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Organisms make ecosystems function

Identifying functional indicators of anthropogenic stress in aquatic ecosystems

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CHAPTER 8

PERSPECTIVES ON FUNCTIONAL ASSESSMENT OF ANTHROPOGENIC STRESSORS ON STREAM ECOSYSTEMS

This chapter is based on the manuscript under review by *Freshwater Science*

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ABSTRACT

Both ecosystem structure and function have been given attention in studies assessing the effect of anthropogenic stressors on running water ecosystems. However, few studies have examined to what extent functional assessment can aid surface water quality assessment compared to more traditional measures of ecosystem structure. This study examined how the functional parameters metabolism and decomposition are affected by different anthropogenic stressors. Although some general trends were identified, the overall impact of anthropogenic stressors on ecosystem functioning was complex, as the processes are largely context dependent and there is usually a combination of multiple stressors involved. We provide perspectives on how to deal with these issues in the future. Next, studies that combined structural and functional measures under anthropogenic stressors both from a mechanistic and assessment-based approach were addressed. It became evident from studies combining structural and functional measures, primarily associated with shredders and decomposition rates, that knowledge on the functional roles of individual species is necessary to understand the relation between structure and function. Based on this notion, we explored ideas on how mechanistic understanding of structure and related processes can improve assessment of stream ecosystems in the future. A way forward would be 1) to increase understanding of the role of individual species in the functioning of stream ecosystems, and 2) to quantify the response of individual species to stressors and combinations thereof. We propose that knowledge on suites of interacting traits that evolved under local environmental abiotic and biotic conditions of all organism groups could help to better comprehend multiple stressor effects on ecosystem structure and function, and thereby aid water management in taking more accurate measures.

INTRODUCTION

Over the last decades, both ecosystem structure and function have increasingly been given attention in studies assessing the effect of anthropogenic stressors on running water ecosystems (Dale & Beyeler, 2001; Giller et al., 2004; Young et al., 2008; Von Schiller et al., 2017). Already in 1960, Hynes & Pentelow illustrated patterns in structural and functional parameters after a point discharge of organic waste in a river, using several biological groups and biological oxygen demand as parameters (Hynes & Pentelow, 1960). Structural parameters have since then gained a proven record in water quality assessment, as they are sensitive to a variety of anthropogenic stressors. Communities, especially of macroinvertebrates, are relatively diverse and can thus reflect small changes in species losses (e.g. Clapcott et al., 2012). Moreover, single species trait-based information can provide a causal diagnosis of different anthropogenic stressors (Culp et al., 2011). A large body of evidence is, however, showing that aquatic ecologists should not only study the organisms present within the environment, but also their roles in ecosystem processes or functioning, as changes in species compositions, especially species losses, can alter ecosystem function (Boulton, 1999; Karr, 1999; Loreau et al., 2002; Gücker et al., 2006; Bergfur et al., 2007; Palmer & Febria, 2012). Nevertheless, water quality assessment continued to rely mostly on structural parameters like indicator species, species diversity and species composition (e.g. Rosenberg & Resh, 1993; Bailey et al., 2004). Hereby, a positive relation between structure and function in running water ecosystems is often assumed (Lecerf, 2006).

Studies have considered function from a structural perspective, using food webs (Hladyz et al., 2011a), functional feeding groups (Cummins & Klug, 1979), or other functional traits to better understand and explain ecosystem processes (Dolédec et al., 1999; McGill et al., 2006; Bergfur et al., 2007; Poff et al., 2010; Frainer & McKie, 2015; Raffard et al., 2017; Truchy et al., 2019). However, 'true' ecosystem processes refer to system dynamics, like leaf litter decomposition (Gessner & Chauvet, 2002), ecosystem metabolism (Fellows et al. 2006), primary and secondary production (Wallace et al., 1996; Udy et al., 2006) and the mechanisms behind these processes, like nutrient uptake (Niyogi et al., 2004; Bukaveckas, 2007), carbon flux into the food web (Marcarelli et al., 2011) and oxygen regimes (Cox, 2003). Measurements of functional parameters that provide insights into these "true" ecosystem processes, are relatively inexpensive, straightforward to deploy and in case of metabolism amenable to automation (Collier et al., 2013).

