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Resetting the river template: the potential for climate-related extreme floods to transform river geomorphology and ecology

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SUMMARY

1. Climate change is expected to alter the occurrence of extreme climatic events, including major floods. Future shifts in the frequency and intensity of extreme floods will vary by region and could modify the geomorphological character of riverine habitat.
2. The geomorphological structure of rivers determines the quality and quantity of habitat available for resident biota, and thus, changes to morphology from more extreme floods are likely to affect river ecology over and above the direct effects of the flood events themselves.
3. Extreme floods can exacerbate the effect of multiple anthropogenic stressors, with potentially dramatic effects on freshwater ecosystems. For instance, high flows mobilise nutrients, sediment and toxic chemicals, and aid dispersal of invasive species, whereas land-use change and channelisation impair flood refugia and constrain recolonisation pathways.
4. Extreme floods may also benefit riverine and riparian biota, overwhelming current anthropogenic constraints and infrastructure to increase habitat complexity and floodplain area.
5. Management to protect human life and infrastructure from severe river flooding can alter channel geomorphology, habitat quality and ecology. However, flood prevention engineering that incorporates the natural form of rivers could potentially mitigate anthropogenic flood damage, in turn restoring habitat and historical ecosystem functioning.
6. We examine potential changes in river channel and floodplain geomorphological characteristics resulting from altered extreme flooding regimes and consider likely implications for the management of the world's freshwater biota.

Keywords: climate change, extreme climate events, floods, geomorphology, habitat template, river engineering, river systems

Introduction

Climate change is altering global patterns of precipitation and temperature (IPCC, 2013) and is predicted to modify the occurrence of extreme climatic events, such as heavy rainfall and floods, with potentially dramatic effects on riverine ecosystems (Grantham, Merenlender & Resh, 2010; Aldous *et al.*, 2011; IPCC, 2013). Floods affect riverine organisms directly, by killing or displacing them, and indirectly, by changing food resources and habitat availability that influence post-flood recovery (Death & Zimmermann, 2005; Death, 2008). Although the direct effects of floods on river ecosystems are well known (e.g. Lake, 2000; Death, 2008), indirect effects arising as increasingly large or frequent floods alter geomorphology and habitat remain uncertain.

Changes in geomorphology arising from extreme floods could markedly alter the quality and quantity of habitat available for river organisms. The geomorphological form and function of rivers is a product of catchment geology, drainage network morphometry, riparian vegetation, slope, discharge and sediment supply. These factors in turn determine the distribution, size and variability of habitats such as riffle, run, pool sequences,

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substratum composition and the extent of deposited fine sediment. River hydromorphology is a key driver of ecology enshrined in many conceptual models of river ecosystem structure and functioning (e.g. Vannote *et al.*, 1980; Thorp, Thoms & Delong, 2006). However, how future increases in flood frequency and intensity might affect river geomorphology and benthic habitat is uncertain and remains an important avenue for future research.

Although there may be a perception that the frequency and intensity of floods are already beginning to increase (Jones *et al.*, 2013), the events we observe in some regions currently are no larger or more severe than those that have occurred within the last 200–300 years (Macklin, Lewin & Woodward, 2012; Foulds, Macklin & Brewer, 2014a). Nevertheless, the major challenge for researchers is to apply our current understanding to forecast the hydrological, geomorphological and ecological effects of possible future changes in climate (Table 1). We need to identify the critical hydrological parameters of change, design studies for floods that extend the current hydrological envelope, and increase our understanding of the critical linkages between habitat and ecological mechanisms (Table 1).

Many of the world's river systems have been severely altered by human activities (Vorosmarty *et al.*, 2010). Dam construction, floodplain drainage, water abstraction and water quality degradation all alter river communities and limit the longitudinal and lateral connectivity that confers ecological resilience to recovery from hydrologic extremes. In future, climate change adaptation and catchment management strategies designed to protect infrastructure and human life from intense floods may further modify rivers (Jones *et al.*, 2013; Jongman *et al.*, 2014), yet engineering of river channels and floodplains seldom considers consequences for the instream biota (Gostner *et al.*, 2013; Urbanic, 2014). Although in some regions, such as Europe and U.S.A., river hydromorphology is now being naturalised to mitigate flood effects and restore ecosystems (e.g. Hart *et al.*, 2002; Feld *et al.*, 2011), this is not the case in many parts of the world, including in regions where aquatic biodiversity is high and/or threatened. In all likelihood, many river communities will become increasingly stressed by the intensification of river flow regimes and river engineering to protect human lives and infrastructure in a changing climate.

In this study, we (i) examine how changes in the incidence of large flood events could affect riverine geomorphology and habitat, (ii) evaluate the likely response of biota to these geomorphological and hydrological changes, (iii) discuss how river engineering interventions undertaken to protect humans may interact and inadvertently affect river biota and (iv) make recommendations which we hope will stimulate future research at the interface of geomorphology and ecology (e.g. Table 1).

Table 1 Research priorities to address knowledge gaps on the effects of increased frequency and intensity of extreme floods on river geomorphology and biology

Establish how/whether extreme flood events shape river geomorphology and ecology. For example at what flood magnitude does geomorphological condition change?
Determine which specific hydrological characteristics (e.g. median, floods >3× median, highest flow) are most tightly linked with river geomorphology and ecology, and how they might change with future climate scenarios
Model how increased intensity and frequency of floods interact to affect geomorphology and ecology
Determine how declines in flood intensity and frequency alter natural hydromorphological dynamics and thus ecology
Develop biologically relevant tools for quantification of riverine geomorphology change
Clarify the linkage between changes in hydrology, geomorphology and the availability of critical habitat characteristics
Extend quantitative models linking habitat and abundance of riverine species to identify critical thresholds for species
Downscale global climate and hydrological models to regional and catchment-scale predictions
Create higher resolution maps and predictions of climate change consistent with the scale of species distributions
Develop a river typology of flood response, for example what river or reach types are most sensitive to flood events
Extrapolate dam (and dam removal) studies to make predictions of hydrological change effects on geomorphology and associated river ecology of climate change reductions in flow regimes
Investigate the importance of river channel – flood plain interactions on river communities and how they may differ between river types
Quantify how recolonisation dynamics are affected by increased intensity and frequency of flood disturbance
Establish how recolonisation dynamics are affected by loss of channel and floodplain connectivity from anthropogenic alteration
Determine the threshold flood size from which recovery is not possible for particular species
Determine how climate change effects on terrestrial species feedback to river dynamics and vice versa
Determine how network structure and population fragmentation affect recovery from floods
Quantify how changes in temperature, volume and pattern of flow interact to affect river biota
Establish how current anthropogenic stresses on riverine communities affect their ability to cope with climate-induced flow changes
Determine whether the effects of aseasonal floods are different from those of seasonal floods
Develop species trait database to predict species sensitivity to flow regime change

