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

Piotr Parasiewicz<sup>1,2</sup>, Elise L.King<sup>3</sup>, J. Angus Webb<sup>3</sup>, Mikołaj Piniewski<sup>2</sup>, Claudio Comoglio<sup>4</sup>, Christian Wolter<sup>5</sup>, Anthonie D. Buijse<sup>6</sup>, David Bjerklie<sup>8</sup>, Paolo Vezza<sup>4</sup>, Andreas Melcher<sup>7</sup>, Katarzyna Suska<sup>1</sup>

<sup>1</sup>The Stanisław Sakowicz Inland Fisheries Institute, ul. Oczapowskiego 10, 10-719 Olsztyn 4, Poland

<sup>2</sup>Department of Hydraulic Engineering, Warsaw University of Life Sciences, Nowoursynowska 159, Warsaw, Poland

<sup>3</sup> Environmental Hydrology and Water Resources, Department of Infrastructure Engineering, The University of Melbourne, Parkville, Victoria, 3010, Australia

<sup>4</sup> Turin Polytechnic, Corso Duca degli Abruzzi 24, c/o DITAG, 10129 Torino, Italy

<sup>5</sup> Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310  
12587 Berlin, Germany

<sup>6</sup> Deltares, Daltonlaan 600, 3584 BK Utrecht, Netherlands

<sup>7</sup> Institute of Hydrobiology and Aquatic Ecosystem Management, University of Natural Resources and Life Sciences, Max Emanuelstrasse 17, 1180 Vienna, Austria

<sup>8</sup> Retired, U.S. Geological Survey New England Water Science Center, Connecticut Office 101 Pitkin Street East Hartford, CT 06108 United States .

## **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 flora and fauna. Improved knowledge of natural biological responses to different types of floods and droughts in rivers would allow us to better predict 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 impact of climate change, physical metrics allowing to quantitatively link the physical disturbance attributes to the directions and intensities of biological impacts is needed. The link between the physical change and character of biological response is provided by the frequency of occurrence of the river wave characteristic – i.e. the event's predictability. The severity of impacts of floods is largely related to river wave amplitude (flood magnitude), and of droughts to river wave length (drought duration). Presented analysis of three rivers in Poland demonstrates how river wave characteristics for floods and droughts can be captured with flow duration statistics, and with help of habitat models and Uniform Continuous Under Threshold duration techniques, respectively.

1

2       Keywords: river wave concept, biological response, extreme events, disturbance,  
3       hydromorphology, climate change, river ecosystems, river floods, river droughts,  
4       warming.

5

## 6       **INTRODUCTION**

7       Global climate change is expected to modify patterns of hydrological events in  
8       many regions of the world (Glaser et al. 2010, Garner et al. 2015, Blöschl et al.,  
9       2017, Bormann et al. 2017, Markovic et al. 2017), affecting water temperature  
10       (Markovic et al. 2013, Van Vliet et al. 2013), and changing the temporal  
11       distribution of river flows (Blöschl et al. 2017). Since flow is considered a master  
12       variable shaping riverine ecosystems, such changes are expected to cause  
13       substantial shifts in the composition of aquatic communities (Guse et al. 2015,  
14       Rolls et al. 2016). This could lead to massive extinctions or to the creation of new  
15       traits and adaptations (Myers et al. 2017). The changes may vary depending on  
16       climate change magnitude and geographic location.

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

23       It is widely recognized that extreme events such as floods and droughts are a  
24       major driving force behind the composition of aquatic biotas (e.g. Poff et al. 2007,  
25       Sukhodolov et al. 2009, Wolter et al. 2016, Poff 2018). However, not all floods  
26       and droughts are the same, and therefore different events have different  
27       consequences. Knowledge of the directions and intensities of natural biological  
28       responses to different types of floods and droughts would allow to better  
29       understand and predict the consequences of natural and anthropogenic alterations.