Functional measures inform about how ecosystems operate, while structural measures inform about the condition of the ecosystem (Dale & Beyeler, 2001; Tilman, 2001). A combination of ecosystem structural and functional measures could thus potentially strengthen tools to assess ecosystem integrity and help water management in taking accurate measures (Young et al., 2008; Feio et al., 2010). Although several studies

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have attempted to quantify the response of different stressors on ecosystem processes (e.g. Sponseller & Benfield, 2001; Bergfur et al., 2007; Young et al., 2008; McKie & Malmqvist, 2009; Frainer & McKie, 2015; Bruder et al., 2016; Clapcott et al., 2016; Von Schiller et al., 2017; Frainer et al., 2018), few examined to what extent functional assessment can aid surface water quality or status assessment compared to more traditional measures of ecosystem structure (but see Pascoal et al., 2001; Hagen et al., 2006; Death et al., 2009). Therefore, the purpose of this paper is to provide more insight into the use of ecosystem function in relation to structure in the assessment of anthropogenic stressors on running waters. Hereby, we focused on two main questions: 1) Do functional parameters add to the understanding of the effects of anthropogenic stressors on streams and rivers?, and 2) Do structural and functional parameters provide complementary information on the effects of anthropogenic stressors on streams and rivers?.

We focused on stressors that are commonly caused by human activities and that show general effects on ecosystem structure and functioning, including warming, light increase, nutrient and organic loading, hydro-morphological modification and chemical stress (Birk et al., 2012; Hering et al., 2015). Stress from invasive species was excluded, as their impact on the ecosystem is dependent on the ecology of each species and therefore difficult to generalize (Von Schiller et al., 2017). As functional parameters we included ecosystem metabolism (primary production and respiration) and decomposition of particulate organic matter, which have previously been suggested to be suited for water quality assessment, as they are sensitive to anthropogenic stressors and relatively easy and inexpensive to measure (Young et al., 2008). As structural measures we focused on the most commonly included biological groups, i.e. bacteria, fungi, algae, macrophytes and macroinvertebrates. We did not include all papers published on this topic, but rather attempted to have looked at a relevant set to provide insight and perspectives on whether functional assessment can assist water management in making more effective decisions, building on three major review papers in the field (Webster & Benfield, 1986; Young et al., 2008; Tank et al., 2010).

We start by examining how ecosystem processes (i.e. metabolism and decomposition) are affected by different anthropogenic stressors. Next, we discuss that this relation is context dependent and usually involves a combination of multiple stressors. We provide perspectives on how to deal with these topics in the future. Then we address studies that combined structural and functional measures under anthropogenic stress both from a mechanistic and assessment-based approach. Lastly, we explore ideas on how mechanistic understanding of structure and related processes can improve assessment of stream ecosystems in the future.

METABOLISM UNDER ANTHROPOGENIC STRESSORS

Metabolism is the flux of matter and energy within a stream, encompassing photosynthetic fixation of inorganic to organic carbon, and respiratory loss or mineralization of organic to inorganic carbon (Odum, 1956; Woodwell & Whittaker, 1968; Chapin et al., 2006). Primary production in streams is performed by algae, bryophytes and aquatic macrophytes, while all life forms respire to carry out metabolic activity (Figure 1; Likens, 1975; Brown et al., 2004). Metabolism is usually estimated from measurements of the diel change in dissolved oxygen (DO) concentration in the open channel or by enclosing part of the stream in an air-tight chamber and measuring DO changes in the chamber (Tank et al., 2010; Staehr et al., 2012a). Both techniques estimate metabolism with inherent uncertainty. For the chamber methods containment artifacts and scaling issues are problematic, while for the open-system methods uncertainty is associated with the estimates of DO diffusing between the air and water (reaeration rates). These technical issues are further discussed elsewhere, e.g. Staehr et al. (2012a) and Demars et al. (2015).
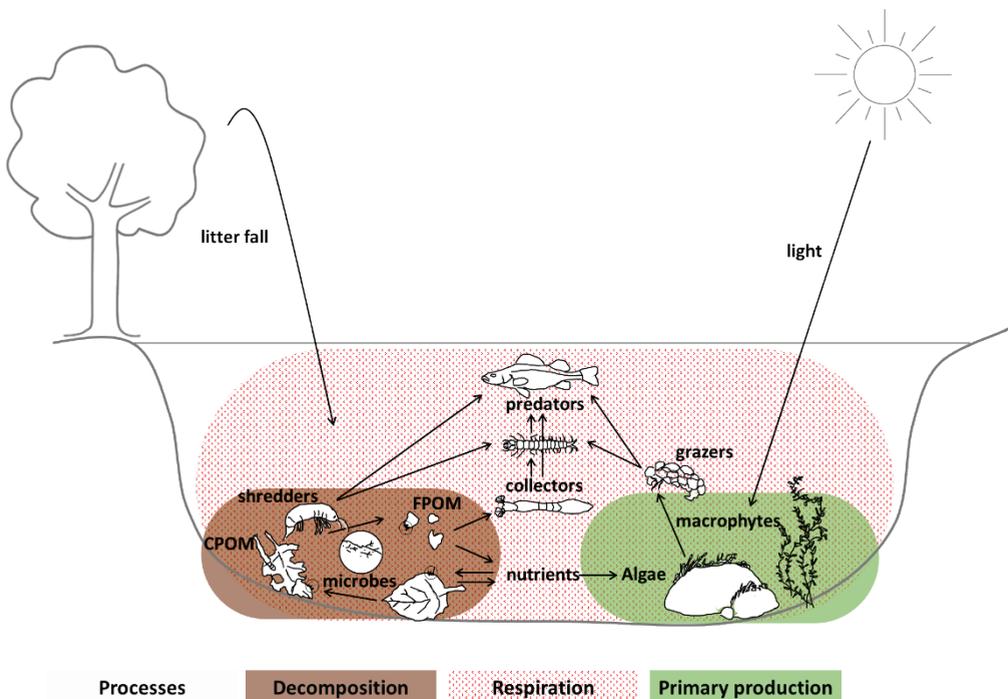

