](#)).

Most e-flow determinations are oriented towards the preservation of low flows only ([Jager and Smith, 2008](#)), whereby the mean annual flow is often only used as a baseline for minimum flow constraints. Standard hydrological methods allot 2.5–30% of average annual flow as e-flow ([Tharme, 2003](#)). Water allocation at this level entails a long-term lowering of the groundwater table within the floodplain and higher areas therein will subsequently dry out ([Dister et al., 1990](#); [Pusch and Hoffmann, 2000](#)). Species reliant upon or preferring moist areas, e.g., pioneer communities of the softwood floodplain zone, are sensitive indicators for long-term reductions of soil moisture availability ([Corenblit et al., 2007](#); [Dister et al., 1990](#); [Egger, 1997](#); [Stromberg et al., 1996](#)). Therefore, it can be expected that minimum flow regulations lead to negative responses of riparian and floodplain vegetation, such as reduced plant growth rate, morphological change, or mortality of recruits, and a decline in native plant species diversity ([Table 2](#); [Merritt et al., 2010](#); [Olivier et al., 2009](#); [Poff et al., 1997](#); [Stromberg et al., 1996](#); [Ward and Stanford, 1995](#)). Water abstraction and lowering of the groundwater table also results in drying and fast disappearing lentic floodplain water bodies, impacting specialized organisms and communities ([Egger, 1997](#)).

As the hydraulic parameters associated with discharges in the mean flow range determine the characteristics of instream habitats, flow reduction promotes alterations of size and pattern of the active channel and geomorphic complexity in the river as well as changes in amount and availability of habitat space and patch size ([Table 2](#); [Graf, 2006](#)). For aquatic organisms, food and cover are reduced and there is greater mortality through competition and predation; migration pathways are also often interrupted ([Graf, 2006](#); [Welcomme, 2008](#)). Filter-feeding or shredding macroinvertebrates (e.g., stone- and caddisflies) which are dependent on swift flow conditions may be repressed by tolerant species if these habitats disappear ([Cortes et al., 2002](#); [Dunbar et al., 2010a, 2010b](#)).

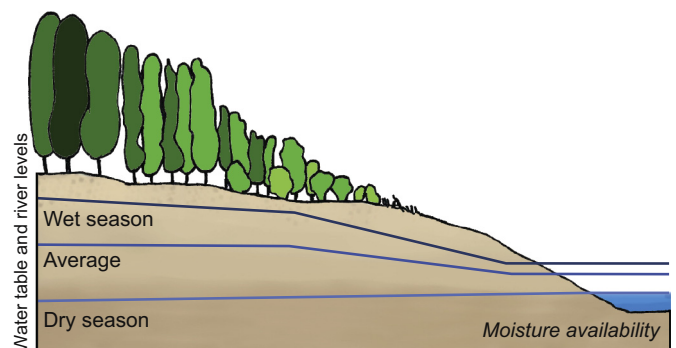


Fig. 3. A schematic sketch of the usual water table distribution in relation to river stage in a temperate floodplain river in a moist environment (shown here: a reach of the high-energy anabranching and braiding Tagliamento River, Italy, with a perennial flashy flow regime, a partly confined morphology, and cobble-gravel-sand as bed material) during the dry and wet season, and the annual average (adapted from [Gurnell et al., 2016](#)).

3.5. Flow and flood pulses

Regarding high flow events, two types can be distinguished (King and Louw, 1998) in terms of magnitude, frequency, and ecological function. Smaller flow pulses occur multiple times per year (Whipple et al., 2017) and serve as habitat maintenance floods. Larger floods act as channel maintenance or flushing floods. These include bankfull discharges which occur, on average, every 1.5 years (Leopold, 1994), and exceeding (overbank) flows that begin to inundate the floodplain (Richter et al., 2006; see Section 3.5.2). In temperate river systems with nival or glacial flow regime components, the timing of seasonal peak discharges are predictable. Floods of a recurrence interval of >5 years can transport major sediment loads and facilitate plant recruitment (Braatne et al., 1996; Wolman and Miller, 1960), whereby a 1-in-10 year or higher flood magnitude is essential for the creation and preservation of complex channel and floodplain morphology (Rood et al., 2005; Trush et al., 2000). It must be noted that flow thresholds for, e.g., sediment mobilization or channel movement rates depend on river type and associated characteristics, whereby less frequent and larger events might be necessary for steep gravel-bed mountain rivers, and more frequent but lower discharges might be sufficient for alluvial sand-bed rivers (Beechie et al., 2006; Rood et al., 2007). Overall, floodplains are formed by the combination of frequent flow pulses and less frequent flood pulses (Grove et al., 2012).