Climate change impacts on flood regimes

In some regions, climate change is expected to increase the frequency, intensity, spatial extent and duration of large floods (Aldous *et al.*, 2011; Dankers *et al.*, 2014). Extreme floods are defined as flows with a 100-year return interval or those with a 1% exceedance probability (Holmes & Dinicola, 2010). To the best of our knowledge, there are no quantitative models of how these extreme flow events will be affected by global warming but Dankers *et al.* (2014) predict that for up to 30% of global land cover (e.g. Asia), current 30-year return interval floods will increase in frequency to become 1-in-5-year events. On the other hand, for *c.* 20–45% of the globe (e.g. Northern Europe, the Mediterranean and Central America), the expectation is that these 30-year return interval floods will decline in frequency (Table 2).

Scenario modelling of climate change impacts on flood regimes is typically conducted at the global scale using coupled climate, hydrology and land surface models that lack the spatial resolution to accurately predict floods at smaller regional or catchment scales (Aldous *et al.*, 2011). Predictions of change in river flow usually involve downscaling global circulation models and linking them with surface and groundwater hydrological models, often ignoring catchment characteristics that shape local impacts. The accuracy and precision of these later models in turn depends on uncertainty in evapotranspiration rates, catchment vegetation responses to climate change and groundwater recharge (Milly, Dunne & Vecchia, 2005; Aldous *et al.*, 2011). Even within small countries, such as New Zealand, the effect of climate change on hydrological regimes is likely to differ among catchments (Clark *et al.*, 2012). In New Zealand, flows are predicted to increase in snowmelt-fed rivers and decrease in groundwater-fed rivers and to increase in western rivers (exposed to the prevailing winds) and decrease in eastern rivers (sheltered from winds) (Clark *et al.*, 2012). Increasing the spatial resolution of the current global models to predict changes in hydrology at the smaller regional and/or catchment scale will make it easier to link likely hydrological changes to specific species.

The seasonal timing of flow peaks and troughs is also likely to change with the climate, with both high and low flow events potentially occurring out-of-phase with flow-related life history events such as spawning and migration (McDowall, 1990; Delong *et al.*, 2001). Shifts in flood timing could be particularly detrimental in monsoon-driven river systems where biological communities are tightly cued to the monsoonal floods (Arunachalam *et al.*, 1991; Brewin, Buckton & Ormerod, 2000). More extreme changes in flow are also expected to occur, with larger floods following lower base flows and/or more extended periods of extreme low flows (e.g. Werritty, 2002).

Table 2 Flooding projections based on an ensemble of 45 models for the world's Giorgi bioclimatic regions for a 'business as usual' greenhouse gas concentration scenario (RCP8.5)

Giorgi region	Median	Interquartile range
Amazon Basin	49	42–63
Central America	53	39–68
Central Asia	51	39–62
Central North America	40	24–57
Eastern Africa	56	48–71
Eastern Asia	70	59–78
Eastern North America	46	34–59
Mediterranean Basin	54	45–67
Northern Asia	61	50–68
Northern Australia	45	37–65
Northern Europe	65	61–76
Sahara	47	41–57
Southeast Asia	77	56–84
Southern Africa	45	28–62
Southern Asia	78	73–80
Southern Australia	40	22–53
Southern South America	45	38–54
Tibet	48	40–62
Western Africa	61	48–70
Western North America	52	40–65

Data from Richardson (2014) are the median percentage, and interquartile range, of the grid points in each region that show a projected increase (unshaded) or decrease (grey) (only the strongest signal is reported for each region) in the frequency of a 1-in-30-year flood event for 2070–99 relative to 1971–2000.

Geomorphic responses to floods and flow changes

Determinants of geomorphologic structure

River geomorphology is conditioned by a range of variables, including discharge (size and variability), slope, sediment supply and size distribution, riparian vegetation and bank composition (e.g. alluvium or bedrock). These factors set the boundary conditions that determine how river channels respond to flow change. For example, extreme flooding in meandering alluvial rivers is likely to increase sinuosity, and widen and/or deepen the channel, whereas similar floods in bedrock channels may effect little change (Fig. 1). The combination of variables that determine channel form vary continuously, both spatially and temporally, producing a continuum of channel forms in a catchment (Schumm, 1977; Fryirs & Brierley, 2013). Within a particular river reach,

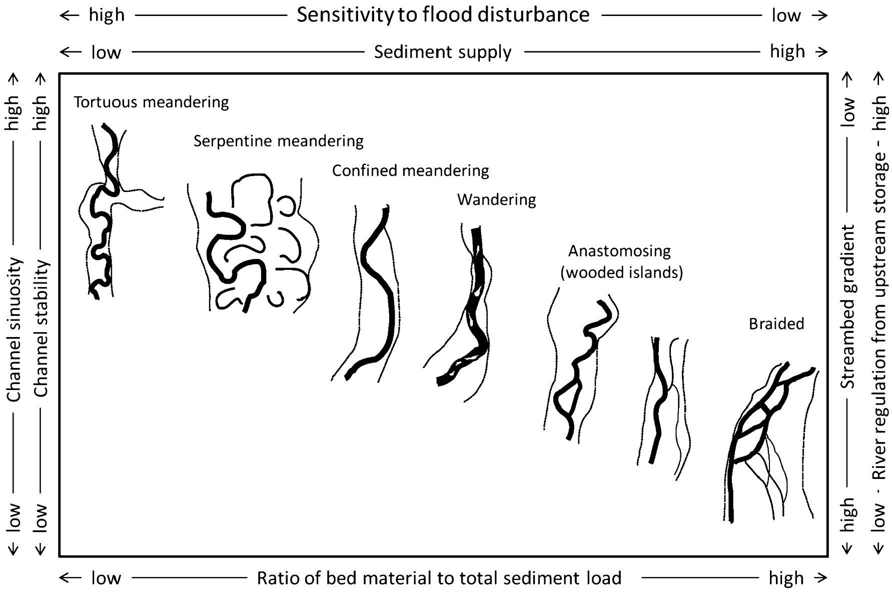

Fig. 1 Continuum of alluvial channel types, after Mosley (1992) (with permission New Zealand Hydrological Society). Sensitivity to flood disturbance increases in the more stable channel forms because these channels are more likely to be significantly perturbed by major flood events, while the less stable channels respond to far smaller and more regular flow events and their morphology is much better adjusted to floods. For example, a '100-year' flood might catastrophically affect a narrow, apparently stable channel (Fuller, 2008), while a similar magnitude flood in a braided river does not generate the same degree of morphological transformation, since the river remains braided.

