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The three Rs of river ecosystem resilience: Resources, recruitment, and refugia

Kris Van Looy[1,2] | Jonathan D. Tonkin[3,4] | Mathieu Floury[2] | Catherine Leigh[5,6] | Janne Soininen[7] | Stefano Larsen[8] | Jani Heino[9] | N. LeRoy Poff[10,11] | Michael Delong[12] | Sonja C. Jähnig[13] | Thibault Datry[14] | Núria Bonada[15] | Juliette Rosebery[16] | Aurélien Jamoneau[16] | Steve J. Ormerod[17] | Kevin J. Collier[18] | Christian Wolter[13]

[1] Institute of Bio- and Geosciences, Jülich, Germany

[2] River Hydro-ecology Lab, Research Unit RiverLY, Irstea Centre de Lyon-Villeurbanne, Villeurbanne Cedex, France

[3] Department of Integrative Biology, Oregon State University, Corvallis, Oregon, USA

[4] School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

[5] Science and engineering faculty, Queensland University of Technology, Brisbane, Australia

[6] Australian Rivers Institute, Nathan, Australia

[7] Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland

[8] Idiv, German Centre of Integrative Biodiversity Research Halle-Jena-Leipzig, Deutscher Pl. 5E, 04103, Leipzig, Germany

[9] Finnish Environment Institute, Oulu, Finland

[10] Department of Biology, Colorado State University, Fort Collins, Colorado

[11] Institute for Applied Ecology, University of Canberra, Canberra, Australia

[12] Department of Biology, Winona State University, Winona, Minnesota

[13] Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

[14] DYNAM Lab, Research Unit RiverLY, Irstea Centre de Lyon-Villeurbanne, Villeurbanne Cedex, France

[15] Grup de Recerca Freshwater Ecology and Management (FEM), Department de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, 08028, Barcelona, Spain

[16] Research Unit Aquatic Ecosystems and Global Change (EABX), Irstea Bordeaux, Cestas Cedex, France

[17] Water Research Institute, Cardiff School of Biosciences, Cardiff University, Cardiff, Wales

[18] Environmental Research Institute, The University of Waikato, Hamilton, New Zealand

Correspondence
Kris Van Looy, Stationsstraat 110, 2800 Mechelen, Belgium.
Email: kris.van.looy@ovam.be

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Abstract

Resilience in river ecosystems requires that organisms must persist in the face of highly dynamic hydrological and geomorphological variations. Disturbance events such as floods and droughts are postulated to shape life history traits that support resilience, but river management and conservation would benefit from greater understanding of the emergent effects in communities of river organisms.

We unify current knowledge of taxonomic-, phylogenetic-, and trait-based aspects of river communities that might aid the identification and quantification of resilience mechanisms. Temporal variations in river productivity, physical connectivity, and environmental heterogeneity resulting from floods and droughts are highlighted as key characteristics that promote resilience in these dynamic ecosystems.

Three community-wide mechanisms that underlie resilience are (a) partitioning (competition/facilitation) of dynamically varying resources, (b) dispersal, recolonization, and recruitment promoted by connectivity, and (c) functional redundancy in communities promoted by resource heterogeneity and refugia. Along with taxonomic and

phylogenetic identity, biological traits related to feeding specialization, dispersal ability, and habitat specialization mediate organism responses to disturbance. Measures of these factors might also enable assessment of the relative contributions of different mechanisms to community resilience.
Interactions between abiotic drivers and biotic aspects of resource use, dispersal, and persistence have clear implications for river conservation and management. To support these management needs, we propose a set of taxonomic, phylogenetic, and life-history trait metrics that might be used to measure resilience mechanisms. By identifying such indicators, our proposed framework can enable targeted management strategies to adapt river ecosystems to global change.

KEYWORDS

disturbance, functional redundancy, recruitment, resilience trait, resource partitioning

1 | INTRODUCTION

Flow-related disturbances, such as floods or droughts, are characteristic phenomena in river systems that can act as a dominant structuring force on lotic communities (Death, 2010; Poff & Ward, 1989; Resh et al., 1988; Townsend, Scarsbrook, & Doledec, 1997). Some river biota can be highly resilient to such disturbances, either by resisting their effects and persisting or by recovering rapidly following disturbance through recolonisation (Naiman, Décamps, & Mcclain, 2005; McCluney et al., 2014). Mechanisms of river resilience are, however, being challenged by human-caused alterations to the characteristic properties of river systems: the primacy of hydrologic disturbance regimes, dendritic network connectivity, and tightly coupled longitudinal and lateral resource flows (Angeler & Allen, 2016; Müller et al., 2016; Oliver et al., 2015). The interplay between climate change, land-use intensification, and human population growth is likely to bring new challenges to the management and conservation of freshwater ecosystems globally, highlighting the need for a better understanding of and adaptive management approaches for ecosystem resilience.

Because a disturbance is an event that disrupts ecosystem and community structure through changes in resources, habitat availability, and/or environmental conditions (White & Pickett, 1985), we can identify three mechanisms for assessing ecological resilience. Floods and droughts induce fundamental disturbances to the ecosystem in three ways (Figure 1): (a) productivity shifts rendering resources unavailable or pulsed, strongly influencing river community assembly and food webs (Junk, Bayley, & Sparks, 1989; Uehlinger, 2000), (b) increasing and/or interrupting physical connectivity, which has repercussions for habitat availability and metacommunity structure (McCluney et al., 2014), and (c) altering environmental conditions, impacting habitat quality and heterogeneity, which regulate community diversity (Lake, 2000; Poole, 2002). These flow regime fluctuations can be seasonally predictable or irregular and unpredictable (Poff & Ward, 1989) and lead to pulse disturbances such as nutrient and sediment pulses, rapid connection disconnection of habitats (e.g., through floodplain inundation), and extreme physicochemical conditions (e.g., highest shear forces at bank-full flows, high temperature, and low dissolved oxygen at low flow).

In contrast to natural pulse disturbances, human-induced alterations, such as flow regime alteration, pollutant inputs, climate change, or habitat degradation, mostly take the character of press or ramp disturbances (increasing gradually or incrementally in intensity) in river ecosystems and their communities (Lake, 2000). Human activities such as land cover modification are at the origin of shifts in the seasonality, frequency, and duration of pulse disturbances and thus challenge river resilience mechanisms. Further, the timing of disturbances may be more important than pulse magnitude in terms of effects on resilience capacity (Woodward et al., 2015; Poff et al., 2018). Floods and droughts in river systems show specific effects on resources, connectivity, and habitat heterogeneity. As a result, organisms respond specifically to events, either in benefiting from resource pulses or avoiding flood disturbance by moving away or to seek refuge in a specific niche, rather than some combination of response mechanisms (McMullen, Leenheer, Tonkin, & Lytle, 2017).