3.5.1. Habitat maintenance floods

High flow pulses are an essential element in the variability of a discharge regime. By mobilizing and sorting small- and medium-sized sediments, they contribute to habitat heterogeneity within the river (King et al., 2003). Furthermore, they flush out silt and cleanse coarse sediment from periphyton (Biggs et al., 2008). By washing out fines from the riverbed, clogging of the hyporheic interstitial is inhibited (Brunke and Gonser, 1997). A functioning hyporheic zone ensures the exchange of water and nutrients between surface and groundwater layers. This zone is colonized by bacterial and benthic fauna and has a balancing effect on the temperature regime of the river. An intact hyporheal, maintained by high flow pulses, also benefits the reproduction of lithophilic fish species and the river's nutrient and pollutant load (Brunke et al., 2015; Hauer et al., 2016).

High flow pulses not only sustain physical habitat but are also related to the completion of the life-cycle phases that are dependent on and synchronized with flow events (Lytle and Poff, 2004). Such pulses can trigger migration and spawning of fish and enable longitudinal and lateral connectivity (Hauer et al., 2014; King et al., 2003; Welcomme, 2008). Connected off-channel habitats can provide nutrients, serve as refuges of high flow velocities or low temperature in the main channel, and function as spawning areas and juvenile rearing grounds (EC, 2015; Zeug and Winemiller, 2008). The drift of some macroinvertebrate species may increase (Brittain and Eikeland, 1988). Rising water levels lead to seepage of water from the channel into the groundwater aquifer (Stanford and Ward, 1988) and the infiltration of nutrient-rich groundwater into the floodplain results in a phase of high primary production (Tockner et al., 2000). Thereby floodplain ponds can also be recharged and may serve as spawning habitats for amphibians (Babbitt and Tanner, 2000; Dick et al., 2017; Morand and Joly, 1995). High groundwater levels benefit riparian and floodplain vegetation, such as those of the softwood forest (e.g., Salicaceae) (Corenblit et al., 2007). Both, increased groundwater levels and hydraulic forces from floods, prevent riparian encroachment and establishment of terrestrial species (Miller et al., 2013; Poff and Zimmerman, 2010; Postel and Richter, 2003).

Most residual flow reaches experience a substantial decline in flood events of various magnitudes (Fig. 2). A decrease in magnitude and frequency of high flow pulses alters the spatial range of functional surfaces and the frequency of processes which affects, e.g., the mobility of channel bed and bank material (Table 2; Graf, 2006). Reduced hydraulic

forces change the dominant particle size and often lead to sedimentation of the riverbed with fines, which creates an almost impermeable layer (Hancock, 2002; Schälchli, 1992). This has negative implications for aquifer exchange, water quality, and aquatic organisms (Brunke and Gonser, 1997; Hancock, 2002). Sedimentation of fines and the absence of flushing flows may constrain the occurrence of macroinvertebrates (Jones et al., 2012; Wood and Armitage, 1999), but also perturb life-history stages of lithophilic or benthic fish (Kemp et al., 2011; Milhous, 1998; Welcomme et al., 2006). A loss of seasonality severely affects flora and fauna adapted to these peaks and may favor invasive species (Bunn and Arthington, 2002). As groundwater layers are not adequately recharged, long-term dehydration of riparian habitats (Graf, 2006) results in a terrestrialization of riparian species (Poff and Zimmerman, 2010).