30       To be precise in predictions useful for climate adaptation planning it is necessary  
31       to identify the appropriate quantitative metrics of disturbance that correlate with  
32       biological responses. Thus, the role that floods and droughts play in biological  
33       cycles needs to be better understood. Specifically, the following questions need to  
34       be answered:

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

1 While there is a substantial body of literature relating to various aspects of floods  
2 and droughts, the information is disjointed and not synthesized in a fashion that  
3 allows to fully understand the driving forces and mechanisms leading to biological  
4 responses. Therefore, the purpose of this paper is to:

- 5 • provide a systematic overview of the topic based on a review of the recent  
6 literature;
- 7 • identify practical, quantitative metrics that may be used to estimate the  
8 climate-induced modifications of flow patterns that determine biological  
9 response.

10 The paper concludes with an application of the identified metrics in three case  
11 studies for rivers in Poland.

## 12

### 13 **FLOODS AND DROUGHTS AS ECOLOGICAL DISTURBANCE** 14 **PROCESSES**

15 For the ecology of a system, floods and droughts are considered physical  
16 disturbances, i.e. stochastic events forcing normal system environmental  
17 conditions substantially away from the mean (Stanford and Ward, 1983,  
18 Puckridge et al. 1998, Death et al. 2015, Fuller et al. 2019). Physical disturbance  
19 is a natural component of aquatic ecosystems, and aquatic biotas are adapted to  
20 deal with these disturbances (Resh et al., 1988; Fisher & Grimm, 1991; Lake,  
21 2000, Lytle & Poff 2004, Van Looy et al. 2019).

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

### 32 **HABITAT CHANGES**

33 Functionally, disturbance changes the quantity and quality of habitat available,  
34 which can directly modify community composition as well as affect biotic  
35 interactions (Fisher et al., 1982; Grossman et al., 1982, 1998; Reice, 1985; Frissel  
36 et al. 1986, Junk 2005, Parasiewicz et al., 2012, Winemiller et al. 2014, Gurnell et  
37 al. 2016, Leigh & Datry 2017). The processes triggered by floods or droughts can  
38 create two types of changes: concurrent i.e. occurring only during the event; and

1 post-event changes that persist after the event for a considerable time (Pearsons et  
2 al. 1992, Bork & Kranz 2008, Death et al. 2015, Leigh & Datry 2017).

3

#### 4 **HABITAT CHANGES CAUSED BY FLOODS**

5 Floods affect habitat elements such as stream substrate composition, stability,  
6 refugia, river channel cross-section and planform morphology, and the flow  
7 regime (Poff, 1992; Lake, 2000; Lake, 2007). However, as floods are pulse  
8 disturbances, their effects are most strongly related to the magnitude of the event  
9 (Molles, 1985; Grimm and Fisher, 1989, Pearsons et al. 1992, Wetter et al. 2010,  
10 Stolz et al. 2013, Herget et al. 2015). The effects of flooding may vary from minor  
11 geomorphological changes caused by small spates or freshets, to alteration of the  
12 entire structure of the stream channel caused by extended, powerful high  
13 discharge events (Costa and O'Connor, 1995; Bork & Kranz 2008, Dotterweich  
14 2008, Hauer & Habersack 2009). Wolman and Miller (1960) showed that floods  
15 of bankfull discharge cause most geomorphological change because they have  
16 significant stream power and occur relatively frequently. Out-of-season floods are  
17 acknowledged to create more significant changes to river morphology than those  
18 that occur during typical wet seasons (Lytle, 2003; Giller, 2005, Wetter et al.  
19 2010).

#### 20 **Concurrent changes**

21 At the onset of a natural flood event, the increasing discharge raises flow  
22 velocities, and the thalweg of the river channel deepens and widens (Figure 2).  
23 Subsequently mobilization and deposition patterns reverse: pools are scoured and  
24 deposition takes place at the riffle areas, with little difference in water depth and  
25 velocity between pools and riffles (velocity-reversal phenomenon, Keller and  
26 Florsheim, 1993; Thompson et al., 1999, Hogan and Church, 1989). The  
27 temperature can either increase (e.g. in consequence of warm thunderstorms) or  
28 decrease (e.g. snowmelt waters), but it generally becomes more diverse across a  
29 cross-sectional profile (Tockner et al., 2000).