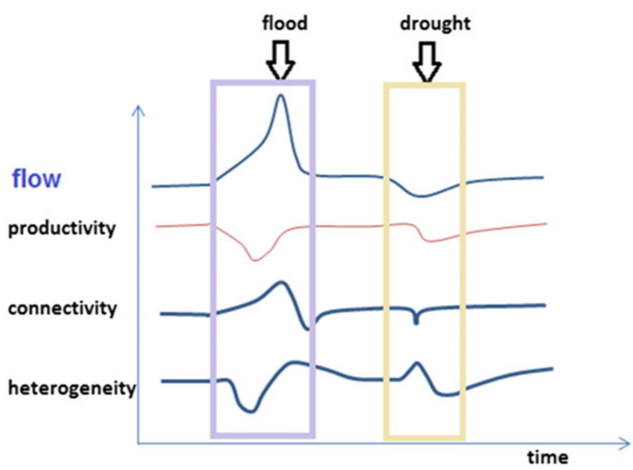

FIGURE 1 River disturbances induced by high ("flood") and low ("drought") flows and potential effects on three distinguished ecosystem properties (based on published works referred to in the text) [Colour figure can be viewed at wileyonlinelibrary.com]

Taxonomic-, phylogenetic-, and trait-based approaches have been proposed to interpret community responses to disturbance across disturbance types, levels of biological organization, and multiple biogeographic regions (Cadotte, Arnillas, Livingstone, & Yasui, 2015; Kremer et al., 2016). The aim of this paper is to present a conceptual framework that enables the core mechanisms of ecological resilience—the "three Rs" of resources, recruitment, and refugia—to be determined jointly and interactively at the river ecosystem and community levels. For this purpose, we (a) identify resource provision/productivity, spatial connectivity, and habitat heterogeneity as the three mechanism axes related to ecosystem response to disturbance, (b) identify resource competition/facilitation, recruitment dynamics, and refugia's functional redundancy as the respective community-level mechanisms, and (c) advise how to operationalize this concept through application of biological indices and species' life history traits, presenting three case studies that illustrate the power of the proposed framework.

2 | THE THREE RS CONCEPTUAL FRAMEWORK

The ensemble of individual species' responses to disturbance through competition/facilitation for resources, movement that avoids mortality, or persistence through adapted traits in specific niches, result in resilience at the community level through one or more of three resilience mechanisms. First, resource competition/facilitation is the mechanism for species that can take advantage of changed (either pulsed or depleted) resource conditions during disturbance. Competition and/or facilitation can occur in response to disturbance-driven resource pulses (Stachowicz, 2001), resulting in a reassembled community following the disturbance. Second, recruitment recovery depends on species' abilities to move through space and time (Heino et al., 2015). This can occur either by active dispersal or by resting stages and serves to avoid disturbance and/or rapidly recolonize afterwards. Recruitment is supported by life history traits such as high mobility and fecundity. Third, functional redundancy in refugia results in persistence of functions at the community level and depends on the variation in responses to environmental change by species within a functional group (response diversity, Elmqvist et al., 2003). Refugia are environments characterized by heterogeneity and continuity in habitat conditions favouring increased species survival and hence functional redundancy, as more species of the same functional group will coexist and show variation in response to disturbance. Species differ in their ability to find and use refugia, but the more heterogeneous the habitat, the more likely many species will survive (Keppel et al., 2012; Scherrer & Körner, 2011).

These types of responses thus reveal three key community resilience mechanisms related to resources, recruitment, and refugia. Because they evolved over time, the prevailing mechanisms will also depend on the ecosystem's historical disturbance characteristics, which vary substantially across climatic, geologic, and land-cover gradients (Rinaldi, Surian, Comiti, & Bussettini, 2015). Thus, we assume that rivers with strong resource pulses will host communities that reassemble more readily, whereas those in river networks with high connectivity can recover quickly through recolonization after disturbance, and rivers with high habitat heterogeneity at local and riverscape scales offer refugia that promote species persistence and functional redundancy.

2.1 | Resource competition/facilitation

Resources and productivity are principal determinants of a community's recovery potential (Brown & Williams, 2015). Resource competition and facilitation are the two opposite interspecies response mechanisms to temporal resource variation. In response to resource pulses, the resilience mechanism at the community level involves internal reorganization, that is, reassembly, based on biotic interactions including intraspecific and interspecific competition and facilitation (Connell & Ghedini, 2015). Resource pulses induce trophic responses at the community level as possible compensatory effects, that are, species' density adjustments to the new resource levels (Connell & Ghedini, 2015). When the disturbances exceed any such compensatory effects, resource scarcity or resource pulses will engender community reorganization through resource competition and facilitation internally or through altered external subsidies between different ecosystem compartments like the river's aquatic and terrestrial riparian zone, depending on food web interaction strength (Altena, Hemerik, & Ruiter, 2016; Yang, Bastow, Spence, & Wright, 2008). Rivers and adjacent terrestrial ecosystems have permeable boundaries that are frequently crossed by two-way resource subsidies, for example, from flooding, insect emergence, and vice versa, for example, floodplain feeding by fish, leaf litter input in autumn (Larsen, Muehlbauer, & Marti, 2016). Adaptations to both pulses and subsidies exist and are reflected in flexible timing in resource use (Holt, 2008).

With disturbances such as floods and droughts, resource availability and abundance can be pulsed (Yang & Naeem, 2008), leading to numerical responses at the population level (de Senerpont Domis et al., 2013; Richardson & Sato, 2015) and indirect effects through subsidies between ecosystem compartments and community functional groups (Greig et al., 2012). Functionally different groups of taxa respond differently to resource dynamics, for example, primary producers may not be detrimentally affected by nutrient pulses but are sensitive to disturbance of light intensity. In contrast, consumers are not limited directly by light availability but depend on undisturbed, continuous organic food resource provision of suitable quality. Furthermore, species' interrelationships can shift from facilitation to competition due to interannual resource dynamics, such as change in

TABLE 1 Identification of characteristic taxonomic, phylogenetic, and functional traits for the three resilience mechanisms

Indices	Resources	Recruitment recovery	Refugia
Taxonomic	Richness/ abundance, Shannon diversity	Taxonomic similarity, beta diversity	Taxonomic richness
Phylogenetic	Species relatedness	Community similarity	Distinctness and diversity
Functional traits	Feeding habits, trophic groups	Dispersal traits, reproduction traits	Habitat guilds and specific life history traits

timing and amplitude of low or high flows or rainfall pulses (Liancourt, Choler, Gross, Thibert-Plante, & Tielbörger, 2012; Tielbörger & Kadmon, 2000).