3.5.2. Channel maintenance and overbank floods

Flood pulses evoke similar ecological responses as the smaller flow pulses, however, due to their larger magnitude, they serve further purposes such as mobilizing and transporting larger bed-load fractions or maintaining river channel and floodplain morphology (King et al., 2003; Trush et al., 2000; Opperman et al., 2010). Together with geomorphological characteristics (e.g., slope, grain size, material properties of river bed and banks that determine erosive resistance, and sediment budget), the magnitude and frequency of bed-forming flows determine channel width and geomorphological river type (Ahmari and Da Silva, 2011). Peak discharge events mobilize coarse bed sediments, flush fines and organic material out of the river, and clear the channels from macrophytes, encroaching riparian vegetation, and alien species (Bejarano and Sordo-Ward, 2011; Biggs et al., 2008; Renöfält et al., 2010; Schälchli, 1992). In this regard, the interrelation between hydrology and vegetation is central in ensuring the geomorphological stability of the river or contributing to its changes (Corenblit et al., 2007; Grabowski et al., 2014; Gurnell et al., 2016). Flow-induced retrogression of vegetation is followed by progression into newly created pioneer sites, which are principal areas for riparian plant establishment (Caruso et al., 2013; Corenblit et al., 2007; Egger et al., 2013; Ward et al., 2001). The recruitment of cottonwood and willow is associated with floods occurring every five or ten years, whereby the flood peak must be aligned with photoperiod and temperature which determine flowering and seed release (Braatne et al., 1996; Mahoney and Rood, 1998). Optimal conditions for plant recruitment comprise a medium to high flood pulse with a rapid rise in river stage, followed by a slow recession. The flood pulse purges and creates river bars and raises the groundwater level (Hughes and Rood, 2003; Mahoney and Rood, 1998; Rood et al., 2007). Seeds are dispersed and germinate underwater to become established on the moist, open gravel bars (Meier, 2008). Recruitment in sand-bed rivers is successful if roots can grow with the slowly receding water levels until the plants can reach base flow groundwater levels (Amlin and Rood, 2002; Mahoney and Rood, 1998; Meier, 2008; Rood et al., 2007). In gravel-bed rivers, the occurrence of a coarse substrate layer over finer material has a rock mulching effect, which provides soil moisture to seedlings even if water input is not significant for some time (Meier, 2008). Furthermore, flushing floods supply dead trees to the river, thereby also shaping the river structure. Washed up dead wood alters streamflow patterns and sedimentation around log jams creates islands or extends bank zones which will be colonized by vegetation (Collins et al., 2012; Gurnell et al., 2012; Karrenberg et al., 2002; Naiman et al., 2008).

In addition to infiltration and subsurface runoff from precipitation, flood pulses recharge the floodplain aquifer until a hydrological equilibrium between the high water level of the channel and floodplain aquifer is reached or river flows start to drop (Stanford and Ward, 1988). Peak discharge events connect floodplain habitats (side channels, oxbows, ephemeral ponds, etc.) with the river channel and provide an influx of fine sediment, nutrient, eggs, and seeds (King et al., 2003). The nutrient input leads to an increase in primary production in the floodplain (Sims

and Colloff, 2012). Life cycle stages of many faunal species (e.g., spawning or larval drift) are synchronized with these flood pulses and coinciding rising temperatures (Baumgartner et al., 2014; Junk et al., 1989; Postel and Richter, 2003; Trush et al., 2000). The common toad, *Bufo bufo*, matches spawning with hydrology by utilizing temporary water-filled habitats and exhibiting quick metamorphosis (Tockner et al., 2006). Amphibians require water submersion until the completion of their aquatic life history stage in early summer (Trush et al., 2000). Jager (2014) demonstrated that seasonal, floodplain-inundating flow pulses might benefit salmon production through accelerated fish growth, facilitated by higher water temperature and prey availability (see also Opperman et al., 2010; Sommer et al., 2001, 2005). Although the erosive forces of flood pulses present serious abiotic stressors, native species have adapted to their occurrence (Hering et al., 2004; Marchetti and Moyle, 2001; Valdez et al., 2001; Yarnell et al., 2015). Fish may seek shelter in the bank zone (Biggs et al., 2008) and macroinvertebrates in the pervious hyporheic interstitial (Brunke et al., 2015; Stubbington, 2012), whereas non-native species may be reduced (Marchetti and Moyle, 2001).