changes to the composition of morphological units, such as bars, riffles, pools and runs, and changes in substratum size and heterogeneity from floods will also be determined by sediment calibre and channel morphology (Thorp *et al.*, 2006; Poole, 2010; Elosegi & Sabater, 2013).

The influence of a flood event on a reach of river channel and its assemblage of morphological units is thus determined by a range of factors, not least the sensitivity of the reach to changes in sediment supply and size, sediment load, channel sinuosity and stability (Fig. 1; Downs & Gregory, 1995; Brunsden, 2001). Reach sensitivity to external change is greatest where the channel system is primed for instability and lies close to a geomorphic threshold (*sensu* Brewer & Lewin, 1998). For example, removal of a wooded island in a braided channel makes the channel extremely sensitive to further high flows and channel meandering will increase until eventually some new steady state is achieved. Large bedload sediment pulses can also alter river channel pattern (e.g. from meandering to braided) (Fig. 1) (Macklin & Lewin, 1989; Wathen & Hoey, 1998). The extent to which channel form is changed by extreme floods will therefore depend on both the nature of that channel form (Fig. 1) and how close it is to a transition into an alternative channel formation.

Are extreme or smaller floods more important in determining river geomorphology?

The role of floods in fluvial geomorphology has been controversial (Lewin, 1989), with much debate over the relative importance of infrequent large floods versus cumulative effects of frequent small events. Wolman & Miller (1960) argued that channels were broadly adjusted to frequent events, with geomorphic work maximised at a discharge approximate to the modal value for the frequency distribution of floods (Baker, 1977). This implies river morphology should reflect the average flood, such that bankfull discharge (achieved every 1–2 years), rather than extremes, is the most significant geomorphological event for channel development (Leopold & Maddock, 1953). If this is the case, channel systems may adjust to flood events with recurrence intervals (RI) of up to 2 years, whereas smaller events (RI 14–30 times a year) modify morphology created by the 2-year event (Harvey, Hitchcock & Hughes, 1979).

The role of more extreme events in determining channel form is also slowly being recognised (Reid & Frostick, 1994). Geomorphic responses to extreme floods can be catastrophic, resulting in large-scale morphological transformation of reaches (e.g. Hauer & Habersack, 2009; Thompson & Croke, 2013), although where stream power is low, there may be limited impact. Floods of similar magnitude and frequency may thus produce dissimilar morphological responses and accomplish different amounts of geomorphic work depending on the physical thresholds for change within a given reach or system (Costa & O'Connor, 1995). For example, a major flood in the Cimarron River, Kansas, in 1914 initiated large-scale channel widening as stability thresholds were exceeded (Schumm & Lichty, 1963). However, subsequent large floods in the much wider floodplain resulted only in continuous minor floodplain aggradation without any major morphological change because much of the stream power was dissipated over the larger floodplain (Schumm & Lichty, 1963). The debate as to whether bankfull averages or extreme events are more important in the geomorphological structuring of river channels will no doubt gain impetus as the climate changes.

The geomorphological response to extreme floods will also differ among river types globally. Monsoonal-driven river systems, for example, have always experienced large floods and will therefore be less affected by an increasing frequency of extreme events. Analysis of historical and palaeo-records has shown that the frequency of high-magnitude floods in monsoonal-driven rivers has increased in recent decades (Kale, Pramod & Baker, 1997), but with no obvious effects on river morphology (Macklin *et al.*, 2012; Muhammad *et al.*, 2013). Large lowland river systems have similarly been structured for considerable time by large floods and will be unlikely to show major geomorphological response to big floods in future (e.g. Croke *et al.*, 2013b). In contrast, the geomorphology of spring-fed streams and rivers has been influenced by the slow dissolution and erosion of limestone; extreme floods in these systems could potentially cause dramatic change.

Extrapolating to general predictions

Variability in the extent of geomorphic change and response to flood disturbance within and between catchments is strongly affected by local thresholds of flood power, channel configuration and river plan geometry (Fuller, 2007). It is therefore difficult to predict for a given river how substratum composition and size, mesohabitat type (e.g. pools, runs and riffles) and channel movement may change with increased extreme floods. However, the importance of floods for geomorphic maintenance of biological habitat is very clear. Dam construction around the globe has removed or altered flood flows, changing geomorphology and habitat for river biota to the extent that many species are now extinct or threatened (Poff *et al.*, 2007; Liermann *et al.*, 2012). Dam removal studies confirm this with often rapid ecological recovery as flows and geomorphology are restored (Hart *et al.*, 2002; Tullos, Finn & Walter, 2014). We know effects will occur, but not exactly how, where and in what circumstances.

Despite the uncertainties in geomorphic responses to extreme floods, it is possible to make some broad predictions regarding potential responses of river channels and floodplains to an increasing frequency of geomorphically effective floods (Fig. 1). Channels may widen, with increased bed erosion causing channel entrenchment. Deposition of fine sediments will accelerate on channel margins, and channels will straighten (Croke, Fryirs & Thompson, 2013a; Thompson & Croke, 2013). Notwithstanding idiosyncratic responses in individual river reaches, geomorphological change will tend to have consequences for the quantity and quality of habitat for instream biota. For example, channel entrenchment and straightening result in the loss of riffles, backwater and undercut bank habitat that in turn will suppress or extirpate species dependent on these environments. As with ecological systems, understanding and predicting critical transitions in geomorphic responses to extreme floods, from no impact to catastrophic change, is a priority for research (Scheffer *et al.*, 2012).