Table 1 presents taxonomic, phylogenetic, and functional trait indices that can be used as indicators for the resilience mechanisms. For resources, taxonomic indices (Table 1), such as Shannon diversity, which captures changes in species relative abundances, allow inference of community-level consequences of shifts in resource dynamics. Among the phylogenetic indices, species relatedness within a specific order or family can indicate competitive or facilitative responses to resource fluctuation. Closely related species are assumed more likely to overlap in habitat and resource use (Poff et al., 2006). Facilitation can promote phylogenetic diversity, due to longer term effects of mutualism and/or segregation (Angelini et al., 2016). Traits related to feeding habits and guilds should directly reflect changes in resource availability. Traits of trophic position (predator-prey) and strategy (detritivore-omnivore), combined with landscape and habitat specialization (niche breath and selectivity) for aquatic and terrestrial communities of river ecosystems can inform the extent to which resource competition/facilitation and subsidies influence communities and hence indicate their sensitivity to environmental changes (Comte, Murienne, & Grenouillet, 2014; MacLean & Beissinger, 2017). Resource subsidies between ecosystem compartments offer resilience to environmental change and specifically to resource pulses under specific conditions of timing or periodicity. The linkage between resilience, subsidy pulses, and asynchrony between different resources across ecosystems or compartments, is formulated as the subsidy-stability hypothesis (Jones & Lennon, 2015; Richardson & Sato, 2015). Both climate and land-use changes can alter the local productivity and pulsing of resources, potentially disrupting subsidy-stability (Soininen, Bartels, Heino, Luoto, & Hillebrand, 2015). The trait-based representation of these relationships allows for a better understanding of these interactions and can potentially inform adaptive resilience management (Larsen et al., 2016). Current knowledge in this domain of species interactions and food webs already offers tools for assessing strength and resilience of food web interactions (Wootton & Emmerson, 2005).

2.2 | Recruitment

The recruitment mechanism of resilience relies on metacommunity dynamics based on habitat connectivity, species' dispersal abilities, and size of the regional species pool. Many recent works elucidate the role of dispersal, landscape connectivity, and exchange processes in the resilience of communities and ecosystems (Earn, Levin, & Rohani, 2000; Hughes, Bellwood, Folke, Steneck, & Wilson, 2005). River network properties, such as their hierarchical dendritic structure and drainage density (Benda et al., 2004; Coté, Kehler, Bourne, & Wiersma, 2009; Fausch, Torgersen, Baxter, & Li, 2002), as well as the spatial arrangement of habitat patches across the landscape (Erös, Olden, Schick, Schmera, & Fortin, 2012; Grant, Lowe, & Fagan, 2007; Phillipsen & Lytle, 2013), influence how communities are organized and respond to disturbances (Altermatt, 2013; Tonkin et al., 2018). River network configuration may affect community structure through a variety of mechanisms that relate to the relative influence of local and regional processes (Altermatt, 2013; Altermatt, Seymour, & Martinez, 2013; Brown & Swan, 2010). The position of a site within the network may influence the rate at which a site is recolonized post-disturbance; sites at more isolated upstream positions may receive a lower rate of recruitment following disturbances than sites at more central network positions resulting from a poorer connection to the regional species pool (Tonkin, Stoll, Jähnig, & Haase, 2016). Yet the more connected downstream sites may, at the same time, be less resilient to disturbances through a greater level of spatial homogenization resulting from a stronger relative influence of mass effects compared with species sorting (Brown & Swan, 2010).

Recovery of riverine biotic communities is presumed to be largely based on dispersal capacity in metacommunities as source-sink dispersal and drift rates are particularly high in river networks (Heino et al., 2015; McCluney et al., 2014). We may expect that dispersal capacities affect recovery rates, with strong dispersers recovering rapidly depending on proximity to source areas. Specialist dispersal traits can also explain species persistence to extreme disturbance; for instance, benthic invertebrate taxa with mobile larvae and/or terrestrial adult stages prove significantly more resilient to extreme events (Poff et al., 2018). In addition to dispersal, some species may also form seedbanks or resting stages that survive unsuitable periods (e.g., floods or drought-induced drying) inside the sediments. This can be understood as "temporal dispersal" or "travelling in time," observed for both riparian plants (Honnay, Jacquemyn, Van Looy, Vandepitte, & Breyne, 2009) and aquatic invertebrates in intermittent rivers (Stubbington & Datry, 2013) or floodplain soils (Catlin, Collier, & Duggan, 2017). The traits of resting and dispersal stages will determine the rate of community recovery following disturbance. For example, if species' dispersal abilities are poor, recovery may be comparatively slow, and the associations between environmental conditions and community structure become weak (dispersal limitation). On the other hand, if species have strong dispersal abilities, recovery may be faster, and community structure is strongly affected by high dispersal rates through mass effects. Stronger dispersing lotic invertebrates, for example, tend to have more similar communities among sites in river networks than their weaker dispersing counterparts (Datry, Bonada, & Heino, 2016; Leigh & Datry, 2017; Thompson & Townsend, 2006), suggesting a greater ability to recover rapidly following local disturbances. However, recovery rate will also depend on whether invertebrates disperse most strongly by air (e.g., as flying adults) or water (e.g., by drift), with out-of-channel dispersal by air across river reaches and drainage divides being associated with more similar communities among rivers at the landscape scale (Datry et al., 2016; Leigh & Datry, 2017). Recruitment recovery can optimally be measured at the network level, over adjacent sites with a measure of community similarity (beta diversity, Table 1). The capacity for movement or survival to enable recovery is a strongly structuring phylogenetic aspect driven by ecosystem (dynamics) characteristics, measurable as community phylogenetic similarity (Tedesco et al., 2012).

Through their greater connectivity, downstream locations may be more influenced by mass effects (i.e., high dispersal rates from favourable "source" to unfavourable "sink" localities; Pulliam, 1988) than more isolated headwaters (Brown & Swan, 2010) and thus be more resilient through stronger recruitment recovery. In contrast, species sorting should be stronger in headwaters because high dispersal rates typical of mainstems do not interfere with local dynamics in the headwaters (Brown & Swan, 2010; Grönroos et al., 2013). This is especially true for benthic invertebrate communities that appear highly influenced by connectivity to upstream parts (i.e., sources for drift dispersal; Göthe, Angeler, & Sandin, 2013). By contrast, fish community response to disconnection is mostly determined by local conditions in combination with barriers to dispersal in downstream sections (Van Looy, Tormos, & Souchon, 2014). For passively yet efficiently dispersed mobile benthic diatoms, environmental filtering is considered to play a primary role in structuring metacommunities, although the influence of mass effects and dispersal limitation on community structure has also been highlighted in relation to connectivity at larger spatial scales (Bottin, Soininen, Alard, & Rosebery, 2016).