30 The extent of habitat change is also a function of river type and morphology (e.g.,  
31 Tockner et al., 2000; Magoulick and Kobza, 2003). In constrained rivers, floods  
32 raise flow velocity and shear stress, creating major changes in channel  
33 morphology through the scouring and filling of the streambed (Gordon et al.,  
34 2004; Vezza et al., 2014). In lowland rivers with extensive floodplains, flood  
35 energy is more easily dissipated and water velocity and shear stress may not  
36 increase significantly. Nutrients previously deposited on the floodplain are also  
37 mobilized, affecting water quality and potentially greatly increasing rates of  
38 primary production (Edwards et al., 2012, Davis et al. 2018). Floods fill wetlands,  
39 anabranches and flood runners with a slow-moving flow that recedes slowly, and  
40 deposits sediments and organic particles upon the floodplain.

1 **Post disturbance effects**

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

10 **HABITAT CHANGES CAUSED BY DROUGHTS**

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

18 **Concurrent changes**

19 During a drought, precipitation, runoff, soil moisture, groundwater levels and  
20 stream flow decline sequentially (Changnon, 1987; Grigg, 1996; Dahm et al.,  
21 2003). Similar to floods, there are both direct and indirect effects on stream  
22 habitat during the drought. Direct effects include loss of habitat area for aquatic  
23 organisms and loss of stream connectivity (Lake, 2003, Magoulick & Kobza 2003,  
24 Matthews & Marsh-Matthews 2003, Marshall et al. 2016, White et al. 2016).

25 Loss of habitat is caused by a lack of flow replenishment from upstream and may  
26 be exacerbated by evaporation and loss of water into the ground. Indirect effects  
27 include deterioration of water quality caused by increased concentration of  
28 organic matter that occur despite lower overall input of nutrients (Dewson et al.,  
29 2007; Golladay and Battle, 2002; Zielinski et al., 2009). The ratio of inorganic to  
30 organic nutrients declines, potentially causing a shift in stream metabolism (Dahm  
31 et al., 2003). Due to reduced sediment transport capacity, fine particles and  
32 organic matter are deposited on the river bed and into interstitial spaces  
33 (McKenzie-Smith et al., 2006). An increase in the density of aquatic organisms, as  
34 well as growth of algae and cyanobacteria feeding on the concentrated nutrients,  
35 may lead to oxygen depletion and potentially hypoxic conditions (Suren et al.,  
36 2003). During hot periods, a continuous increase of water temperature is  
37 sometimes accompanied by reduced inflow of cooler groundwater and consequent  
38 loss of thermal refugia (Elliot, 2000; Torgersen et al., 1999) and lower oxygen  
39 solubility. Higher temperatures increase decomposition rates and thus, further  
40 reduce oxygen concentrations. During cold weather periods, droughts may lead to

1 lowering of water temperature, ice and frazil ice formations. Frazil ice tends to  
2 scour river bottoms causing morphological change (Lake, 2003). Overall, habitat  
3 area and quality decline during droughts.

#### 4 **Post disturbance effects**

5 Long-term changes depend on drought intensity, duration and the ability of the  
6 ecosystem to recover. The changes are mostly of a morphological and/or chemical  
7 nature, and among others are consequences of ice-induced scour or sedimentation.  
8 Growth of macrophytes and riparian vegetation during droughts can create new  
9 morphological patterns after the event (Gurnell 2014, Gurnell et al. 2016a,  
10 2016b). However after drying, the bare ground undergoes important chemical  
11 changes, increasing phosphate retention and re-oxidisation of sulphur that may  
12 lead to acidification after re-wetting (Baldwin and Mitchell, 2000; Lamontagne et  
13 al., 2006).