The importance of geomorphology in riverine ecosystems

Stream ecologists have long viewed river and catchment geomorphology as a key determinant of benthic communities (Hynes, 1970, 1975). River geomorphology forms the basis of many syntheses in stream ecology such as the river continuum concept (Vannote *et al.*, 1980), intermediate disturbance hypothesis (Connell, 1978), network dynamics hypothesis (Benda *et al.*, 2004), shifting habitat mosaic (Stanford, Lorang & Hauer, 2005) and riverine ecosystem synthesis (Thorp *et al.*, 2006; Thorp, 2008). However, although we know the general changes in structure and functioning of river ecosystems as rivers transition from small headwater streams to meandering mid-catchment channels and eventually onto lowland floodplains, we are not able to quantify those changes (e.g. Vaughan *et al.*, 2009; Poole, 2010). For example, we recognise substratum size affects invertebrate communities but do not know what level of fine sediment cover results in communities transitioning from EPT (Ephemeroptera, Plecoptera and Trichoptera) dominance to molluscs, oligochaetes and chironomids (Burdon, McIntosh & Harding, 2013). We know pools are critical for many salmonids, but not what size or density they should be to maintain healthy salmonid populations (Wheaton *et al.*, 2010). More research is needed to quantify the relationships among essential habitat characteristics and identify critical thresholds to maintain healthy populations of target species so these can be maintained or restored as floods and human mitigation of flood effects alter river geomorphology (Table 1).

Although stream ecologists have described the general changes in ecological communities as rivers transition downstream, geomorphologists have worked more explicitly on specific geomorphological changes of river morphology and processes that might affect riverine biota (e.g. Newson & Newson, 2000; Brierley *et al.*, 2010; Poole, 2010). Much of the focus has been on developing a geomorphological typology (e.g. braided, anastomosing, wandering and meandering) for understanding the relative roles of channel-shaping processes, both spatially and temporally. For example, braided rivers have high bedloads, are laterally unstable and are very dynamic morphologically, whereas meandering rivers usually have deeper, more stable channels, with high suspended sediment and more homogenous habitats. Questions remain as to whether these river typologies link with particular assemblages or species (e.g. Vaughan & Ormerod, 2010; Gorski *et al.*, 2013a; Gostner *et al.*, 2013). For instance, does the change from a braided river to a deeper entrenched wandering channel alter biological communities?

The linkages between geomorphology and ecology have been considered most thoroughly within the context of salmonid fishery management (e.g. Kondolf, 2000; Wheaton *et al.*, 2010). The commercial and recreational benefits of salmonids have driven research to understand their geomorphological requirements and determine how these may be affected by human activities, such as water abstraction. Many salmonids require large pools for adult habitat, riffles for invertebrate food and clean, well-aerated gravels for spawning. The geomorphological requirements for a variety of other freshwater fish species have also been determined (Helfman, 2007; Gorski *et al.*, 2013a; Koehn & Kennard, 2013) although less extensively. Geomorphological influences on invertebrates have also received less attention than the Salmonidae, although it is well known that there are differences in invertebrate assemblages between pools and riffles (e.g. Brown & Brussock, 1991; Carter & Fend, 2001), that substratum composition can strongly influence many invertebrate species (Death, 2000; Barnes, Vaughan & Ormerod, 2013) and that disturbance regimes can have a strong effect on diversity and life history traits (Death, 2008; Lytle, Bogan & Finn, 2008; Death & Barquín, 2012). The importance of these geomorphological drivers on riverine biological community structure is often overlooked in more focussed experimental studies (e.g. on disturbance and recolonisation) and really only gets consideration in attempts to place the smaller scale experiments into a larger framework such as the RCC or riverine ecosystem synthesis.

Stream ecologists certainly couch their research within the framework of a riverscape (Fausch *et al.*, 2002; Allan, 2004). But the overriding influence of catchment processes and dynamics (including climate and land-use change) on biology is greatly underestimated because most stream ecologists investigate freshwater ecosystems at dramatically different spatiotemporal scales than most geomorphologists. Few ecologists would investigate the differences in invertebrate faunas between a large gravel-bedded braided river, a deep entrenched bedrock channel river and a low-energy meandering lowland river because the differences, determined by the channel form, are obvious. Instead, most research is focussed on ecological responses to a particular environmental variable, such as human pressure or flow disturbance, within one type of stream or river, usually in only one location. Emphasis should be placed on studies at larger scales to evaluate how river channel and floodplain dynamics interact with the flood regime and sediment supply in different river types, and how this in turn affects the sensitivity of biological assemblages to climate-induced changes in these dynamics (but see Reckendorfer *et al.*, 2006, 2013).

Identification of biologically relevant geomorphic change

Smaller floods (RI 14–30 times a year) are often critical for maintaining suitable habitat and ecological integrity but generally have little effect on geomorphology beyond localised scouring and filling within the active channel (Clausen & Biggs, 1997; Death, 2008). Such small geomorphological effects are critical, however, as they prevent substratum armouring, fine sediment accumulation and excessive periphyton proliferation that can cause cascading trophic changes and reduce ecological condition (Poff *et al.*, 1997; Death, 2008; Lessard *et al.*, 2013). In many regions, ecologically important smaller floods may be lost as precipitation patterns change (Table 2) and/or water abstraction increases (Dewson, James & Death, 2007). For instance, change in Mediterranean climates may increase the occurrence of droughts and reduce floods (Alcamo, Florke & Marker, 2007; Filipe, Lawrence & Bonada, 2013). The ecological impact of such change is uncertain but may be similar to that observed where dams are constructed (Poff *et al.*, 1997).

It is difficult to predict at which point flood magnitude exceeds that to markedly alter geomorphic condition, but when the tipping point is reached, change is often extensive and rapid. As sediment movement drives geomorphic change, large or frequent sediment-mobilising events can accelerate geomorphic change. Erosion and deposition occur primarily in the wetted channel and low elevation bar platforms. However, in more geomorphically sensitive reaches (e.g. steeper slopes, smaller substrata), dramatic habitat change can be effected by even small events (Schwendel, Fuller & Death, 2010). Even in some small headwater streams, significant structural change associated with channel avulsion, bar destruction and bar formation can occur. Nevertheless, the likelihood of channel change typically increases with increasing flood magnitude (Fuller, 2007; Fuller *et al.*, 2012), with geomorphic outcomes contingent upon the steepness and geology of the catchment (cf. Croke *et al.*, 2013b; Thompson & Croke, 2013).