Because the recruitment recovery of riverine biota after disturbance is presumed to be largely based on dispersal capacity and connectivity within and between river networks, the dispersal traits (functional traits, Table 1) of organisms and the physical connectivity of the landscape should interact to moderate resilience (Heino et al., 2017; Tonkin, Altermatt, et al., 2018). This interaction may be species specific with respect to dispersal routes and dispersal rates. For example, even if diatom species dispersal is primarily passive, their metacommunity dynamics appear to be under both local and regional connectivity control, in relation to flow disturbance regimes (Biggs, 1995; Dong et al., 2016; Göthe et al., 2013; Soininen, Jamoneau, Rosebery, & Passy, 2016).

In addition to dispersal capabilities, reproduction traits foster recruitment and recovery after disturbances. Life history traits promoting regeneration comprise high fecundity with the production of many eggs or seeds and seed banks. For fish, multiple spawning (iteroparity) or batch spawning in combination with a protracted spawning season insure successful reproduction at broad ranges of environmental fluctuations.

2.3 | Refugia

Habitat heterogeneity is generally acknowledged to provide ecological resilience to communities through the functional redundancy mechanism driven simultaneously by organisms' response diversity and habitat specialization (Angeler & Allen, 2016). Functionally similar organisms that respond differently to disturbances will sustain the structure and function of communities in space and time (Nash, Graham, Jennings, Wilson, & Bellwood, 2016). Community resilience can result from compensatory interactions among species in response to environmental fluctuations (Angeler & Allen, 2016; Peterson, Allen, & Holling, 1998). Fluctuations in the abundances of species with different adaptive modes to disturbance may be one mechanism stabilizing community function in a varying environment (McNaughton, 1977) and interannual fluctuations of species with broad environmental tolerances another.

Most resilience literature puts forward functional redundancy as the principal mechanism by which communities persist through disturbances (Angeler & Allen, 2016). The response to disturbance is determined in species habitat-specific resistance and resilience mechanisms that are generally described with life history traits that promote survivorship, such as behavioural and morphological traits (e.g., Lytle & Poff, 2004). The mechanism behind functional redundancy is the functional similarity of species in one trait but their speciation or conditional differentiation in others.

The role of landscapes as refugia is ruled by local and riverscape scale environmental heterogeneity, together with the continuity of provision of a habitat mosaic under changing environmental conditions (Keppel et al., 2012; Scherrer & Körner, 2011). River ecosystems offer refugia from disturbance through a mosaic of habitat patches that confer habitat heterogeneity and promote specialization of organisms (Townsend & Hildrew, 1994). The redundancy response to disturbance is most directly indicated by taxonomic richness (Table 1)—under this mechanism vulnerable species are lost to disturbance but afterwards species richness recovers via recolonization during more "stable periods" (Leigh et al., 2016). The changes in taxonomic richness correspond to a constant functional diversity under the functional redundancy mechanism. The continuity and habitat heterogeneity characteristics of refugia should also result in high and persistent phylogenetic distinctness and diversity indicating the longer term community composition impact of the river's disturbance regime.

2.4 | Specific functional traits per resilience mechanism for different biotic groups

For the three R mechanisms, we can identify specific functional traits and levels of community organization. Understanding how communities are shaped by abiotic and/or biotic factors has been an enduring theme in ecology, for example, by analysing species coexistence, species traits, and evolutionary relatedness (Cavender-Bares, Ackerly, Baum, & Bazzaz, 2004; Dijkstra, Monaghan, & Pauls, 2014; Kraft, Cornwell, Webb, & Ackerly, 2007; Múrria et al., 2012; Webb, Ackerly, McPeek, & Donoghue, 2002). In general, species acquire traits and diverge through evolution and selection and are subsequently filtered from the regional pool through abiotic and biotic factors that act on traits (Saito, Cianciaruso, Siqueira, Fonseca-Gessner, & Pavoine, 2016; Webb et al., 2002). In river ecosystems, floods and droughts are thought to be the major drivers of community organization and resilience (Death, 2010; Lytle & Poff, 2004; Resh et al., 1988). Such events indeed can act as strong abiotic filters that might select for specific traits, resulting in functional and phylogenetic clustering of closely related species that have similar traits matching the requirements of their environment (i.e., what is good for one species will be good for closely related species; Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015; Kraft et al., 2007; Saito et al., 2016). The traits fostering resilience should be beneficial and thus conserved in river systems because they have evolved in disturbance-dominated (i.e., flowing) systems. Tolerant, large-bodied taxa may be resistant—some may withstand the variation in currents and also tolerate variation in chemistry, whereas small-bodied taxa may not be resistant but recover rapidly due to short generation times. In addition to size, the shape and ability to resist flow also affects recovery ability. Taxa with high dispersal and regeneration capacity recover fast from disturbances if colonists remain available in the local or regional species pools. The incorporation of phylogeny and evolutionary information into functional-trait-based approaches is one way to understand responses to disturbance.

Many functional trait metrics and indices of disturbance response exist. In fish, for instance, responses to fluctuations of resources have been observed in batch spawning and extended spawning seasons, whereas for recruitment recovery, high fecundity promotes resilience (Table 2). By contrast, multiple spawnings per year increase the probability at least some of the offspring will encounter favourable environmental conditions (Wolter, Buijse, & Parasiewicz, 2016). For benthic invertebrates, mobility by larvae, high drift rates, or a hard exoskeleton (or shell) can provide resistance to flow disturbances (Poff et al., 2018). Further, mobility of all stages is seen as a recovery mechanism to both droughts (Leigh & Datry, 2017) and floods (Woodward et al. 2016; Poff et al., 2018). Dispersal through drift, swimming, and adult flight ability implies important functional traits in this regard. With disturbance, associated resource pulses/fluctuations should mean generalist species with high fecundity and short life cycles (multivoltine) have more chances in recolonization. The refugia and redundancy mechanism, on the other hand, should be promoted by the presence of specialists, like those species that have strategies of oviposition by aerial adults or survive with buried eggs or under anoxic conditions. The nature of the disturbance regime (magnitude, frequency, timing) of individual streams will result in different expectations of which "mechanism" is dominant based on the local spatio-temporal dynamics. For plants, Grime (1974) introduced the C-S-R strategy triangle to classify species according to their response to stress and disturbance. Competitors ("C") respond strongly to the resource conditions and pulses to survive stress and disturbances at the expense of other species in the community; ruderals ("R") have strategies for quick recruitment and recovery after disturbance (like many seeds/long-lived seed banks or strong resprouting roots); and stress tolerant-resistant ("S") specialist species are adapted to the disturbance or present in specific undisturbed niches.

