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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 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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