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The role of floods and droughts on riverine ecosystems under a changing climate

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Abstract

Floods and droughts are key driving forces shaping aquatic ecosystems. Climate change may alter key attributes of these events and consequently health and distribution of aquatic species. Improved knowledge of biological responses to different types of floods and droughts in rivers should allow the better prediction of the ecological consequences of climate change-induced flow alterations. This review highlights that in unmodified ecosystems, the intensity and direction of biological impacts of floods and droughts vary, but the overall consequence is an increase in biological diversity and ecosystem health. To predict the impact of climate change, metrics that allow the quantitative linking of physical disturbance attributes to the directions and intensities of biological impacts are needed. The link between habitat change and the character of biological response is provided by the frequency of occurrence of the river wave characteristic—that is the event's predictability. The severity of impacts of floods is largely related to the river wave amplitude (flood magnitude), while the impact of droughts is related to river wavelength (drought duration).

KEYWORDS

biological response, climate change, disturbance, extreme events, hydromorphology, river droughts, river ecosystems, river floods, river wave concept, warming

1 | INTRODUCTION

Global climate change is expected to modify patterns of hydrological events in many regions of the world (Blöschl et al., 2017; Bormann & Pinter, 2017; Garner, Van Loon, Prudhomme, & Hannah, 2015; Glaser et al., 2010; Markovic, Carrizo, Kärcher, Walz, & David, 2017), affecting water temperature (Markovic, Scharfenberger, Schmutz, Pletterbauer, & Wolter, 2013; Van Vliet et al., 2013) and changing the temporal distribution of river flows (Blöschl et al., 2017). Since flow is considered a master variable shaping riverine ecosystems, such changes are expected to cause substantial shifts in the composition of aquatic communities (Guse et al., 2015; Rolls, Heino, & Chessman, 2016). This could lead to massive extinctions or to the creation of new traits and adaptations (Myers et al., 2017).

Understanding functional relationships between flow patterns and biological consequences is of the utmost importance for planning adaptation measures to climate change and for sustainable river management. Identifying elements of the hydrological regime directly responsible for shifts in community composition is necessary. Subsequently, the attributes determining the direction and magnitude of the shift can be identified.

It is widely recognised that extreme events such as floods and droughts are a major driving force behind the composition of aquatic biotas (Poff, 2018; Poff, Olden, Merritt, & Pepin, 2007; Sukhodolov, Bertoldi, Wolter, Surian, & Tubino, 2009; Wolter, Buijse, & Parasiewicz, 2016). However, not all floods and droughts are the same, and therefore, different events have different consequences. Knowledge of the directions and intensities of natural biological responses to different types of floods and droughts should allow improved understanding and ability to predict the consequences of natural and anthropogenic alterations.

To make precise predictions useful for climate adaptation planning, it is necessary to identify the appropriate quantitative metrics of disturbance that correlate with biological responses. Thus, the role that floods and droughts play in biological cycles needs to be understood better. Specifically, in this review the following questions are addressed:

- What are the functional mechanisms between physical patterns and biological response?
- Which attributes of floods and droughts are most closely related to population shaping phenomena?
- Which of these attributes are most sensitive to climate change effects?

While there is a substantial body of literature relating to various aspects of floods and droughts, the information is disjointed and not synthesised in a fashion that allows a full understanding of the driving forces and mechanisms leading to biological responses. Therefore, the purpose of this paper is to:

- provide a comprehensive overview of the topic based on a review of the recent literature;
- identify practical quantitative metrics that may be used to estimate the climate-induced modifications of flow patterns that determine biological response.

2 | FLOODS AND DROUGHTS AS ECOLOGICAL DISTURBANCE PROCESSES

For the ecology of a system, floods and droughts are considered physical disturbances, that is stochastic events forcing normal system environmental conditions substantially away from the mean (Death, Fuller, & Macklin, 2015; Fuller, Gilvear, Thoms, & Death, 2019; Puckridge, Sheldon, Walker, & Boulton, 1998; Stanford & Ward, 1983). Physical disturbance is a natural component of aquatic ecosystems, and aquatic biotas are adapted to deal with these disturbances (Fisher & Grimm, 1991; Lake, 2000; Lytle & Poff, 2004; Resh et al., 1988; Van Looy et al., 2019).

Lake (2000) described three types of disturbance: pulse, press and ramp, which trigger three different processes that alter populations. A pulse disturbance causes an instantaneous alteration in animal or plant densities and possibly diversity, while a press disturbance causes a sustained change in abundance or composition. Ramps have been defined as disturbances that increase in strength (and often spatial extent) over time (Lake, 2000). These definitions occur within a temporal scale experienced by individual organisms, and for aquatic organisms, the spatial scale is that of the reach. At this scale, floods are most often pulse or press disturbances, and droughts tend to be ramp. At coarser temporal scales, all disturbances may be considered as pulses (Lake, 2003; Poff, 1992).