The absence of channel forming flows (and natural sediment fluxes) and the application of minimum e-flow rules are often highlighted as some of the reasons for the loss of aquatic and terrestrial habitats as well as geomorphological river transitions (Auble et al., 1994; Tockner et al., 2010; Petts and Gurnell, 2005; Trush et al., 2000). Reductions of flood magnitude and frequency may reduce channel width and promote change of the morphological river type (e.g., from braided to wandering) (Trush et al., 2000; Surian and Rinaldi, 2003; Ahmari and Da Silva, 2011). Gravel-bed rivers adjust mostly via channel degradation and bed armoring, whereby their response time is usually slower than for rivers of finer grain sizes as bed-mobilizing discharges occur less frequently (Grant, 2012). Under such altered flows, fine sediment is deposited along the channel margins, allowing vegetation to encroach into formerly non-vegetated zones. Plants begin to follow low water levels and are no longer uprooted or eroded by regular floods (Aguar et al., 2016; Grant, 2012; Rivaes et al., 2015, 2017). Subsequently, vegetation establishes itself in these areas, stabilizes the location, resists flood erosion and traps further sediments, while narrowing the channel (Corenblit et al., 2007; Petts and Gurnell, 2005; Trush et al., 2000). Hence, a reduction of flood dynamics impedes dynamic morphological processes and formation of river structures (Poff et al., 1997). Through the above-described interactions, vegetation can change the hydraulic structure of instream habitats (Rivaes et al., 2017) and the floodplain can transform from a heterogeneous mosaic towards dryer soil-moisture forest formations, as the connectivity between channel and floodplain diminishes and groundwater resources are lost (Corenblit et al., 2007; Surian and Rinaldi, 2003; Trush et al., 2000).

Adverse implications for floodplain organisms can be detected if hydrological characteristics of peak flows are changed, especially regarding life history cycles such as spawning and rearing (Table 2). Therefore, reduced peak flows often favor exotic species over native ones, as introduced species can cope better with such hydrological alterations (Gurnell et al., 2016; Marchetti and Moyle, 2001).

3.6. Flow variability

Temperate river flow regimes exhibit natural flow fluctuations on multiple scales. The seasonal and yearly flow variability between (the above-described) low, mean and high flows is crucial for ecological functions and processes of floodplain ecosystems (Caruso et al., 2013; Naiman et al., 2008). The rise and fall of river stage from flood pulses facilitates numerous processes, such as the flushing of organic and

inorganic matter into and out of the floodplain, the incorporation of terrestrial carbon into the aquatic food web and vice versa, or the exchange between surface water and groundwater aquifers (Junk and Wantzen, 2004). Furthermore, these events maintain the balance of species in aquatic, riparian and floodplain communities (Postel and Richter, 2003). The flooding regime and moisture distribution within the floodplain essentially determine where which species can flourish (Meitzen et al., 2013; Stromberg et al., 1991). Apart from the variation between these two extremes, the flow variability within the channel (i.e., below bankfull discharge) is vital for enhancing floodplain productivity (Tockner et al., 2000).