TABLE 2 Identification of characteristic functional trait classifications for the three resilience mechanisms for fish (Wolter et al., 2016), benthic invertebrates (Poff et al., 2006), diatoms (Passy, 2007), and macrophytes (Grime, 1974)

Indices	Resources	Recruitment recovery	Refugia
Fish	Feeding opportunism, habitat generalist, short lived, r-strategy, long spawning season, batch spawning	Fecundity, iteroparity, swimming/ migration ability, small bodied, strong disperser	Habitat specialist, longevity, swimming performance, endemism, k-strategy
Invertebrates	Multivoltine, generalist	Drift, crawling, swimming, flight ability, high fecundity	Resistance forms, eggs, shells, habitat specialist
Diatoms	Generalists/ ubiquists	Strong dispersers (flattened shape)	Resistors
Macrophytes	C-strategy (competitor)	R-ruderal producing many seeds, seed banks, buoyancy	S-stress tolerator-resistor, habitat specialist

3 | FRAMEWORK TO ASSESS ECOSYSTEM RESILIENCE IN MANAGEMENT PERSPECTIVE

To be applicable in river management, the recognition of the three R's and their quantitative assessment with the presented indices requires a framework to infer how the mechanisms described above contribute to community resilience.

The framework in Figure 2 shows the three mechanisms as axes that can be used to measure the strength of resilience, and the arrows highlight the external drivers of specific community resilience mechanisms. Strong resource dynamics drive organisms to resource competition or facilitation; high connectivity allows dispersal and recolonization; and increasing habitat heterogeneity promotes species survivorship and functional redundancy. Hence, community composition as reflected in the prevailing traits indicates the relative contribution of the three specific mechanisms and thus can indicate a community's potential sensitivity and resilience to specific types of disturbance. A community with a majority of good dispersing species, for example, might be vulnerable to strong resource pulses, whereas a community with many trophic or habitat specialists might be vulnerable to changes in ecosystem connectivity or changes in resource dynamics, which might provide opportunities for generalists to dominate. This framework can be applied to measure the community resilience over the three axes, as illustrated in Figure 3 for the example of the lost resilience of the Upper Mississipi River with the river regulation mid-20th century (Example 2 in the box). In this example, the variance of trophic position of fish guilds indicates the functional diversity for the Refugia mechanism. Measured in "decadal trophic position

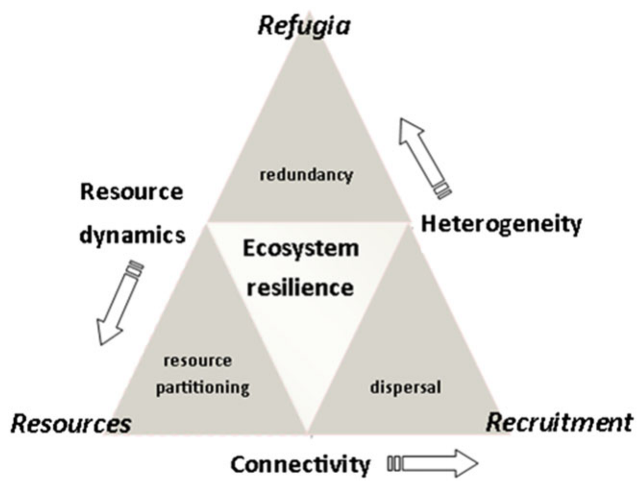

FIGURE 2 Conceptual river resilience framework representing the three mechanisms driving resilience of communities: resource competition/facilitation, dispersal-based recruitment recovery, and refuge-mediated functional redundancy. The extrinsic drivers at the ecosystem scale (arrows) that steer the prevalence of specific mechanisms are resource dynamics, landscape connectivity, and environmental heterogeneity [Colour figure can be viewed at wileyonlinelibrary.com]

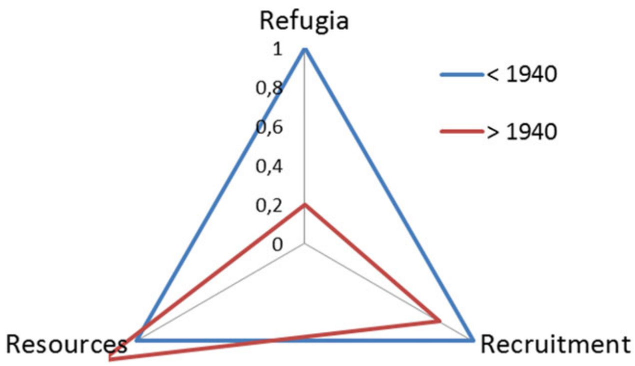

FIGURE 3 Illustrative radar chart presentation of the resilience of the Upper Mississippi River communities of fish before and after the construction of the locks and dams (Example 2 in box). The post-1950 resilience surface is strongly reduced due to diminished functional diversity [Colour figure can be viewed at wileyonlinelibrary.com]

diversity," we observe a strong decrease along the refugia axes. In the resulting resilience surface, recruitment also diminished slightly through partial loss of connectivity by the lock-and-dam construction (loss of diadromous fish species), and resources increased slightly through the increase in peaks of algal blooms due to flow regulation.

In this way, the framework can also inform possible management interventions aimed at river resilience. For resource dynamics, communities characterized by resource resilience traits indicative of specific resource dynamics can be managed around "constraining" or restoring resource pulses and fluctuations, while preserving heterogeneity and connectivity. For recruitment recovery, for communities dominated by species with high dispersal capacities, management should focus on preserving well-connected systems (removing barriers/obstacles for dispersal). Where poor dispersal abilities dominate at the community level connections should focus primarily on lateral connectivity with floodplain habitats. Finally, for refugia, communities with many habitat specialists can be preserved by maintaining habitat heterogeneity and managing for environmental quality conditions (even for extreme conditions such as in alpine streams).

Through the identification of the specific traits of the extant community, the predominant resilience mechanism at the community level can be determined. Consequently, we postulate that the three resilience mechanisms (resources, recruitment, and refugia) are complementary and interact with landscape/ecosystem characteristics, as represented in a three-dimensional framework (Figure 2). The conceptual framework in Figure 2 can help guide the assessment and prediction of patterns of community changes in response to prevailing extrinsic drivers and resilience in response to environmental disturbances.