3 | HABITAT CHANGES

Functionally, disturbance changes the quantity and quality of available habitat, which can directly modify community composition and affects biotic interactions (Fisher, Gray, Grimm, & Busch, 1982; Frissell, Liss, Warren, & Hurley, 1986, Junk, 2005; Grossman, Moyle, & Whitaker, 1982; Grossman, Ratajczak, Crawford, & Freeman, 1998 ; Gurnell, Rinaldi, et al., 2016; Leigh & Datry, 2017;Reice, 1985; Winemiller et al., 2014). The processes triggered by floods or droughts can create two types of changes: concurrent that is occurring only during the event; and post-event changes that persist for a considerable time after the event (Bork & Kranz, 2008; Death et al., 2015; Leigh & Datry, 2017; Pearsons, Li, & Lamberti, 1992).

3.1 | Habitat changes caused by floods

Floods affect habitat elements such as stream substrate composition, stability, refugia, river channel cross-section and planform morphology, and the flow regime (Lake, 2000, 2007; Poff, 1992). However, as floods are pulse disturbances, their effects are most strongly related to the magnitude of the event (Grimm & Fisher, 1989; Herget et al., 2015; Molles, 1985; Pearsons et al., 1992; Stolz, Grunert, & Fülling, 2013; Wetter et al., 2011). The effects of flooding may vary from minor geomorphological changes caused by small spates or freshets, to alteration of the entire structure of the stream channel caused by extended, powerful high discharge events (Bork & Kranz, 2008; Costa & O'Connor, 1995; Dotterweich, 2008; Hauer & Habersack, 2009). Wolman and Miller (1960) showed that floods of bankfull discharge cause most geomorphological change because they have significant stream power and occur relatively frequently. Out-of-season floods are acknowledged to create more significant changes to river morphology than those occurring during typical wet seasons (Giller, 2005; Lytle, 2003; Wetter et al., 2011).

3.1.1 | Concurrent changes

At the onset of a natural flood event, the increasing discharge raises flow velocities, and the thalweg of the river channel deepens and widens. Subsequently, mobilisation and deposition patterns reverse: pools are scoured and deposition takes place at the riffle areas, reducing the difference in water depth and velocity between pools and riffles (velocity-reversal phenomenon, Hogan & Church, 1989; Keller & Florsheim, 1993; Thompson, Wohl, & Jarrett, 1999). The temperature can either increase (e.g. in consequence of warm thunderstorms) or decrease (e.g. snowmelt waters), but it generally becomes more diverse across a cross-sectional profile (Tockner, Malard, & Ward, 2000).

The extent of habitat change is also a function of river type and morphology (Magoulick & Kobza, 2003; Tockner et al., 2000). In constrained rivers, floods raise flow velocity and shear stress, creating major changes in channel morphology through the scouring and filling of the streambed (Gordon, McMahon, Finlayson, & Gippel, 2004; Vezza, Parasiewicz, Spairani, & Comoglio, 2014). In lowland rivers with extensive floodplains, flood energy is more easily dissipated and water velocity and shear stress may not increase significantly. Nutrients previously deposited on the floodplain are also mobilised, affecting water quality and potentially greatly increasing primary production rates (Davis, Pusey, & Pearson, 2018; Edwards, Baker, Dunbar, & Laize, 2012). Floods fill wetlands, anabranches and flood runners with a slow-moving flow that recedes slowly, and deposits sediments and organic particles upon the floodplain.

3.1.2 | Post-disturbance effects

Floods reshape the distribution and composition of habitat. The consequences may range from spatial rearrangement of habitats, but maintaining a similar quantitative distribution, to complete destruction of habitat for some species and creation of habitats for others (Arthington, Balcombe, Wilson, Thoms, & Marshall, 2005; Roghair, Dolloff, & Underwood, 2002). In some cases, the morphology of the channel returns to pre-flood conditions (dynamic equilibrium), but this depends on lower flows being sufficiently powerful to move sediments. Thus, recovery is partly determined by river and sediment type.

3.2 | Habitat changes caused by droughts

Droughts can be divided into those that cause predictable, seasonal press disturbances and those that cause less predictable, protracted 'ramp' disturbances (Humphries & Baldwin, 2003). Droughts can either be periodic, seasonal or supra-seasonal events. Seasonal droughts are press disturbances, whereas supra-seasonal droughts are ramps marked by an extended decline in rainfall (Lake, 2003). Droughts tend to be more spatially extensive than floods, which are frequently limited to individual basins (Edwards et al., 2012).