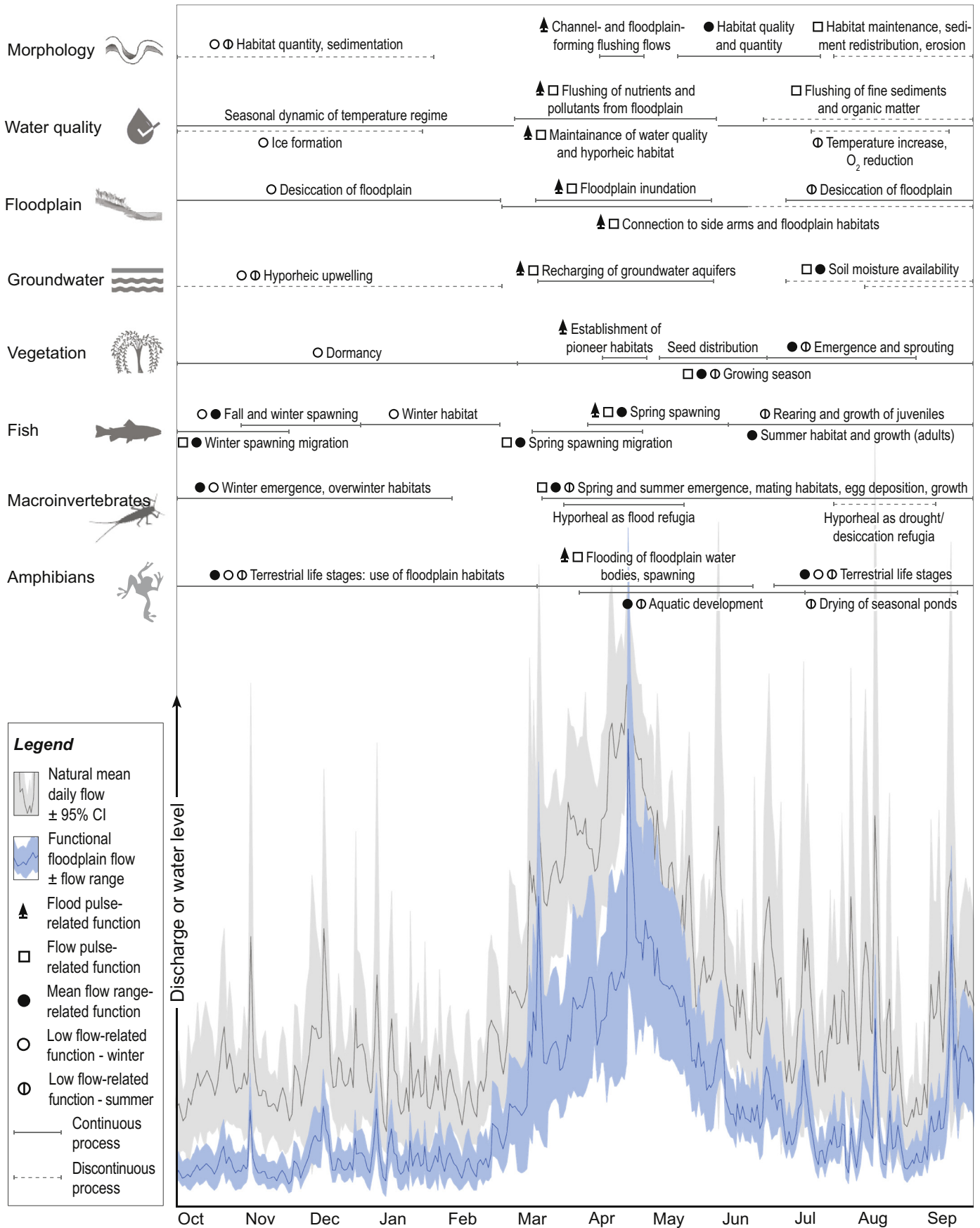
The life-history requirements of numerous aquatic and semiaquatic species are synchronized with spatially and temporally varying habitat availability caused by fluctuating flows (Tockner et al., 2010). To complete its life cycle, a species relies on qualitatively and quantitatively adequate habitat for each life-history phase (Fisher et al., 2012; Wolter et al., 2016). Thereto related is also the ecologically-significant seasonal variability of water temperature (Caissie, 2006; Naiman et al., 2008; Olden and Naiman, 2010; Tockner et al., 2000). For macroinvertebrates, river stage may determine adult emergence, egg-laying, drift, or diapause stage (Hancock and Bunn, 1997; Lytle and Poff, 2004; O'Hop and Wallace, 1983). Amphibians require seasonally inundated water bodies for aquatic life stages and non-inundated, moist areas for terrestrial ones (Indermaur et al., 2009a, 2009b; Tockner et al., 2006; Trush et al., 2000). The aquatic life stages of both, amphibians and macroinvertebrates, are also affected by the thermal regime (King et al., 2008; Tockner et al., 2010). The longitudinal migration of many fish species, their spawning behavior, larval emergence, rearing of juveniles, and lateral movements into the floodplain are interlinked with the natural timing of specific discharge and temperature events (Fenkes et al., 2016; Lobón-Cerviá and Rincón, 2004; Lytle and Poff, 2004; Melcher and Schmutz, 2010; Tockner et al., 2000; Unfer et al., 2011).

Changes in the seasonality or return of flow events may, therefore, influence riverine biota as life-history stages are disconnected from necessary components of the flow or thermal regime (Bunn and Arthington, 2002; Tockner et al., 2010). Mims and Olden (2013) demonstrate that dam-induced flow variability reductions and seasonality shifts transformed fish communities across the United States by favoring equilibrium strategist life-history species over opportunistic ones. Auble et al. (1994) suggest that riparian vegetation can change considerably without alteration of the mean annual flow but through adjustments of minimum and maximum flows. However, responses of distinct guilds can be linked to different components of the flow regime (Merritt et al., 2010). Similarly, temperature regime alterations also affect ecological (Olden and Naiman, 2010) and geomorphological functions and processes (Rood et al., 2007).