Geomorphic responses to flooding are thus both geographically and temporally highly varied, being both site and event specific. Nevertheless, geomorphic evidence of past floods can be used to assess flood magnitude–frequency relationships and identify flood regimes likely to generate the greatest geomorphic change in particular catchments or regions. Foulds *et al.* (2014b) used dated lichen growing on river boulders to infer past boulder-moving flood events in streams in south-west England. This study extended flood history back to *c.* 1800 and revealed that the period 1820–1940 was a time of widespread and occasionally large floods. Thus, any future geomorphic change is likely to require flood events of greater magnitude and duration then those observed in this period. We require more research along these lines to identify the critical flood size thresholds of geomorphic and biological change in specific rivers. Floods in future that exceed these thresholds are then likely to be those that cause the greatest geomorphic change.

Given the large spatial and temporal variation in the potential geomorphic effects of flood events, it is challenging to make specific predictions about what, how and where biologically relevant changes are likely to occur in response to future extreme events (Table 1). Some of the geomorphological changes that may be driven by extreme flood events are listed in Table 3 with their corresponding likely biological effects. Perhaps the most pervasive changes will result from increasing channelisation and sediment deposition in main river channels, but also from increasing separation of river channels from the floodplain. Within the suite of extreme event characteristics considered in this special issue (frequency, intensity, spatial extent, duration and timing), increases in frequency and/or intensity are likely to have the greatest biological effects. Figure 2 outlines how frequency and intensity interact to alter the driving forces on community structure. Where the frequency of events increases, floods may lack the power to effect geomorphic change, and thus, the recolonisation process will be the major determinant of biological composition, with communities dominated by taxa with strong colonising abilities (i.e. mobile life stages, short life cycles) (Death, 2008). If flood frequency declines, algae and sediment may accumulate, and communities may become dominated by biota tolerant of deposited sediment and poor water quality (Clausen & Biggs, 1997). However, where the intensity of flood events increases, greater geomorphological change may occur, modifying benthic habitat (Fuller, 2007). Increases in the intensity of floods are also likely to result in greater human intervention in channel form, and thus habitat, through engineering to prevent floods (Vaughan *et al.*, 2009). If both flood intensity and frequency increase, then change to habitat and recolonisation dynamics will both be important in shaping community structure.

Biological responses to extreme floods

The effects of more frequent and larger floods

Model forecasts of the future occurrence of extreme floods have a high degree of uncertainty (Milly *et al.*, 2005; Aldous *et al.*, 2011; Dankers *et al.*, 2014). It is therefore difficult to predict the likely impact of changes in the occurrence of extreme flood events on river geomorphology and ecology. By their very nature, studies of extreme floods are also relatively rare and often serendipitous (Hering *et al.*, 2004). The effects of the few studied past extreme events are highly variable, but suggest that the biota is highly resilient to the events unless there are corresponding marked geomorphological changes. Two extreme floods (100-year events) in Germany had relatively minor effects on floodplain beetles, molluscs, plants and instream biota, as geomorphology was relatively unchanged (Hering *et al.*, 2004; Ilg *et al.*, 2008). The main response seemed to be an increase in unvegetated gravel beds and large woody debris and a short-term decline in Carabidae. In contrast, a 100-year flood in an Alaskan glacial river resulted in major geomorphic change with channel incision and narrowing, and sediment deposition with concomitant declines in salmon, macroinvertebrates and meiofauna (Milner *et al.*, 2013). The meiofauna recovered rapidly, salmon abundance recovered within 5 years, but the macroinvertebrate fauna was reset to the composition of more recently created glacial rivers and was slow to recover even after 2 years. It appears the biota is able to recover rapidly from even extreme flow events provided river geomorphology is not also reformed; however, if

Table 3 Geomorphological characteristics and associated habitat changes of biological importance that may be affected by increasing extreme floods

Flood characteristic	Geomorphological characteristic	Instream habitat characteristic	Biological characteristic	Selected references
Intensity/ Frequency	More bank and catchment erosion	More deposited fine sediment	Lower invertebrate diversity	Ryan (1991), Waters (1995), Bond & Downes (2003), Downes *et al.* (2006), Matthaei *et al.* (2006), Herbst *et al.* (2012), Burdon *et al.* (2013)
			Less suitable substratum for fish spawning	Acornley & Sear (1999), Curry & MacNeill (2004), Scheurer *et al.* (2009), Sternecker & Geist (2010), Wheaton *et al.* (2010)
		Greater recruitment of wood into stream channel	More habitat heterogeneity and channel stabilisation	Johnson *et al.* (2000), Pettit & Naiman (2005), Pettit, Latterell & Naiman (2006), Naiman *et al.* (2008)
	More channelised flow	Homogenised sediment size distribution	Changed invertebrate diversity and composition	Minshall (1984), Kunkel *et al.* (2010), Barnes *et al.* (2013)
		Changed hydrological conditions	Changed invertebrate and fish community composition	Lamouroux & Capra (2002), Lamouroux & Souchon (2002), Tharme (2003), Lancaster & Downes (2010), Booker *et al.* (2015)
		Fewer large substratum refugia and microform bed clusters	Lower fish and invertebrate diversity. Slower recolonisation	Matthaei *et al.* (1996), Biggs *et al.* (1997), Matthaei, Arbuckle & Townsend (2000), Matthaei & Huber (2002), McEwan & Joy (2013)
		More scouring of periphyton and macrophytes	Less primary productivity	Robinson & Minshall (1986), Biggs (1995), Biggs & Thomsen (1995), Matthaei, Guggelberger & Huber (2003), Death & Zimmermann (2005), Parsons & Thoms (2007)
		Fewer and smaller pools	Less available habitat for many fish	Jowett & Richardson (1989), Wiley, Kohler & Seelbach (1997), Hayes, Stark & Shearer (2000), Nicola, Almodovar & Elvira (2009), Frank, Piccolo & Baret (2011)
			Fewer pool invertebrates	Brown & Brussock (1991), Brussock & Brown (1991), Rosenfeld & Hudson (1997), Carter & Fend (2001)
		Reduced connection with floodplain or complete loss of floodplain	Fewer refugia and recolonisation sources	Rempel, Richardson & Healey (1999), Matthaei & Townsend (2000), Gray & Harding (2009)
			Less floodplain vegetation	Johnson, Burgess & Keammerer (1976), Auble, Friedman & Scott (1994)
			Lower floodplain ecosystem functions	Gray *et al.* (2011), Pingram *et al.* (2012), Gorski *et al.* (2013b), Reckendorfer *et al.* (2013), Pingram *et al.* (2014)
			Less wet season habitat	Moss (1988), Helfman (2007), Jardine *et al.* (2012), Warfe *et al.* (2013)
		Reduced instream ecosystem functions	Less nutrient, litter and organic matter retention and breakdown	Elosegi, Díez & Mutz (2010), Elosegi & Sabater (2013)
	Fewer ecologically important moderate-size floods that mobilise substrata	More sediment, organic matter and periphyton accumulation	Changed invertebrate and fish diversity, abundance and composition	Clausen & Biggs (2000), Parsons & Thoms (2007), Death (2008)
		More invasive species	Changed invertebrate and fish diversity, abundance and composition	Meffe (1984), Jowett & Richardson (1989), Strange, Moyle & Foin (1992), Jowett & Richardson (1994)