3.2.1 | Concurrent changes

During a drought, precipitation, runoff, soil moisture, groundwater levels and streamflow decline sequentially (Changnon, 1987; Dahm, Baker, Moore, & Thibault, 2003; Grigg, 1996). Similar to floods, there are both direct and indirect effects on stream habitat during the drought. Direct effects include loss of habitat area for aquatic organisms and loss of stream connectivity (Lake, 2003; Magoulick & Kobza, 2003; Marshall et al., 2016; Matthews & Marsh-Matthews, 2003; White, McHugh, & McIntosh, 2016).

Loss of habitat is caused by a lack of flow replenishment from upstream and may be exacerbated by evaporation and loss of water into the ground. Indirect effects include deterioration of water quality caused by increased concentration of organic matter that occurs despite lower overall input of nutrients (Dewson, James, & Death, 2007; Golladay & Battle, 2002; Zieliński, Gorniak, & Piekarski, 2009). The ratio of inorganic to organic nutrients declines, potentially causing a shift in stream metabolism (Dahm et al., 2003). Due to reduced sediment transport capacity, fine particles and organic matter are deposited on the river bed and into interstitial spaces (McKenzie-Smith, Bunn, & House, 2006). An increase in the density of aquatic organisms, as well as growth of algae and cyanobacteria feeding on the concentrated nutrients, may lead to oxygen depletion and potentially hypoxic conditions (Suren, Biggs, Kilroy, & Bergey, 2003). During hot periods, a continuous increase of water temperature is sometimes accompanied by reduced inflow of cooler groundwater, and consequent lower oxygen solubility and loss of thermal refugia (Elliott, 2000; Torgersen, Price, Li, & McIntosh, 1999). Higher temperatures increase decomposition rates and, thus, further reduce oxygen concentrations. During cold weather periods, droughts may lead to lowering of water temperature, and ice and frazil ice formation. Frazil ice tends to scour river bottoms causing morphological change (Lake, 2003). Overall, habitat area and quality decline during droughts.

3.2.2 | Post-disturbance effects

Long-term changes depend on drought intensity, duration and the ability of the ecosystem to recover. The changes are mostly of a morphological and/or chemical nature, and among others are consequences of ice-induced scour or sedimentation. Growth of macrophytes and riparian vegetation during droughts can create new morphological patterns after the event (Gurnell, 2014; Gurnell, Corenblit, et al., 2016; Gurnell, Rinaldi, et al., 2016). However, after drying, the bare substrate undergoes important chemical changes, increasing phosphate retention and re-oxidisation of sulphur that may lead to acidification after re-wetting (Baldwin & Mitchell, 2000; Lamontagne, Hicks, Fitzpatrick, & Rogers, 2006).

4 | BIOLOGICAL RESPONSE

There are two generally recognised forms of biological response to disturbance: resistance (the capacity of the biota to withstand the disturbance) and resilience (the capacity to recover from the disturbance) (Lake, 2000). A third type of response is opportunistic utilisation of habitats that are created by the disturbance, such as spawning or feeding habitats (Górski et al., 2011; Górski, Winter, De Leeuw, Minin, & Nagelkerke, 2010; Grift et al., 2001; Phelps, Tripp, Herzog,

& Garvey, 2015; Van Looy et al., 2019; Welcomme, 1979). Resistance is observed concurrently with disturbance events, while resilience is expressed during the post-disturbance phase. Opportunism can be observed in both phases. Figure 1 represents this concept for the example of floods.

Biological responses are triggered by changes in habitat area and quality that fall outside the typical range. Physico-chemical habitat quality attributes are related to flow velocity, water depth, substrate stability, temperature and water quality. These factors affect organisms at the scale at which they perceive their environment (i.e. river element and hydraulic unit; see Gurnell et al., 2014). Once the factors exceed the typical suitable range, they cause resistance reactions that include changes in habitude (i.e. organisms occupy sub-optimal habitats when favourable habitats are lost), behaviour (e.g. the drag-minimising body posture and adhesive anchoring observed in some invertebrates (Schnauder, Rudnick, Garcia, & Aberle, 2010) or body size-related swimming performance (Radinger & Wolter, 2014; Wolter & Arlinghaus, 2003)) and a search for areas offering refuge (Lancaster & Belyea, 1997; Meffe, 1984). Resilience is driven by the availability of refugia, connectivity and the organism's fecundity as well as flexibility of life history strategy (Arlinghaus & Wolter, 2003; Klemetsen et al., 2003; Van Looy et al., 2019; Wolter et al., 2016). Opportunism is a function of species being able to take advantage of circumstances during the disturbance.