4. Functional floodplain flow

For a long time, stable minimum flows over an entire year or season were considered adequate to maintain an acceptable ecological status of residual flow reaches. Therefore, constant flow allotments without dynamic components are widespread until today. Recent research, however, shows that multiple elements of the natural annual hydrograph are necessary to maintain the ecological integrity of riverine ecosystems and their related components (river, floodplain, groundwater). To preserve their long-term sustainability, central hydrological aspects can be identified and management criteria derived (see Table 2). Here, we present a *functional floodplain flow* (*ff-flow*) approach which aims to establish the basis for an ecologically-relevant e-flow regime for the restoration of temperate floodplain rivers impacted by flow regulation (Fig.

Fig. 4. The conceptual curve of the functional floodplain flow (*ff-flow*) approach integrates ecological functions and processes (top) with principal flow regime components and their seasonality (bottom; the natural mean daily flow is depicted in grey). The presented environmental flow hydrograph (depicted in blue) does not establish intra-annual flow thresholds. Instead, it is understood to be a guide towards key aspects of the annual hydrograph and their implications for various elements of floodplain ecosystems.



4). The depicted hydrological regime represents all temperate regimes as it contains pluvial, nival, and glacial components. Note that the primary outputs of this conceptual model address ecological benefits but do not reflect social or economic services, though the approach could be adapted to integrate these aspects as well.

The central element determining the structure and functioning of floodplain ecosystems is the shift between dry and wet phases, determined by flood pulses and groundwater dynamic. This entails erosion and sedimentation processes as well as exchanges between surface and groundwater aquifers. Therefore flow stabilization alone is not a viable solution for hydrological restoration of dam-impacted floodplain rivers. Instead, an e-flow regime should emulate the natural distribution of flow events. While the importance of flow variability is well recognized (Acreman et al., 2009), the danger of favoring simplistic, constant e-flow allocations remains (Naiman et al., 2008). As fauna and flora are adapted to intra- and inter-annual flow variability, it can be expected that flows which mimic the natural hydrograph lead to sustainable e-flow rules (Richter et al., 2012; Ritchie et al., 2004).

By establishing the relationship between river morphology and biology with the natural flow regime, the *ff-flow* (Fig. 4) advocates that e-flow regimes must be function- and process-oriented (Yarnell et al., 2015). Above, we demonstrated how different river flows enable these features in natural systems. Mean flows, flow pulses, and floods especially, are most severely affected by diversion or abstraction dams and their restoration, therefore, must be emphasized in modern e-flow assessments. Water management must ensure that all central flow regime components occur correctly timed, with the right frequency as well as duration. In addition, the rate-of-change between flow seasons (Yarnell et al., 2015) must be preserved. Furthermore, the *ff-flow* approach suggests restoring the sediment budget by transporting sediment downstream during high flows (García de Jalón et al., 2017; Kondolf et al., 2014; Wohl et al., 2015). These guidelines ensure that morphological processes are sustained and that native species can fulfill all of their life-history phases (see management recommendations in Table 2). The conceptual curve of the *ff-flow* (blue band in Fig. 4) is, therefore, a graphical e-flow proposal that aims at maintaining fundamental seasonal flow-dependent functions and processes of floodplain rivers as described in the literature and depicted in the top section of Fig. 4. Following, we accentuate these links by describing the dynamic e-flow hydrograph in its seasonal sequence and its importance for abiotic and biotic elements.

To ensure the maintenance of ecological functions and processes, e-flow allocations need to overlap with natural flow patterns: The beginning of the hydrological year in fall is generally characterized by low to mean flows. The floodplain slowly falls dry, and vegetation becomes dormant. The release of flow pulses, which naturally occur due to precipitation events, promote migration and breeding of winter spawners. During winter low flows, hyporheic upwellings facilitated by earlier high flows add to in-channel flow which safeguards the upkeep of aquatic habitat quantity and provides refugia during cold or even freezing water temperatures.