#### 14 ***BIOLOGICAL RESPONSE***

15 There are two generally recognized forms of biological response to disturbance:  
16 resistance (the capacity of the biota to withstand the disturbance) and resilience  
17 (the capacity to recover from the disturbance) (Lake, 2000). A third type of  
18 response is opportunistic utilization of habitats that are created by the disturbance,  
19 such as spawning or feeding habitats (e.g., Grift et al., 2001; Welcomme, 1979,  
20 Gorski et al. 2010, 2011, Phelps et al. 2015, Van Looy et al. 2019). Resistance is  
21 observed concurrently with disturbance events, while resilience is expressed  
22 during the post-disturbance phase. Opportunism can be observed in both phases.  
23 Figure 1 represents this concept for the example of floods.

24 Figure 1 here

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

1

## 2 **BIOLOGICAL RESPONSE TO FLOODS**

### 3 **Concurrent response**

4 Floods increase the overall wetted area, although much of this area may be  
5 uninhabitable due to high velocities, suspended solids or chemical loads (e.g.,  
6 Moffett, 1936; Hoopes, 1974). This is followed by change of habitude from, for  
7 example, foraging to refuge seeking (Bolland et al. 2015). In rivers without  
8 floodplains, the consequence is a reduction of abundance and diversity of  
9 macroinvertebrates and juvenile fish (Bischoff & Wolter 2001). Adult fish may  
10 also be affected by displacement and injury caused by moving debris and bed  
11 instability, or by a shortage of food (Jensen and Johnsen, 1999; Lusk et al., 1998;  
12 Weng et al., 2001, Hogberg & Pegg 2015). Extreme events may scour eggs and  
13 prevent hatching (Peterson et al. 2000, Carline and McCullough, 2003; Cowx and  
14 de Jong, 2004; Phillips et al., 1975, Dusterhoff et al. 2017).

15 In terms of opportunism, salmonids for example are well adapted to high  
16 velocities and use floods to reach spawning grounds that are not accessible or  
17 suitable during lower flows (DeVries, 1997). Inundation of the floodplains of low  
18 gradient rivers causes a net increase in habitat area for many fish species, and  
19 offers refuge and foraging habitat (Schwartz & Herricks 2005, Beesley et al.  
20 2014). The available flooded areas will also determine fish productivity, growth  
21 and survival and, accordingly, density of juvenile year classes, especially in spring  
22 (Copp 1989, Holčík 1996, Coops et al. 2008, Gorski et al. 2010, 2011, 2013,  
23 2014). The additional influx of nutrients supports rapidly-growing populations of  
24 macroinvertebrates (Hickey and Salas, 1995). Allochthonous inputs and high  
25 autochthonous floodplain production dominate ecological processes (Humphries  
26 et al., 2014, Davis et al. 2018). This creates an abundance of prey for fish (Allen,  
27 1993; Junk et al., 1989). The abundance of phytophilous and phytolithophilous  
28 species increases due to higher food and shelter availability (Jurajda et al., 2004,  
29 Schomaker & Wolter 2011). However, such a situation is less common during  
30 winter floods.

### 31 **Post-disturbance effects**

32 Overall the most important consequence of flooding is shift of the species  
33 composition towards fish species that are better adapted to, or even dependent on,  
34 floodplain habitats (Bayley, 1991; Jurajda et al., 2006; Maher, 1994; Leitman et  
35 al., 1991, Bischoff & Wolter 2001, Schomaker & Wolter 2011). Due to high  
36 mobility of aquatic organisms, the recolonization of highly disturbed areas rapidly  
37 takes place, although the rate is strongly dependent on availability and quality of  
38 refugia (Magoulick and Kobza, 2003; Townsend, 1989) and species-specific  
39 dispersal ability (Radinger & Wolter 2015, Radinger et al. 2017, 2018).



1 Furthermore, species composition and densities after recovery depend on many  
2 morphological changes caused by floods (Elwood and Waters, 1969).