4.1 | Biological response to floods

4.1.1 | Concurrent response

Floods increase the overall wetted area, although much of this area may be uninhabitable due to high velocities, suspended solids or chemical loads (Hoopes, 1974; Moffett, 1935). This is followed by change of habitude from, for example foraging to refuge seeking (Bolland, Nunn, Lucas, & Cowx, 2015). In rivers without floodplains, this leads to a reduction in abundance and diversity of macroinvertebrates and juvenile fish (Bischoff & Wolter, 2001). Adult fish may

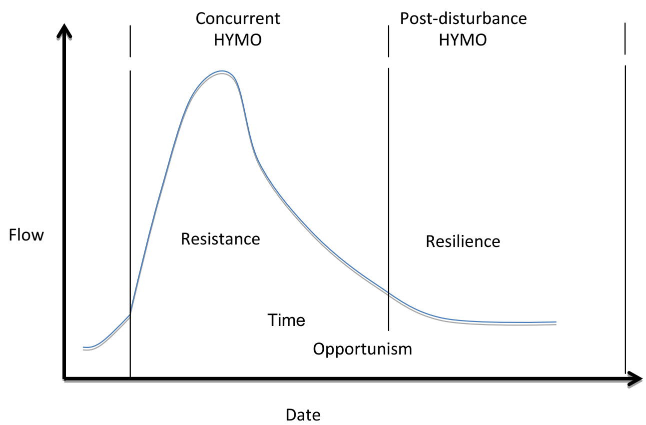

FIGURE 1 A concept of hydromorphologic (HYMO) changes and biological response types during the flood event. Blue line represents flow in the river [Colour figure can be viewed at wileyonlinelibrary.com]

also be affected by displacement, and injury caused by moving debris and bed instability, or by a shortage of food (Hogberg & Pegg, 2016; Jensen & Johnsen, 1999; Lusk, Halačka, & Lusková, 1998; Weng, Mookerji, & Mazumder, 2001). Extreme events may scour eggs and prevent hatching (Carline & McCullough, 2003; Cowx & de Jong, 2004; Dusterhoff, Sloat, & Ligon, 2017; Peterson, Conrad, & Quinn, 2000; Phillips, Lantz, Claire, & Moring, 1975).

In terms of opportunism, salmonids, for example, are well adapted to high velocities and use floods to reach spawning grounds that are not accessible or suitable during lower flows (DeVries, 1997). Inundation of the floodplains of low gradient rivers causes a net increase in habitat area for many fish species and offers refuge and foraging habitat (Beesley et al., 2014; Schwartz & Herricks, 2005). The available flooded areas will also determine fish productivity, growth and survival, and consequently, density of juvenile year classes, especially in spring (Coops et al., 2008; Copp, 1989; Górski et al., 2010, 2011; Holčík, 1996). The additional influx of nutrients supports rapidly growing populations of macroinvertebrates (Hickey & Salas, 1995). Allochthonous inputs and high autochthonous floodplain production dominate ecological processes (Davis et al., 2018; Humphries, Keckeis, & Finlayson, 2014). This creates an abundance of prey for fish (Allen, 1993; Junk, 2005). The abundance of phytophilous and phytolithophilous species increases due to higher food and shelter availability (Jurajda, Ondračková, & Reichard, 2004; Schomaker & Wolter, 2011). However, such a situation is less common during winter floods.

4.1.2 | Post-disturbance effects

Overall, the most important consequence of flooding is a shift of species composition towards fish species that are better adapted to, or even dependent on, floodplain habitats (Bayley, 1991; Bischoff & Wolter, 2001; Jurajda, Reichard, & Smith, 2006; Leitman, Darst, & Nordhaus, 1991; Maher, 1993; Schomaker & Wolter, 2011). Due to the high mobility of aquatic organisms, the recolonisation of highly disturbed areas occurs rapidly, although the rate is strongly dependent on availability and quality of refugia (Magoulick & Kobza, 2003; Townsend, 1989) and species-specific dispersal ability (Radinger et al., 2017; Radinger, Hölker, Horký, Slavík, & Wolter, 2018; Radinger & Wolter, 2015). Furthermore, species composition and densities after recovery depend on many morphological changes caused by floods (Elwood & Waters, 1969).