By raising water levels at the onset of spring, the *ff-flow* approach initiates a series of ecological functions in floodplain rivers. Flushing waste products and pollutants downstream restores water quality. The gravel riverbed is scoured from organic matter and fines, which re-establishes the water exchange between surface and hyporheic habitats, enhancing successful spawning of rheophilic fish and supporting macroinvertebrate gravel and cobble communities. Lateral water seepage replenishes water tables in the river bank and floodplain which stimulates plant growth. Emulating the snow and glacier melt and their corresponding natural sediment load, the e-flow increases in magnitude, and side arms and heterogeneous floodplain habitats become connected to the main channel. Biota such as fish and amphibians receive ecological spawning cues as well as habitats for rearing and feeding. Flushing flows can transport (trapped) sediment downstream (Kondolf et al., 2014) and ensure that the river channel and its floodplain are

maintained by redistributing fluvial sediment through erosion and sedimentation, and by resetting successional processes. For safeguarding sediment transport and morphological processes, high flows must exceed the critical shear velocity threshold to mobilize and transport various particle sizes (Meitzen et al., 2013).

Pioneer habitats created by the released flood peaks at a timing and recession rate which emulate the characteristics of the falling hydrograph limb under natural conditions (as flows shift from spring flood pulses to summer low flows) are particularly vital for the establishment of floodplain and riparian plant seedlings. A natural timing and recession rate of these declining flows also allows the safe return of fish into permanent aquatic habitats and amphibians can finish their aquatic development phase before their temporal habitats fall dry.

The *ff-flow* also suggests recreating the typical summer dry-season flow conditions. Though these low flows may produce stressful conditions for native biota, for example, through temperature increase or diminished habitat connectivity, they also incite ecological functions such as rearing and growth of juvenile fish or the desiccation of the floodplain. The drying of seasonal floodplain ponds is a prerequisite for predator-free spawning sites for amphibians. At the same time, the effects of previous flood pulses and occasionally occurring higher flows prevent the potential negative impacts of low flows by providing soil moisture for plants or hyporheic refugia for aquatic biota.

The value of minimum e-flows and regular flooding events is widely recognized (Yang et al., 2016), however, few studies highlight the importance of higher seasonal flows and the role of groundwater to sustain functioning riverine floodplains. During the vegetation period, floodplain flora requires higher flow allocations (Foster and Rood, 2017) and certain biotic guilds (e.g., rheophilic fish) also depend upon hydraulic conditions established by higher flows, especially during spawning (Jungwirth et al., 2000). The capacity of phreatic groundwater layers to contribute to low river flows depends upon seasonal flood pulses that recharge its aquifer (Smakhtin, 2001). Moreover, Miller et al. (2013) predict that the encroachment of terrestrial vegetation into hydrologically altered river channels can be reduced through increased base flows and the release of high flow pulses. Hence, the *ff-flow* approach proposes a dynamic e-flow regime, underlining the importance of emulating the natural flow regime with its seasonal variability, flow magnitude, frequency, event duration, and rise and fall of the hydrograph. By incorporating these flow regime attributes, we hypothesize that the *ff-flow* regime will sustain self-regenerating floodplain forests, as it fulfills their four essential requirements, i.e., regular, correctly timed flows, the establishment of regeneration sites, the provision of water table conditions, and the propagation of needed materials (Hughes et al., 2012).

In summary, the *ff-flow* approach emphasizes the influence of hydrological key factors and their seasonal variation to sustain or restore ecological and morphological components of temperate floodplain rivers by targeting process-form relationships. The presented intra-annual e-flow hydrograph does not, however, establish exact thresholds. Instead, it is understood to be a guide towards functional key aspects of the annual hydrograph and their implications for abiotic and biotic elements of floodplain ecosystems. In modified rivers, the proposed flow management may not be effective if geomorphological impacts on e-flow releases (and vice-versa) are not considered (Meitzen et al., 2013), for example, if levees or riverbed incision prevent floodplain connectivity (Opperman et al., 2010; Richter and Thomas, 2007). In this regard, the combination of hydrological and morphological measures is often considered the most beneficial and cost-effective restoration measure (EC, 2015; García de Jalón et al., 2017; Greimel et al., 2017; Opperman et al., 2010). Moreover, since dams not only alter water flows but also sediment supply and transport, modern e-flow management must administer hydrological and sediment regimes concurrently (García de Jalón et al., 2017; Wohl et al., 2015). If the hydrology (e.g., flood pulses) is restored without considering the restoration of the sediment budget deficit, unanticipated riverbed degradation may occur

(Schmidt and Wilcock, 2008). Therefore, especially in floodplain rivers, an e-flow assessment must regard the reciprocal interactions between water flow, sediment, and also vegetation, as these determine physical processes (e.g., erosion and deposition) at different dynamic riparian zones (Corenblit et al., 2007, 2009a, 2009b; Gurnell et al., 2016; Gurnell and Petts, 2002).