Table 3 (Continued)

Flood characteristic	Geomorphological characteristic	Instream habitat characteristic	Biological characteristic	Selected references
Spatial extent	More widespread geomorphological change	Fewer refugia upstream and in catchment for recolonisation after flood	Less recolonisation	Woodford & McIntosh (2010, 2011)
		More area of riparian riverbed	More habitat for terrestrial riverbed bird, invertebrates, plants and reptiles	Hering *et al.* (2004), O'Donnell (2004), Baxter *et al.* (2005), Keedwell (2005), Steward *et al.* (2011)
Duration	More severe geomorphological change	Fewer species and individual organisms	Slower recolonisation	Limited research on effect of fewer longer floods versus multiple smaller events but see Lake *et al.* (1989)
Timing of extreme flows	Aseasonal flood events		Flood-initiated life history events do not occur, or occur at wrong time of year	McDowall (1990), Poff *et al.* (1997), Helfman (2007), Gorski *et al.* (2010, 2013a)
			Scouring of fish eggs and fry from stream substrata	Erman, Andrews & Yoderwilliams (1988), Montgomery *et al.* (1999), Fausch *et al.* (2001)
			Washing away of nesting birds	Keedwell (2005), Whitehead *et al.* (2008)

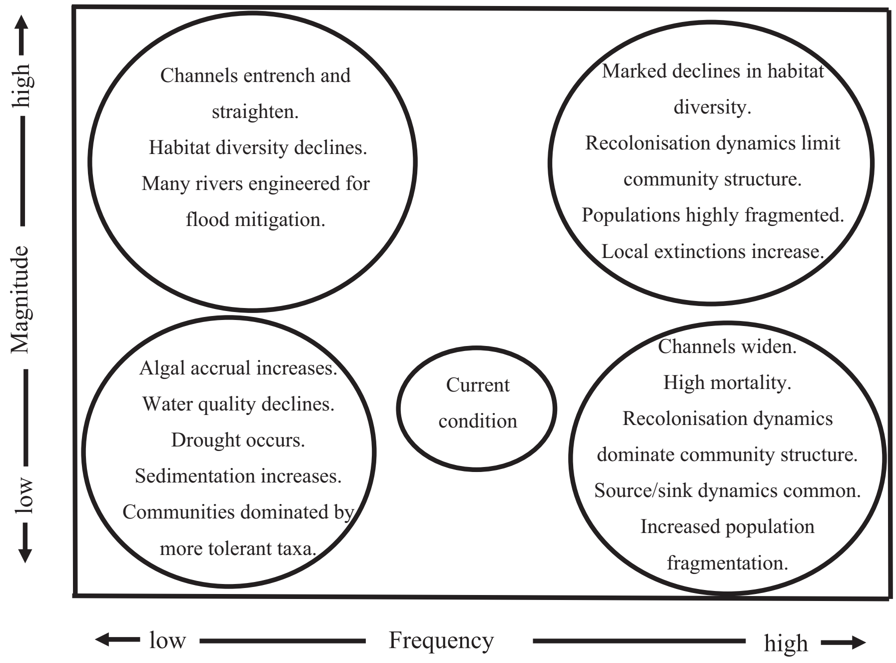

Fig. 2 Conceptual habitat template of the relative importance of extreme flood frequency and magnitude in determining drivers of biological change associated with climate change. Of the five characteristics of extreme floods, increases in frequency and magnitude are postulated to have the greatest influence on biological communities.

instream habitat is dramatically affected, then recover will be much slower, if at all.

While our understanding of the effects of extreme floods is limited, we do know a considerable amount about the effects of current flood regimes on biological communities (Lake, 2000; Death, 2008; Lytle, 2008). Research is needed to expand that knowledge to anticipate the potential effects of the more frequent and severe floods forecast by models. In particular, we need to expand both the temporal and spatial scales of investigation. For example, how important are large historical floods in determining the types of biological habitat available currently (Table 1)? Do floods in rivers disconnected from their floodplains have the same effect on community stability as those in rivers where upstream and side channels are still well linked? In many of the world's river systems currently characterised by frequent floods, we would contend that extreme floods that alter the types and availability of habitat will have the biggest effects on the future structure of river communities.

Floods remove biota from river substrata and they usually recover within weeks (Lake, 2000; Ilg *et al*., 2008; Hauer & Habersack, 2009), yet questions remain as to how recovery rates vary with flood size, frequency of occurrence and refuge availability (Death, 2008, 2010; but see Lake, Doeg & Marchant, 1989). It is uncertain whether there are thresholds of flood size that reduce recovery rates for some species, and how the frequency and intensity of flood impacts are related (i.e. 'Do single large floods have the same ecological impact as several small floods?' (Table 1)). Research is also required to determine the extent to which large floods structure channel geomorphology, sediment characteristics and the frequency of hydrogeomorphic units (pools, riffles and runs) (Croke *et al*., 2013a), and to quantify geomorphology–biology relationships to enable prediction (Elosegi & Sabater, 2013; Urbanic, 2014). For instance, how many pools per km of river channel are required to sustain a riverine *Salmo trutta* population?