4.2 | Biological response to droughts

4.2.1 | Concurrent response

Reduction of habitat area during drought conditions is not only due to a smaller wetted area, but also reduced habitat suitability (e.g. due to excessive temperatures or nutrients). Many fish change their behaviour, adjusting to the new conditions (Davey, Kelly, & Biggs, 2006; Dekar & Magoulick, 2007; Elliott, 2000, 2006). For organisms that prefer shallow and low-velocity zones (e.g. invertebrates and juvenile fish), or that are tolerant to high temperature and low oxygen, the amount of suitable habitat may initially increase (Reid, Farrell, Luke, & Chapman, 2013). As wetted area further declines, the densities of these organisms increase (Dewson et al., 2007; Matthews, Harvey, & Power, 1994; McIntosh, Benbow, & Burky, 2002). Soon food availability declines and predation increases. The numbers of invertebrates decline and fish assemblage structure changes as a consequence (Arthington et al., 2005; White et al., 2016; Wood, Agnew, & Petts, 2000).

In perennial streams, the richness of macroinvertebrate species declines due to the loss of habitat diversity. By contrast, the same phenomenon leads to local increases in fish species richness in remnant pools. However, this is an artefact of relocation of fish from de-watered areas (Pires, Pires, Collares-Pereira, & Magalhães, 2010). Again, predation by fish and other vertebrates becomes a limiting factor for macroinvertebrates (Labbe & Fausch, 2000; Maceda-Veiga, Salvadó, Vinyoles, & De Sostoa, 2009).

Since large portions of aquatic zones become terrestrial, sedentary and sessile species, such as freshwater mussels, are at risk of stranding, desiccation and predation. The temperature increase in expanding shallow margins also exposes such organisms to thermal shock (Castelli, Parasiewicz, & Rogers, 2011).

4.2.2 | Long-lasting effects

The overall consequence of drought is a change in species composition towards drought-tolerant, small-bodied species, that is those for which habitat conditions have actually improved (Boix et al., 2010; Leigh & Datry, 2017; Ruhí, Holmes, Rinne, & Sabo, 2015; Schomaker & Wolter, 2011). As drought persists and water quality exceeds critical thresholds, the numbers of individuals rapidly declines (Extence, 1981). For fish, the timing of drought is important, as it may affect sensitive life history stages such as spawning or egg incubation. This shapes community composition in future years by potentially causing the failure of entire year classes. Fish and macroinvertebrates can recover quickly from short-term droughts, but availability of refugia during the drought is critical for this (Covich, Crowl, & Scatena, 2003; Fenoglio, Bo, & Bosi, 2006; Matthews & Marsh-Matthews, 2003). If cease-to-flow conditions occur, populations may go locally extinct unless aquatic dispersers have made it to permanent water. Populations can re-establish through subsequent high-flow events. Recovery from longer-term droughts that span multiple years is slower because of the smaller pool of surviving organisms or greater distances over which recolonisation must occur. The impacts of supra-seasonal droughts are difficult to predict because of limited experience of these events (Lake, 2007; Ruhí et al., 2015).

4.3 | What affects the intensity and direction of biological response?

The above sections describe a general pattern of biological response. Floods and droughts may lead to a change in aquatic community composition, impacting upon the organisms less adapted to the disturbance and promoting those better adapted. During flooding, the mechanisms leading to these changes are drift, injury, dislocation, and concurrent and post-disturbance habitat modifications. However, the flood is not solely a damaging disturbance, but also a major regenerator of biodiversity and production. Drought, by contrast, leads, at coarse scales, to a net loss of populations through habitat limitation, predation and food shortages. Consequently, a general observation is that predictable floods tend to increase fish species richness, abundance and biomass, whereas droughts lead to a decline (Figure 2).

However, the conceptual model in Figure 2 is generic and some studies have found different results for individual cases (Piniewski et