The listed indices in Tables 1 and 2 are a selection of generally acknowledged resilience traits or indices. Many more examples exist of specific resilience traits and trait-based indices of specific disturbances in rivers such as drought (Chessman, 2009), flow intermittence (Leigh & Datry, 2017), floods (Poff et al., 2018), sedimentation (Glendell, Extence, Chadd, & Brazier, 2013), or pollution (Liess & Beketov, 2011). Here, we emphasize the application of a variety of taxonomic, phylogenetic, and functional traits, to be able to capture the prevailing mechanism. Prevalence of resilience mechanisms at the community level will depend on population density and resources (Oliver et al., 2015; Weaver, Paquet, & Ruggiero, 1996), connectivity and dispersal ability ranging from fine-scale migration (e.g., organisms moving into interstitial spaces of a river bed) to regional scale dispersal (e.g., organisms moving over long distances for reproduction; Pedersen, Marleau, Granados, Moeller, & Guichard, 2016), and landscape heterogeneity and refugia availability (Nimmo, Mac Nally, Cunningham, Haslem, & Bennett, 2015; Pyne & Poff, 2017). Responses to and the relative importance of mechanisms operating at the community level will also vary with the severity and predictability of the disturbance (Dong, Lytle, Olden, Schriever, & Muneepeerakul, 2017; Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017). Accordingly, relative changes of trait composition at the community level might offer strong indications of the dominant mechanisms and the strength of community resilience to specific disturbances.

3.1 | Box examples of application of taxonomic, phylogenetic, and functional trait indices to assess resilience

3.1.1 | Example 1. Need for multiple indices to reflect different mechanisms

The trait-based approaches to appraise the mechanisms behind community resilience can be illustrated using a case study from the Lynn Brianne Stream Observatory (Wales, United Kingdom: see Ormerod & Durance, 2009). A long-term time series of benthic invertebrate communities monitored in multiple catchments shows overall stability in taxonomic richness and suggests resilience to environmental changes (Larsen, Chase, Durance, & Ormerod, 2018). Different responses to environmental change can be inferred from taxonomic and phylogenetic indices (respectively taxonomic richness and taxonomic distinctness, Figure 4) because the two metrics show specific variations that can each be linked to specific types of environmental change, involving large flow variations and high temperatures.

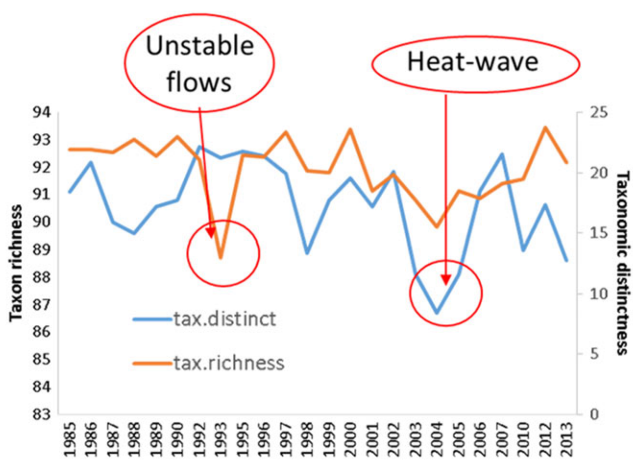

FIGURE 4 Temporal pattern of taxonomic richness and distinctness from a 28-year study of benthic invertebrates at 10 streams in the Lynn Brianne Stream Observatory. Taxonomic distinctness is based on the phylogenetic affiliation among taxa (increasing distinctness indicates assemblages with more phylogenetically distant taxa) [Colour figure can be viewed at wileyonlinelibrary.com]

Taxonomic richness appears more sensitive to the large variations in discharge preceding the spring of 1993, whereas taxonomic distinctness responded more strongly to low flows coupled with the European heat wave in 2003. This might be due to the specific selection effect of increased water temperature that filters out sensitive taxa, thus lowering community distinctness. Conversely, unstable flows in 1993 presumably removed a wide range of species nonselectively to taxonomic affiliation (thus lowering overall richness but not distinctness). Detailed functional trait-based approaches might further help to understand the mechanisms that allow species to withstand specific disturbances and how their responses scale up at the community level (cfr. Woodward et al. 2016). In this case, detailed information on the ability of species to resist flow variations (e.g., higher mobility that allows organisms to move to favourable microhabitats) and drought (e.g., more efficient respiration enables survival with lower dissolved oxygen concentration), could provide important additional insights.

In this case study, a measure of taxonomic richness can indicate the community response in redundancy most clearly, where the phylogenetic diversity provided a strong indicator for recruitment recovery and for selective responses (specialists resistant to heat wave). In conclusion, most studies find that responses are difficult to reveal with single indices and that community-level aspects of niche breath and specialization often are necessary to analyse over longer time intervals to fully detect and interpret responses of communities to disturbances (Larsen et al., 2018).

3.1.2 | Example 2. Resilience lost in the regulated Mississippi River due to diminishing temporal and spatial heterogeneity

A major change in the riverine landscape of the Upper Mississippi River occurred in 1935–1939 with the construction of locks and dams that stabilized summer water levels to maintain a navigable channel during the summer. Applied to a 120-year period encompassing both the predam and post-dam phases, a trait-based analysis detected functional changes in communities based on trophic position and feeding traits of fish, mussels, and snails. Carbon and nitrogen stable isotope ratios were used to calculate trophic position of fish feeding guilds, revealing marked variation in trophic position in response to hydrological conditions during the predam period, whereas reduced variation in trophic position was evident during the post-dam period (Figure 5). In essence, the functional diversity of the communities—observed as variation of trophic position—diminished after 1940 with completion of the lock and dam system, even during periods of both high and low discharge. This loss of resilience identified in loss of functional diversity over the years, is likely a result of changes in niche space, particularly in areas immediately above each dam where habitat heterogeneity has been greatly diminished. Also, changes in resource availability are a contributing factor. Where large shifts in the contribution of benthic and pelagic resources supporting the food web characterized the predam period, this variance was lost with the diminished hydrological variability following the flow modification (Delong & Thoms, 2016; Delong, Thorp, Thoms, & McIntosh, 2011). Managing for restoring the ecosystem's resilience should consider allowing for some degree of flow fluctuation to restore the resource pulses and shifts and at the same time the "original" habitat heterogeneity. Traditionally, most recommendations on dam impact remediation orient to resolving disrupted connectivity. The broader trait-based orientation, proposed in our framework, revealed that resources and habitat heterogeneity are the main drivers to community resilience and should be a key focus of management.