Floodplains and extreme floods

Extreme events will also affect riparian communities (Hering *et al*., 2004; Ilg *et al*., 2008). Many organisms are both affected by, and alter, river geomorphology as ecosystem engineers (e.g. riparian trees, wetland plants, macrophytes and beaver) (Pollock *et al*., 1995; Gurnell, 2014). How climate change will affect the distribution and activity of these engineers and how that in turn will feed back to affect river geomorphology is uncertain. Rare extreme events may play an important role in maintaining habitat complexity by recruiting large woody debris into streams (Johnson *et al*., 2000; Hering *et al*., 2004; Pettit & Naiman, 2005). In turn, some ecosystems may modulate disturbances associated with extreme events; wetlands are well known to lessen the impact of high flows (Ogawa & Male, 1986; Acreman & Holden, 2013), while beaver dams can both exacerbate and alleviate flood flows (Hillman, 1998; Andersen & Shafroth, 2010). The feedbacks between the effects of more floods on river engineers and their effects on the floods are difficult to predict. For example, will more wetlands be lost as the climate warms, reducing their flood mitigation services, or will flood intensification increase the areal extent of wetlands, thereby mitigating flood impacts in the longer term? Research at greater spatial scales will be required to consider how these interactions will play out in future climate scenarios (Table 1).

Riparian areas are also critical habitat for many species, and the exposed dry area of river beds created by floods is used by a wide range of birds, reptiles, plants and invertebrates (Baxter, Fausch & Saunders, 2005; Keedwell, 2005; Steward *et al*., 2011). More frequent or more extreme events may in fact yield more habitat for these organisms but changes to the timing and size of floods may also be detrimental to seasonally breeding organisms such as birds (Keedwell, 2005; Ilg *et al*., 2008; Whitehead *et al*., 2008).

Climate change may increase the spatial extent of extreme floods and alter historical routes of recolonisation from disturbances across the riverscape. We have only recently begun to explore the effect of river channel typology on patterns of biodiversity and connectedness in river systems (Rodriguez-Iturbe *et al*., 2009; Hermoso, Kennard & Linke, 2012; Seymour & Altermatt, 2014). Floods maintain river ecosystems by transporting organisms and resources among habitats, but ecosystem health relies on the preservation of refugia, and recolonisation pathways from those refugia, to enable recovery of biota after floods. Widespread flooding could defaunate historical refugia (e.g. floodplains, headwaters, hyporheic zone) and limit recovery. Furthermore, the greater disconnection within river networks as a result of anthropogenic alteration may also limit recolonisation pathways. For instance, fish can recolonise disturbed habitat from estuaries or adjoining rivers but recovery may be limited where connections with source habitats are blocked by dams, culverts, canals or even point sources of pollution (Baker & Montgomery, 2001; Olden *et al*., 2010). We have limited knowledge of the relative importance of potential refugia (Death, 2008, 2010), the specific pathways of recolonisation (Winterbourn & Crowe, 2001; Seymour & Altermatt, 2014) and how they may interact to determine diversity and species persistence (Colomer *et al*., 2014; Mari *et al*., 2014).

It has proven challenging to derive firm predictions about how large floods will impact riverine biota given current gaps in knowledge of geomorphological and ecological responses to extreme events. For instance, the influence of river network structure and population fragmentation on recovery processes remains to be tested for the majority of river biota (Swan & Brown, 2011; Woodford & McIntosh, 2011; Hermoso *et al*., 2012), although recent research on amphibians has begun to explore the relationships between extreme floods, species persistence and recolonisation at the scale of the river network (Colomer *et al.*, 2014; Mari *et al.*, 2014). Restoration attempts on many rivers have highlighted that simply restoring local habitat does not result in community recovery, unless the pathways for species to colonise following restoration or a flood are also present (Blakely *et al.*, 2006; Hagen *et al.*, 2012; Tonkin *et al.*, 2014). Similarly, feedback loops between floods and many natural river engineers remain to be explored to test whether these interactions shift systems to new equilibria or spiral to alternate communities. Although some of the effects of temperature change on these complex biological interactions are known, less consideration has been given to expected increases in extreme floods (Rahel & Olden, 2008; Woodward, Perkins & Brown, 2010). We urgently need more research (see, e.g. Table 1) to quantify how increased (or decreased) levels of flooding influence riverine and floodplain species and their interaction with a changing geomorphology, to evaluate impacts of aseasonal floods, and determine the interaction between floods and multiple anthropogenic stressors.

To focus conservation efforts for river biology in the face of more extreme events, one of the most useful tasks would be to develop a trait-based framework of species responses to hydrological disturbance, just as we have for thermal tolerance, which could be used to map species vulnerability in parts of the world where extreme flood events are forecast to increase. We also need to develop quantitative, simple and cost-effective methods for linking riverine geomorphological characteristics to the organisms that inhabit those geomorphic units (Gostner *et al.*, 2013). As the former are easier to monitor, particularly with increasingly available and more accurate earth observation capabilities, this should provide some early warning as to whether a species habitat is threatened (Diffenbaugh & Field, 2013).

Human amplification of climate change impacts

Multistressor interactions

Increasing extreme climatic events in and of themselves are likely to have a large effect on riverine biodiversity. However, a considerable proportion of the world's waterways are already under extreme environmental stress (Strayer & Dudgeon, 2010; Vorosmarty *et al.*, 2010). Larger floods will thus occur in systems already stressed by high nutrient and contaminant loads, increased deposited sediment, water abstraction, invasive species and a variety of other stressors (Moss, 2010). Staudt *et al.* (2013) argued that ecosystems already severely stressed by a wide range of multiple human pressures are likely to be less resistant and resilient to climate change. Research is now needed to determine whether eutrophic rivers, those with altered flow regimes from water abstraction and those transformed by invasive species are more or less sensitive to changes in flood regimes (but see Gafner & Robinson, 2007). More frequent flooding could result in increased rates of bank erosion and sediment deposition in rivers already choked with sediment slugs. Furthermore, some of the mobilised sediment may contain pollutants, such as heavy metals, from historically contaminated floodplains (Macklin *et al.*, 2006). This has already occurred following major flooding in northern England in 2000 (Dennis *et al.*, 2003) and mid-Wales in 2012 (Foulds *et al.*, 2014a). Recent flooding in mid-Wales resulted in livestock deaths with cattle being poisoned as a consequence of being fed lead-contaminated silage cut from floodplains affected by the summer 2012 floods (Foulds *et al.*, 2014a). Again, we need to give more consideration to how flood-induced interactions with the land will impact instream biota.