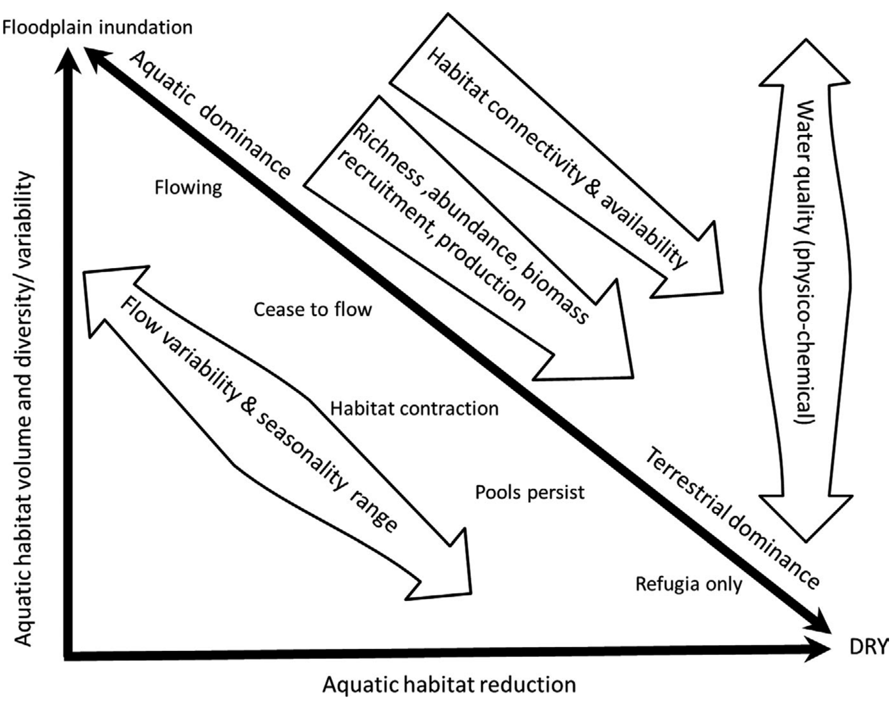

FIGURE 2 Conceptual overview of fish responses to change in flow habitat characteristics (modified from Webb et al., 2010). The model hypothesizes that with reduction of flow, there will be negative effects on the behavioural and reproductive characteristics of native fish and a decrease in population and community composition measures. Conversely, the same changes in flow habitat are hypothesized to increase the dominance, spread and abundance of terrestrial fauna and flora. The figure highlights the generic relationships between reductions in flow habitat and freshwater fish. Reduction in discharge is leading to overall reductions in habitat, it also leads to reduce diversity in habitat and reduce water quality

al., 2017). One of the more significant covariates causing such deviations is the morphological variability of rivers and floodplains. The presence of refugia has a direct effect on the survival of animals and is therefore important for the speed and scale of recolonisation. Spatial variability not only mitigates deleterious impacts by providing refugia, but also by offering a diversity of habitats that increase richness, abundance, biomass, recruitment and productivity prior to any disturbance. Habitat shifts also occur for aquatic biota, caused by changes in discharge and resulting changes in flow velocities, shear forces and water levels (Wolter et al., 2016). For example, in lowland floodplain rivers, the occurrence of hydraulically inhospitable habitats (i.e. very fast flowing) is compensated for by the creation of vast areas of attractive spawning and larval rearing habitats on the floodplain (Górski et al., 2010, 2011; Stoffels, Rehwinkel, Price, & Fagan, 2016; van de Wolfshaar, Middelkoop, Addink, Winter, & Nagelkerke, 2011). In high-gradient rivers, floods create access to tributaries, effectively expanding accessible habitat area (Sukhodolov et al., 2009).

The intensity of biological response also depends upon factors such as geographic location and seasonality. For example, a drought of the same magnitude will have different consequences in northern and southern Europe. In some Mediterranean streams, adaptation to climatic regimes means that fish can survive severe droughts, which would be lethal to any northern organisms (in review, in press).

Similar differences in response are seen with the timing of disturbance. For example, in many rivers of the northern hemisphere, severe flooding in summer has different biological consequences than during the spring (spawning) time. Since summers are characterised by low-flow conditions, many animals utilise habitat for rearing and growth, with extensive nursery habitats (Olaya-Marín, Martínez-Capel, & Vezza, 2013). Unpredictable floods (e.g. aseasonal or happening with higher frequency than in the past) have been documented as having very deleterious effects on fish assemblages (Bischoff & Wolter, 2001; George, Baldigo, Smith, & Robinson, 2015; Hogberg & Pegg, 2016).

Consequently, the intensity of biological responses to disturbance events depends on their predictability; populations become adapted to the conditions that are most common, and the frequency of occurrence in the past is a driver of the predictability.

5 | PREDICTING IMPACT OF CLIMATE CHANGE ON HYDROLOGICAL REGIMES

Recent work projecting hydrological response to future weather data, derived from various IPCC global circulation models for the state of New Hampshire, USA provides some insight on how climate change could modify hydrological patterns (Bjerklie & Sturtevant, 2018). This state-wide analysis documented a common pattern characterised by an increase of higher flows in cold seasons and lower flows during spring and summer. The study also projected increased variability of flows, with changes to the magnitude of baseflows (groundwater inflow) varying depending on elevation and micro-climatic factors related to location. The variability of flow responses to climate change within the state is demonstrated by comparing flows of a relatively small coastal river, the Oyster River and the larger Pemigewassett River (Bjerklie, Ayotte, & Cahillane 2015); the above-described trend is more pronounced in the Pemigewassett River. The Oyster River has a little topographic relief and sandy soils, while the Pemigewassett River is located in the upland and more mountainous terrain (Bjerklie et al., 2015).