3

#### 4 **BIOLOGICAL RESPONSE TO DROUGHTS**

##### 5 **Concurrent response**

6 Reduction of habitat area during drought conditions is not only due to a smaller  
7 wetted area, but also to reduced habitat suitability (e.g. due to excessive  
8 temperatures or nutrients). Many fish change their behavior, adjusting to the new  
9 conditions (Elliot, 2000, 2006; Davey et al. 2006, Dekar and Magoulick, 2007).  
10 For organisms that prefer shallow and low-velocity zones (e.g. invertebrates and  
11 juvenile fish), or that are tolerant to high temperature and low oxygen, the amount  
12 of suitable habitat may initially increase (Reid et al. 2013). As wetted area further  
13 declines, the densities of these organisms increase (Matthews et al. 1994, Dewson  
14 et al., 2003; McIntosh et al., 2002). Soon food availability declines and predation  
15 increases. The numbers of invertebrates decline and fish assemblage structure  
16 changes as a consequence (Arthington et al., 2005; Wood et al., 2000, White et al.  
17 2016).

18 In perennial streams, the richness of macroinvertebrate species declines due to the  
19 loss of habitat diversity. In contrast, the same phenomenon leads to local increases  
20 in fish species richness in remnant pools. However, this is an artefact of relocation  
21 of fish from dried up areas (Pires et al., 2010). Again, predation by fish and other  
22 vertebrates becomes a limiting factor for macroinvertebrates (Labbe and Fausch,  
23 2000; Maceda-Veiga et al., 2009).

24 Since large portions of aquatic zones become terrestrial, sedentary and sessile  
25 species such as freshwater mussels are at risk of stranding, desiccation and  
26 predation. The temperature increase in expanding shallow margins also exposes  
27 such organisms to thermal shock (Castelli et al., 2012).

28

##### 29 **Long lasting effects**

30 The overall consequence of drought is a change in species composition towards  
31 drought-tolerant, small-bodied species, i.e. those for which habitat conditions have  
32 actually improved (e.g. Boix et al, 2010, Schomaker & Wolter 2011, Ruhí et al.  
33 2015, Leigh & Datry 2017). As drought persists and water quality exceeds critical  
34 thresholds, the numbers of individuals rapidly declines (Extence, 1981). For fish,  
35 the timing of drought is important, as it may affect sensitive life history stages  
36 such as spawning or egg incubation. This shapes community composition in future  
37 years by potentially causing the failure of entire year classes. Fish and  
38 macroinvertebrates can recover quickly from short-term droughts, but the

1 availability of refugia during the drought is critical for this (Covich et al., 2003;  
2 Fenoglio et al., 2006; Matthews and Marsh-Matthews, 2003). If cease-to-flow  
3 conditions occur, populations may go locally extinct unless aquatic dispersers  
4 have made it to permanent water. Populations can be re-established by subsequent  
5 high-flow events. Recovery from longer-term droughts that span multiple years is  
6 slower because of the smaller pool of surviving organisms. The impacts of supra-  
7 seasonal droughts are difficult to predict because of our limited experience of  
8 these events (Lake, 2007, Ruhí et al. 2015).

## 10 **WHAT AFFECTS THE INTENSITY AND DIRECTION OF BIOLOGICAL** 11 **RESPONSE?**

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

23 *Figure 2 here*

24 Still, the conceptual model in Figure 2 is generic and some studies have found  
25 different results for individual cases (Piniewski et al 2016). One of more  
26 significant covariates causing such deviations is the morphological variability of  
27 rivers and floodplains. The presence of refugia has a direct effect on survival of  
28 animals, and is therefore important for the speed and scale of recolonization.  
29 Spatial variability not only mitigates deleterious impacts by providing refugia, but  
30 also by offering a diversity of habitats that increase richness, abundance, biomass,  
31 recruitment and productivity prior to any disturbance. Habitat shifts also occur for  
32 aquatic biota, caused by changes in discharge and resulting changes in flow  
33 velocities, shear forces and water levels (e.g. Wolter et al. 2016). For example, in  
34 lowland floodplain rivers, the occurrence of hydraulically inhospitable habitats  
35 (i.e. very fast flowing) is compensated for by the creation of vast areas of  
36 attractive spawning and larval rearing habitats on the floodplain (Gorski et al.  
37 2010, 2011, van de Wolfshaar et al. 2011, Stoffels et al. 2015). In high-gradient  
38 rivers, floods create access to tributaries, effectively expanding accessible habitat  
39 area (e.g. Sukhodolov et al. 2009).