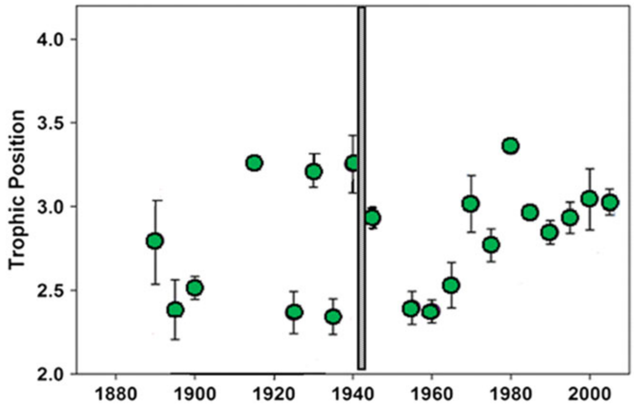

FIGURE 5 The loss of natural fluctuations in the ecosystem leads to a resilience loss, illustrated in the reduced interannual variance in trophic position of fish guilds (loss of natural fluctuations in trophic position of community; mean + *SD*). The mean trophic position of fish over the last century illustrates the reduced interannual variance in trophic position of fish guilds related to changes in hydrology of the Upper Mississippi River. The ecosystem responds to flow regime modifications around 1940, with loss of functional diversity/variability and thus loss of resilience observed in the loss of capacity to respond to changes in hydrological conditions [Colour figure can be viewed at wileyonlinelibrary.com]

3.1.3 | Example 3. Resources partitioning response to climatic disturbance over large spatial scales

The trophic responses of communities to environmental variation can be measured as changes in specific feeding strategies and ratios (e.g., predator-prey) or in composite indices of specialization for feeding strategies and feeding habits, highlighting different resilience mechanisms related to resource provision and pulses. As a case study, analysis of long-term data throughout France has revealed how benthic invertebrates have recovered from decades of water pollution and responded to recent temperature increase, via resource partitioning leading to trophic amplification, that is, the intensification of trophic interactions and pathways through the food web (Floury, Souchon, & Van Looy, 2018; Van Looy, Floury, Ferréol, Prieto-Montes, & Souchon, 2016). This has led to strong responses in community traits related to feeding specialization (measured with a composite trait-based index for specialization in feeding strategies and feeding habits), phosphate reduction (presumably reduced periphyton biomass) and climate warming, that can be described from a more detailed regional scale analysis of feeding specialization for the period 1992–2012 (Figure 6).

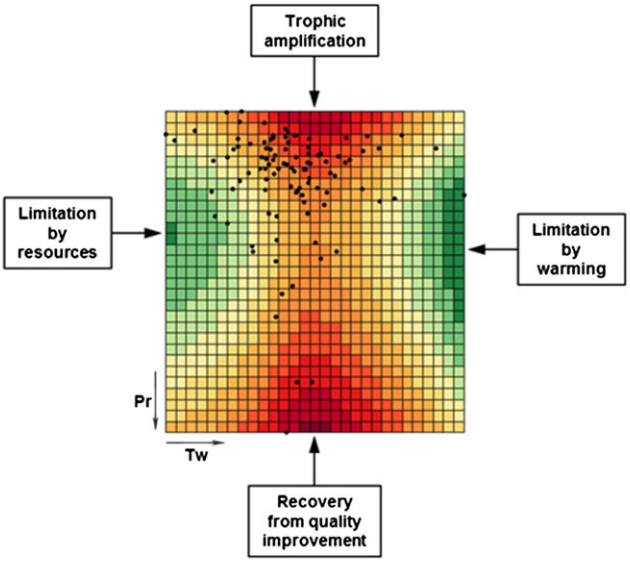

FIGURE 6 Changes in feeding specialization of invertebrate communities in response to long-term trends in phosphate concentration (Pr—Phosphate reduction) and temperature (Tw—temperature warming), for a regional long-term dataset (Auvergne-Rhône-Alpes, France, *n* = 100 sites, 20 years). Green grid cells are associated with a decrease in feeding specialization whereas yellow-to-red colours represent gradual increases in feeding specialization [Colour figure can be viewed at wileyonlinelibrary.com]

A first mechanism (upper sector in Figure 6) reflects long-term increases in feeding specialization resulting from moderate environmental changes (that is, warming) in the absence of marked changes in resources (that is, phosphate concentration). This is the most common case of active resource partitioning that corresponds to the trophic amplification processes where resources are likely to be nonlimiting, allowing moderate temperature increases to enhance productivity and promotes specialists for different resource types (e.g., Yvon-Durocher et al., 2015). Conversely, two mechanisms of limitation—associated with little resilience—resulted where either resources (left sector in Figure 6) or warming (right sector in Figure 6) were likely to limit specialist organisms. In both cases, conditions would provide too few resources because nutrient availability and temperature gain were either too weak or too strong to enhance productivity. Finally, the strongest reduction in phosphates allowed the recovery of vulnerable species (bottom sector in Figure 6) as well as significant increase (recovery) in the proportion of feeding specialists (see Floury, Usseglio-Polatera, Féreol, Delattre, & Souchon, 2013). Consistently with the nationally observed trends, most of the sites studied (c. 70–80%) tended to follow the first mechanism, supporting a predominant effect of trophic amplification.

This case study shows how resilience over large spatial and temporal extents can reflect trophic changes controlling long-term biodiversity patterns and responses to environmental change. Although these observations are sometimes counterintuitive in the global warming context, they reveal how trophic processes can provide insurance against biodiversity loss while underpinning ecosystem resilience (Mori, Furukawa, & Sasaki, 2013; Peterson et al., 1998). It underscores that resource pulses increase resilience for nonresource limited systems, for which the reduced resource competition can apparently increase food web complexity and functional diversity. Such a conclusion, together with the role of resource pulses to subsidies and food web stability in river ecosystems, puts forward a strong emphasis on temporal resource dynamics in management for resilience and adaptation to global changes.

4 | NEEDS AND FUTURE DIRECTIONS

For the proposed trait indices of Tables 1 and 2 to be adopted by environmental managers as resilience indicators, the ranges, boundaries, and projected responses under disturbances for specific environmental conditions need to be determined. For specific conditions, specific rules and indicator values will apply. For example, abundant generalist species might be very resilient under frequent disturbances but recover less after an extreme event; therefore, community resilience will depend on the initial abundance of generalists. This rule might apply differently, however, for large and small rivers. Thus, although we have offered a framework to identify the relative importance of different resilience mechanisms, to truly assess the effective strength of resilience and the specific management options to preserve resilience and thus ecosystem functions and services, a more detailed analysis of environmental conditions and community assets will still be necessary. The signals apparent at the level of communities will depend on whether we focus on taxonomic, phylogenetic, or trait data. It might also be that different time scales operate for different indices in the form of shorter term functional responses (ecological tolerance), midterm taxonomic responses, and longer term phylogenetic responses.