The majority of model-based climate change impact studies address biological consequences by defining changes in 'ecologically relevant' flow regimes (Dhungel, Tarboton, Jin, & Hawkins, 2016; Döll & Zhang, 2010; Laizé et al., 2013; Morales-Marin, Rokaya, Sanyal, Sereda, & Lindenschmidt, 2019; O'Keeffe et al., 2018; Piniewski, Laize, Acreman, Okruszko, & Schneider, 2014; Stagl & Hattermann, 2016; Vigiak et al., 2018; Van Vliet et al., 2013). Ecological relevance in this case is usually assessed based on available literature. This approach is better suited for large-scale analyses: from global (Döll & Zhang, 2010), through continental (Laizé et al., 2013; Van Vliet et al., 2013), to national (Dhungel et al., 2016) and large river basin scale (O'Keeffe et al., 2018; Stagl & Hattermann, 2016). Predicted effects of climate change on riverine biota are only implicit in such studies. For example, O'Keeffe et al. (2018) reported a projected increase in high-flow frequency in the Vistula and Odra basins in Poland, which could be beneficial for northern pike due to more frequent floodplain inundation and better river-floodplain connectivity. On the other hand, abnormally high streamflow could wash away the fish and eggs.

In a more complex approach, but typically applied at finer spatial scales, climate change forcing is propagated through a modelling cascade consisting of a hydrological model loosely coupled with a habitat suitability or species distribution model (Jaeger, Olden, & Pelland, 2014; Kakouei et al., 2018; Kuemmerlen et al., 2015; Morid, Delavar, Eagderi, & Kumar, 2016; Muñoz-Mas, Lopez-Nicolas, Martinez-Capel, & Pulido-Velazquez, 2016; Mustonen et al., 2018; Viganò et al., 2015; Woznicki, Nejadhashemi, Tang, & Wang, 2016). For example, Jaeger et al. (2014) predicted a higher frequency of zero-flow days in an intermittent stream in Arizona, United States, which would inevitably lead to increased channel fragmentation and a reduced network-wide hydrological connectivity during spawning of native fish.

Still higher levels of complexity can be achieved by including a hydraulic model in the modelling chain, but such approaches are typically applied only at small catchment scales (Guse et al., 2015; Papadaki et al., 2016). Guse et al. (2015) reported variable changes in habitat suitability for fishes in a small stream in northern Germany in response to increased occurrence of seasonal habitat deficits. They also predicted a dampened effect of climate change on stream hydraulics compared with the effects on discharge itself. Papadaki et al. (2016) showed that the West Balkan trout is likely to experience a deterioration in habitat quantity and quality in summer months in a mountainous stream in Greece, also as a result of an increased frequency of low flows.

6 | DISCUSSION

This review underlines the importance of floods and droughts as master driving forces of the riverine ecosystems that shape the biotic communities. Each of these events creates immediate and long-lasting modification of habitat conditions for aquatic species. This in turn causes specific biological response that leads to changes in the composition of aquatic communities, both in short and long terms.

The response may be in the form of resistance, change of habitude and resilience. The intensity and direction of biological impact may vary depending on location and particular climatic and physiographic setting of the watershed. The variety of impact will further diversify if other human-induced alterations to riverine ecosystems are included. For example, the consequences of dam construction are presented in a study on the Tana River, Kenya by Langat, Kumar, Koech, and Ghosh (2019).

Nevertheless, the expected overall long-term consequence of natural floods and droughts regime is an increase in biological diversity and ecosystem health. Hence, floods and droughts can be seen as 'rejuvenating' events essential for ecological equilibrium. Therefore, alteration of floods and droughts patterns expected as a consequence of climate change may cause dramatic changes in the structure and composition of aquatic communities. Quantification of these changes is crucial for predicting the biological consequences of climate change. To capture these modifications at a continental scale, descriptive pattern metrics, which are directly related to biological response, need to be identified.

As presented by Humphries et al. (2014) in the River Wave Concept, river flow may be conceptualised as series of waves varying in shape, amplitude, wavelength, and frequency. Floods are crests and droughts are the troughs of the wave and define its overall characteristics. These attributes can be used as hydrological metrics to characterise the pattern of disturbance events.

As presented above, aquatic organisms have evolved around the hydrological events that are predictable and therefore more common. Hence, event frequency is a wave metric most closely related to disturbance predictability and, consequently, to the intensity of biological response. It is an inverse relationship—that is the higher the natural frequency, the higher the probability of a less severe biological alteration (Figure 3).