40 The intensity of biological response also depends upon factors such as geographic  
41 location and seasonality. For example, a drought of the same magnitude will have

1 different consequences in northern and southern Europe. In some Mediterranean  
2 streams, adaptation to climatic regimes means that fish can survive much more  
3 severe droughts that would be lethal to any northern organisms (Horne et al., in  
4 review).

5 Similar differences in response are seen with the timing of disturbance. For  
6 example, in many rivers of the northern hemisphere severe flooding in summer  
7 has different biological consequences than during the spring (spawning) time.  
8 Since summers are characterized by low-flow conditions, many animals utilize  
9 habitat for rearing and growth, with extensive nursery habitats (Olaya-Marin et al.,  
10 2013). Unpredictable floods (e.g. unseasonal or happening with higher frequency  
11 than in the past) have been documented as having very deleterious effects on fish  
12 assemblages (Bischoff & Wolter 2001, George et al. 2015, Hogberg & Pegg 2015).

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

#### 17 ***PREDICTING IMPACT OF CLIMATE CHANGE ON ECOLOGICALLY-RELEVANT FLOW*** 18 ***REGIMES***

19 A recent work projecting hydrologic response to future weather data derived from  
20 various IPCC global circulation models for the state of New Hampshire, USA  
21 provides some insight on how the climate change could modify hydrologic  
22 patterns (Bjerklie and Sturtevant, 2017). This state wide analysis documented a  
23 common pattern characterised by an increase of higher flows over cold season and  
24 lower flows during spring and summer. The study also projected increased  
25 variability of flows, with changes to the magnitude of baseflows (groundwater  
26 inflow) varying depending on elevation and micro-climatic factors related to  
27 location. The variability of the flow response to climate changes within the state is  
28 demonstrated by comparing flow duration curves of a relatively small coastal river  
29 the Oyster River and the larger Pemigewasset River (Bjerklie et al., 2015).  
30 Although both of them follow the described trend it is more pronounced in the  
31 Pemigewasset River. The Oyster River has little topographic relief and sandy  
32 soils, while the Pemigewasset River is located in the upland and more  
33 mountainous terrain (Bjerklie et al., 2015).

34 The question about the way in which predicted river flow changes will mediate  
35 climate change signal on biota is rather complex due to many confounding factors.  
36 The majority of the model-based climate change impact studies deal with  
37 'ecologically relevant' flow regimes (Dhungel et al. 2016, Döll & Zhang 2010,  
38 Laizé et al. 2013, Morales-Marin et al. 2019, O'Keefe et al. 2018, Piniewski et al.  
39 2014, Stagl and Hattermann 2016, Van Vliet et al. 2013, Vigiak et al. 2018)  
40 whereby 'ecological relevance' is usually assessed based on available literature.  
41 This approach is better suited for large-scale analyses: from global (Döll &

1 Zhang), through continental (Laizé et al. 2013, Van Vliet et al. 2013) to national  
2 (Dhungel et al. 2016) and large river basin scale (O’Keeffe et al. 2018, Stagl and  
3 Hattermann 2016). Predicted effects of climate change on riverine biota are only  
4 implicit in such studies. For example, O’Keeffe et al. (2018) reported a projected  
5 increase in high flow frequency in the Vistula and Odra basins in Poland, which  
6 could be beneficial for northern pike due to more frequent floodplain inundation  
7 and better river-floodplain connectivity. On the other hand, abnormally high  
8 streamflow could wash away the fish and eggs.