5. Conclusion

Research shows that floodplain rivers are dependent upon recurring cycles of hydrological varying river flows which drive ecological and morphological processes and determine the structure and functions of these ecosystems. Due to their dependency on natural flow regimes, floodplain rivers are particularly sensitive to hydrological modifications. There is broad evidence demonstrating that flow abstraction evokes morphological and biological responses (Table 2). The concept of e-flows is considered a solution to these alterations as it endeavors to prevent ecological deterioration of the impacted reach and to preserve a desired ecological state by allotting the affected reach with a certain flow. As most e-flow assessments are biased towards instream flows based on minimum low flow requirements of selected criteria, it was critical to establish a holistic e-flow framework for temperate floodplain rivers.

Present-day water diversion or abstraction schemes normally exceed modern ecological protection thresholds (e.g., max. flow alteration < 10% or 11–20%; Richter et al., 2012), as only water uses above these limits become economically profitable. The presented *ff-flow* restoration approach (Fig. 4) acknowledges these socio-economic constraints by allowing the utilization of a significant proportion of the natural flow. At the same time, the approach moves away from minimum flow prescriptions by propagating the establishment of an e-flow regime capable of restoring the natural functions and processes of impaired floodplain ecosystems through the release of functional elements of the annual hydrograph. Limitations of the *ff-flow* approach include clear water releases and the associated effects of erosional dynamics caused by interrupted sediment transport, e.g., channel incision or bed armoring (Brandt, 2000; Grant, 2012; Kondolf, 1997; Schmidt and Wilcock, 2008), as well as physically modified rivers (García de Jalón et al., 2017; Meitzen et al., 2013). Regarding riparian succession, it shall be noted that once vegetation has established itself in the channel caused by missing floods, even higher flows are necessary to scour these patches (Ryan, 1997; Corenblit et al., 2007). Many studies indicate that native biota benefit from flow restoration (e.g., Caiola et al., 2014; Caruso et al., 2013; Marchetti and Moyle, 2001) yet there still remains the possibility of propagating invasive species through e-flow releases (Stuart and Jones, 2006).

Though e-flow studies conducted in temperate floodplain rivers are scarce (Hughes and Rood, 2003), we conclude that the ecological principles laid out in the presented *ff-flow* approach provide a sound basis for establishing ecologically relevant e-flows and for guiding flow restoration in temperate floodplain rivers (Bunn and Arthington, 2002; Hughes et al., 2012; Tharme et al., 1998, in: Postel and Richter, 2003; Trush et al., 2000), if constraints are considered. The inclusion of inter-annual flows or water management options may improve both ecological and socio-economic outputs, as a dynamic e-flow regime entails, for example, the release of higher flood pulses ('regeneration flows') in wet years and 'maintenance flows' in dry years (Erfani et al., 2015; Hughes and Rood, 2003; Rood et al., 2003, 2005). Further research is necessary to quantify the amount of flow needed for maintaining specific functions and processes in distinct river types and to provide appropriate e-flow assessment tools.

Acknowledgements

The authors express their thankfulness to Rui Rivaes and Alban Kuriqi, as well as two anonymous reviewers for their valuable comments and

suggestions to develop this manuscript. Thanks to Tamika-Chantel Rybinski for creating the graphical icons, and to Pearl Kim Williams for her grammatical improvements. This work was supported by the World-wide Fund for Nature – Switzerland and Austria. CEF is a research unit funded by Fundação para a Ciência e a Tecnologia I.P. (FCT), Portugal (UID/AGR/00239/2013). Daniel S. Hayes benefited from a Ph.D. grant sponsored by FCT (PD/BD/114440/2016).

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