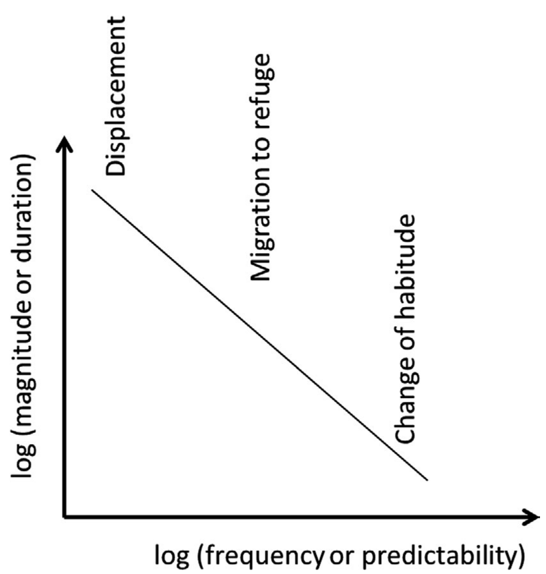

FIGURE 3 Biological response type to disturbance drivers

The relationship between the metrics of event intensity and frequency is generally described by a power law (Bak, 1996). In undisturbed ecosystems disturbances of large magnitude or duration are infrequent and vice versa. Consequently, events of extreme magnitude and/or duration (floods or droughts) can be expected to have a much stronger biological effect; they may even cause a depletion or expansion of populations. The smallest and most frequent events commonly cause a change of habitude, as the migration to refuge sets in (Figure 3).

According to Lake (2000), floods are pulse disturbances and the response to floods is most often of a pulse type. However, extreme floods that create dramatic hydromorphologic changes will cause a press response. In both cases, flood magnitude is a stronger driver than event duration.

Since floods are generally pulse disturbances, the key attributes related to biological response are flood frequency and magnitude. Consequently, there is a functional relationship between these two metrics and the intensity of biological impact of floods. In regions where the hydrological response to climate change is an increasing frequency of high-flow events, the channel cross-section will widen and deepen to accommodate the more frequent flooding. The time frame for the river to adjust to a more stable geometry is associated with the time for instream habitat to adjust. If the response also includes larger flood events, adjustments to channel morphology may also include changes to the planform structure of the river network, including changes to the meandering pattern and associated riverine floodplain features such as wetlands and ponds. Additionally, changes in flood frequency and magnitude will markedly change the amount of woody debris entering the river channel, and the amount of sediment transported to downstream areas. Subsequently, the relative alteration of flood magnitude and frequency that is caused by climate change is tied to, and can be indicative of, biological response to climate change.

Since droughts are presses and ramps, the key driver of biological response is drought duration (Figure 4). In addition, increased frequency even of small disturbance events can also be a cause of ramp responses. For example, increased frequency of smaller drought events that happen during supra-seasonal droughts will further affect the physical condition of fauna and may lead to catastrophic consequences.

The conclusion of this review is that the influence of floods and droughts on aquatic ecosystems under changing climate will be substantial, but by considering floods and droughts in terms of their effects on the river wave, increased understanding and predictability of responses is possible. Ecosystem effects can be directly related to the frequency and magnitude of floods, and frequency and duration of droughts. These metrics can be quantitatively tied to the intensity of biological response and allowed for impact predictions at multiple scales. In future impact modelling studies, the focus should be therefore on the changing River Wave attributes of aquatic ecosystems.

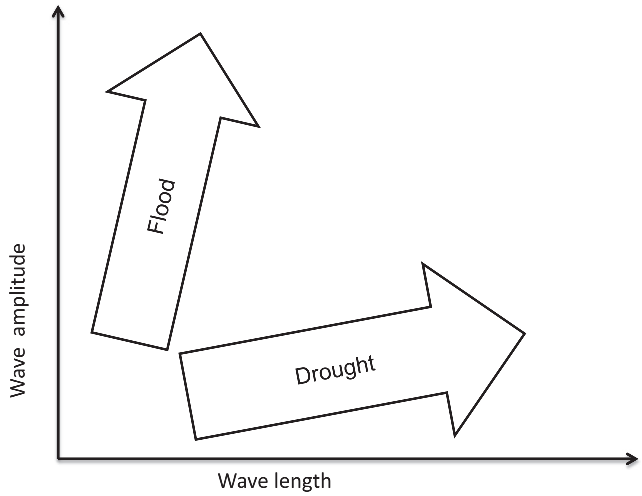

FIGURE 4 Key attributes of river wave affecting the severity of impact of flood and drought

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