9 In a more complex approach, but typically applied at finer spatial scales, climate  
10 change forcing is propagated through a modelling cascade consisting of a  
11 hydrological model loosely coupled with a habitat suitability or a species  
12 distribution model (Jaeger et al. 2014, Kakouei et al. 2018, Kuemmerlen et al.  
13 2015, Morid et al. 2016, Muñoz-Mas et al. 2016, Mustonen et al. 2018, Viganò et  
14 al. 2015, Woznicki et al. 2016). For example, Jaeger et al. (2014) predicted a  
15 higher frequency of zero-flow days in an intermittent stream in Arizona, United  
16 States, which would inevitably lead to more channel fragmentation and a reduced  
17 network-wide hydrological connectivity during spawning of native fish.

18 Yet higher level of complexity can be achieved by including a hydraulic model in  
19 the modelling chain, yet such approaches are typically applied only at small  
20 catchment scales (Guse et al. 2015, Papadaki et al. 2016). Papadaki et al (2016)  
21 showed that the West Balkan trout is likely to expect a deterioration in habitat  
22 quantity and quality in summer months in a mountainous stream in Greece. In  
23 contrast, Guse et al. (2015) reported variable changes in habitat suitability for  
24 fishes in a small stream in northern Germany in response to climate change. They  
25 also predicted a dampened effect of climate change on stream hydraulics  
26 compared to the effects on discharge itself.

## 29 **DISCUSSION**

30 Our review underlines the importance of floods and droughts as a master driving  
31 force of the riverine ecosystems that shape the biotic communities. Each of these  
32 events creates immediate and long lasting modification of habitat conditions for  
33 riverine flora and fauna.

34 This in turn causes specific biological response that leads to change of  
35 composition of aquatic communities, also in short and long term.

36 The response may be in form of resistance, change of habitude and resilience. The  
37 intensity and direction of biological impact may vary depending on location and  
38 particular climatic and physiographic setting of the watershed. The variety of  
39 impact will further diversify if we include other human-induced alterations to  
40 riverine ecosystems. For example, a good demonstration of the consequences of

1 dam construction is presented in a study on the Tana River in Kenya (Langat et al  
2 2019).

3 Nevertheless, the expected overall long term consequence of natural floods and  
4 droughts regime is an increase in biological diversity and ecosystem health. Hence,  
5 floods and droughts can be seen as “rejuvenating” events essential for ecological  
6 equilibrium. Therefore, sudden and dramatic alteration of floods and droughts pattern  
7 as expected in climate change perspective may cause dramatic changes in the  
8 structure and composition of aquatic communities. Quantification of these changes is  
9 therefore key to prediction of biological consequences of climate change. To capture  
10 these modifications descriptive pattern metrics, which are directly related to  
11 biological response need to be identified.

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

17 As presented above the aquatic organisms evolved around the hydrologic events  
18 that are predictable and therefore more common. Hence, the event frequency is a  
19 wave metric most closely related to disturbance predictability and consequently  
20 intensity of biological response. It is in a reverse relationship i.e. the higher the  
21 natural frequency, the higher the probability the less intense the biological  
22 alteration (Figure 3).

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

31 Figure 3 here

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

36 Since floods are generally pulse disturbances, the key attributes related to  
37 biological response are flood **frequency** and **magnitude**. Consequently, there is a  
38 functional relationship between these two metrics and the intensity of biological  
39 impact of floods. In regions where the hydrologic response to climate change is  
40 towards increasing frequency of high flow events, resulting in significant change  
41 to the flow regime, the channel will try to widen and deepen its cross-section to

1 accommodate the more frequent flooding. The time frame for the river to adjust  
2 to a more stable geometry is intricately associated with the time for instream  
3 habitat to adjust. If the response also includes larger flood events, adjustments to  
4 the channel morphology may also include changes to the planform structure of the  
5 river network, including changes to the meandering pattern and associated riverine  
6 floodplain features such as wetlands and ponds. Additionally, changes in flood  
7 frequency and magnitude will markedly change the amount of woody debris  
8 entering the river channel, and the amount of sediment transported to downstream  
9 areas. Subsequently, the relative alteration of flood magnitude and frequency that  
10 is caused by climate change is intricately tied to, and can be indicative of,  
11 biological response to climate change.

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

18 Figure 4 here

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