Tipping points are often searched for in resilience indicators, to determine the critical change from one ecosystem state to another (Scheffer et al., 2015). The highly dynamic nature of natural river ecosystems and their pulsed hydrologic disturbances make the presence of alternative stable states implausible (Lake, 2000), rather they exist on a continuum of states in response to antecedent flow conditions. On the other hand, anthropogenically altered flow regimes, patch and habitat dynamics, pollutant input, or resource depletion can be expected to initiate tipping points. Indications for such tipping points have been observed at the scale of the river section in large rivers with artificial embankments causing significant declines in indicators of community diversity (Van Looy, Meire, & Wasson, 2008; Wolter & Vilcinskas, 1997). Moreover, human modified flow regimes have been predicted to induce threshold changes to riparian ecological network properties under future settings (Tonkin, Merritt, Olden, Reynolds, & Lytle, 2018b). Thus, although unmodified rivers are unlikely to experience alternative stable states, modified ones may be more likely to do so (Hilton, O'Hare, Bowes, & Jones, 2006). Human induced pulse disturbances might furthermore be better buffered in river systems than press disturbances. Correspondingly, increased frequency of extreme events associated with climate change might be better buffered due to the pulsed nature of such events than, for example, land use changes (=press or ramp disturbances; e.g., Woodward et al. 2016). The degree to which evolved resilience to pulse disturbances supports communities under human-induced ramp and press disturbances, must therefore also be determined.

On the other hand, high temporal variation and habitat heterogeneity induced by unpredictable flow dynamics may offer a "portfolio effect"—asynchronous dynamics across patches that reduce broad-scale ecological variability—resulting in enhanced resilience (McCluney et al., 2014). The strength of these portfolio effects and metacommunity dynamics, depending on species dispersal traits, river network connectivity, and habitat heterogeneity, is another field for future research as it determines the resilience of river communities to natural and anthropogenic disturbances, including climatic changes (Campbell, Winterbourn, Ta, & McIntosh, 2015; McCluney et al., 2014).

Functional diversity of communities is proposed as a general measure for biodiversity insurance and resilience (Angeler & Allen, 2016). Still, much uncertainty remains for scale sensitivity and issues of functional diversity measurement and meaning. The same difficulty arises for phylogenetic measures. Some traits that confer resilience to extreme flow variations are not always phylogenetically conserved. For example, the ability to fly long distances as an adult insect is phylogenetically conserved, whereas voltinism or size at maturity are more labile insect traits (Poff et al., 2006). Similarly, certain traits indirectly related to resilience are not conserved phylogenetically, such as feeding habits or the type of locomotion (Pauls, Graf, Haase, Lumbsch, & Waringer, 2008; Poff et al., 2006). Labile traits may be more directly related to the environment than nonlabile traits (Poff et al., 2006; Saito et al., 2016; Verberk, van Noordwijk, & Hildrew, 2013), which in turn suggest that labile traits are better indicators of resilience than phylogenetically conserved traits, at least when considering multiple-trait analysis. In this respect, we have to consider the limits to using phylogenetic and evolutionary information in trait-based approaches of community resilience. The integrated assessment of taxonomic, phylogenetic, and functional traits may thus prove more informative than using one class of metrics alone (see also Example 1 above). For instance, in some studies from river systems, phylogenetic diversity facilitated identification of specific response capacities to climate change, information that was not provided by measures of functional diversity alone (Blanchet, Helmus, Brosse, & Grenouillet, 2014; Comte et al., 2014).

5 | CONCLUSION

A framework is proposed to operationalize resilience research into management applications. The constraints that natural and anthropogenic disturbances place on species persistence, species pools, and dispersal have considerable implications for what actions are targeted when and where to maintain and restore lotic systems. Conservation and restoration outcomes depend on the responsiveness of the biotic community to disturbance regimes, pulses in resources, habitat patch mosaics and connectivity, the availability and quality of refugia, and the regional species pool (Tonkin, Stoll, Sundermann, & Haase, 2014), with heavily degraded regional species pools likely to have low resilience to habitat degradation (Stoll, Breyer, Tonkin, Früh, & Haase, 2016). Alternatively, strong potential to withstand changes have been documented in river networks for fish (Radinger et al., 2017), and there are examples of strong recovery after improvement of water quality for river invertebrates (Van Looy et al., 2016) and diatoms (Morin, Lambert, Artigas, Coquery, & Pesce, 2012) due to the influence of the regional species pools and habitat connectivity. River management and restoration projects should thus focus on the entire species pool, metacommunity and habitat mosaic dynamics, and underlying network connectivity and resource dynamics, rather than on monitoring the dynamics of local communities only.

The conceptual framework presented here, together with the examples for assessing resilience mechanisms and community responses, contribute to better understanding and managing for resilience in river ecosystems. The framework has the capacity to inform river managers of how responsive or vulnerable communities and ecosystems might be to human induced disturbances.

6 | GLOSSARY BOX

Resilience: We adopt the original definition of Holling (1973)—nowadays denoted as ecological resilience—as the amount of disturbance an ecosystem (or community) can tolerate and its capacity to reorganize before it loses its original functions. In this definition, both the resistance to and recovery after disturbance are accounted for.

Resource: Here use of this term is not only restricted to only food but also encompasses elements such as light (especially for primary producers), oxygen (anoxic conditions occur in river sediments), substrate (such as bare sediment for riparian plants and ground beetles or gravel and branches for benthic organisms), and temperature (for thermophilic organisms).

Resource pulses: Strong fluctuations in availability of resources occur under pulsed disturbances of floods and droughts in river ecosystems, with consequences to biotic communities.

Resource facilitation: Facilitation is a significant ecological process that produces community-level effects through individual positive interactions. By increasing access to resources, facilitation can impact community structure and diversity. Such interactions are considered "mutualisms" when both species derive benefit from the interaction.

Recruitment: The processes of regeneration and recolonization that follow disturbance enabling the recovery of the biotic community.

Metacommunity dynamics: Metacommunities are determined by exchanges among populations through dispersal. The strength of these exchanges can be affected by disturbances; recruitment recovery determines the rate of return to preceding exchanges.

Refugia: Used here in a wider sense, that is, sites offering (a) refuge to changing environments and (b) continuity in environmental conditions together with habitat heterogeneity offering opportunities for speciation and specialization. Environments with strong gradients in moisture and temperature like fluvial ecosystems are rich in micro and macrorefugia, respectively, at site and landscape scales.

Functional redundancy: A single function can be supported by more than one species (functional equivalence of species) in a community. If one of the species is lost, the function is maintained for the ecosystem. Associated to response diversity of species, this concept immediately leads to a resilience mechanism in refugial environments characterized by heterogeneity and continuity in conditions.

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ORCID

Kris Van Looy https://orcid.org/0000-0001-5436-2320
Aurélien Jamoneau https://orcid.org/0000-0003-1181-2269
Christian Wolter https://orcid.org/0000-0002-2819-2900

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