The effects of human flood protection activities

The effects of large floods on riverine biological communities will also be exacerbated by engineering work designed to provide flood protection for the increasing threat to human life and infrastructure (Wilby, Beven & Reynard, 2008; Jongman *et al.*, 2014). River management for flood protection (see, e.g. Fig. 3) has tended to focus on maintaining a 'stable' channel form to maximise flood conveyance, which has not usually benefited biota (Darby & Thorne, 1995; Harvey & Wallerstein, 2009). River banks have been protected with concrete and channels straightened, and complexity in geomorphic structure removed, with limited consideration of the interactions between channel morphology and sediment transfer (Darby & Thorne, 1995; Fuller *et al.*, 2011). Where the natural behaviour of the reach or system being managed is not properly understood, engineering failure may occur as the river channel adjusts to remove or work around its imposed engineered 'straightjacket'. Hardening banks and constraining what would otherwise be laterally active channels tend to result in bed scour. This results from excess stream power and deepens the channel. The process is self-perpetuating as the channel deepens, and flows become further confined within-channel and armoured banks, further increasing

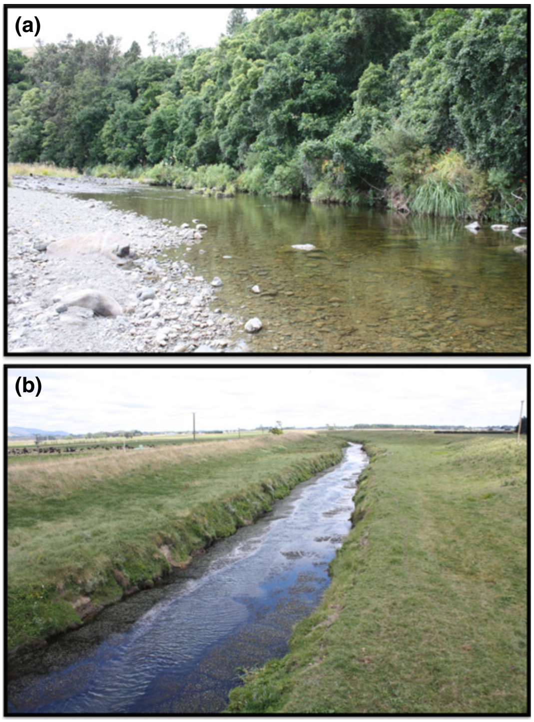

Fig. 3 Tokamaru River, New Zealand, at (a) an unengineered upstream reach illustrating geomorphic and hydrological complexity that supports high biodiversity, and (b) an engineered reach, 8.5 km downstream where the majority of that complexity has been removed.

scour. In containing larger floods and concentrating flows, entrenched channels generate higher transport capacities, resulting in the mobilisation of large volumes of bedload and further bed degradation (Fryirs & Brierley, 2001).

Such degradation is commonly observed in laterally constrained rivers (Gilvear & Winterbottom, 1992; Wishart, Warburton & Bracken, 2008), and these types of channels are frequently engineered, which further reduces geomorphic diversity. In the Rangitikei River in New Zealand, channel straightening to protect urban areas and bridges has channelised a formerly braided river (Fuller *et al.*, 2012), which is now undermining the banks as the channel degrades requiring further engineering works. Engineered reaches thus remain unstable, but often have different dimensions from their natural counterparts.

River engineers are only beginning to consider softer approaches to protecting people and property that allow more natural river behaviour, maintaining and/or restoring connection with the flood plain and in some cases actually restoring river flood plains (Gostner *et al.*, 2013; Urbanic, 2014). Often however, pressure from the public, politicians and insurance companies, and the large number of dwellings that are still built in active floodplains (Macklin & Harrison, 2012) mean the protection of biodiversity is given little or no consideration, even when both people and animals could be protected with a more forward-looking approach. In some regions of the world, policies such as the EU Water Framework Directive (European Commission, 2000) are focussed on improving riverine biological communities through more natural hydromorphology. The Foresight Report (Evans *et al.*, 2004, 2008) and consequent policy changes in the U.K. and mainland Europe also stress working with natural riverine processes to mitigate for extreme flooding, but also to protect, restore and conserve riverine biological communities. This involves modifying riparian areas and floodplains, allowing for natural channel adjustment and encouraging large wood in some headwater streams (Sear & Arnell, 2006).

Flood engineering effects on biology

The geomorphological structure of rivers will determine the species that flourish within them (Parsons & Thoms, 2007; Brierley *et al.*, 2010) and a loss of geomorphological diversity from flood control engineering without consideration of the river's natural form commonly results in a decline in biological diversity (Thorp *et al.*, 2010; Gorski *et al.*, 2013a). Many instream habitats such as larger boulders, logs, backwaters (abandoned channels and chutes), undercut banks and overhanging vegetation are removed to facilitate the rapid removal of water during floods. These all provide habitats for a wide range of biota permanently or during floods. Native galaxiid fish in New Zealand repeatedly sought refuge under particular large boulders during floods despite spending the rest of their time some distance away along the stream reach (McEwan & Joy, 2013). We have limited knowledge of exactly how animals respond just before and during floods. Some fish move away from the main channel, and some invertebrates may similarly be capable of sensing substratum movement and escape to avoid being washed away (Gibbins *et al.*, 2005; Death, 2008; McEwan & Joy, 2013). However, if channelisation and/or fragmentation has removed their escape routes, survival may be impossible. There will clearly be an increasing need for river engineers, geomorphologists and stream ecologists to find more sustainable approaches to flood protection, as in the U.K. and Europe, while at the same time retaining the geomorphological complexity necessary for maintaining biodiversity.

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