Figure 1: Aquatic food web structure in relation to ecosystem processes (primary production, respiration and decomposition).

Light and nutrients are required for photosynthesis and generally lead to higher primary production (e.g. Phinney & McIntire, 1965; Steinman & McIntire, 1987; Bott et al., 2006; Dodds, 2006; Bernot et al., 2010). An increase in these parameters is termed stressors when acting as a debilitating agent or i.e. setting ecosystems in a self-reinforcing motion that creates further degradation (Odum et al., 1979). A positive link is also frequently observed between primary production and warming of stream water. Warming may increase primary production through increased temperature-dependent physiological rates and changes in the trophic structure (Phinney & McIntire, 1965; Petchey et al., 1999; Rasmussen et al., 2011), however, this positive relation is presumably also mediated through increased light availability (Young et al., 2008). The impact of organic pollution is ambiguous as some studies observed an increase (Quinn & McFarlane, 1989; Paul & Meyer, 2001; Bott et al., 2006; Gücker et al., 2006, Aristi et al., 2015) and others a decrease in primary production (Meyer & Edwards, 1990; Minshall et al., 1992; McTammany et al., 2003; Rodríguez-Castillo et al., 2017). Aristi et al. (2015) argued that the specific impact of organic pollution is related to whether the increased nutrient supply promoted activity of primary producers or whether the reduced light availability suppressed the activity of primary producers. In terms of hydrological stress, studies commonly observed a decrease in primary production under high flows and floods (e.g. Uehlinger et al., 2003; Roberts et al., 2007; Val et al., 2016), while the opposite was the case for low flows and droughts (e.g. Marcarelli et al., 2010; Acuña et al., 2010; Val et al., 2016). High flows and floods generally related to decreased substrate stability and the resulting increase in turbidity may reduce light conditions (Uehlinger, 2000; Morgan et al., 2006; Leggieri et al., 2013). Furthermore, scouring may reduce the biomass of epiphytic and benthic algae and abundance and diversity of macrophytes (Riis & Biggs, 2003; Vilches & Giorgi, 2010) and as such reduce primary production. Other authors have, however, reported that after a flood epiphyton was more productive because of the greater availability of nutrients (Stevenson, 1990). Low flows and droughts may enhance primary production through increased substrate stability, reduced shear stress on periphyton, enhanced macrophyte establishment, increased light availability and increased nutrient concentrations due to decreased dilution (Marcarelli et al., 2010; Val et al., 2016). Morphological alterations of natural streams are diverse, ranging from the removal of large instream wood to the construction of new artificial channels (Elosegi & Sabater, 2013). The change in primary production due to morphological alterations is, therefore, dependent on whether the channel cross-sectional area is increased or decreased, resulting in different flow velocity patterns, shear stress and sediment transport (Gücker et al., 2009). Lastly, toxicants and other forms of chemical pollution may inhibit primary production if the present algae and macrophytes are sensitive to the particular substance (Peters et al., 2013), however, this effect may be offset by

nutrients in toxic discharge (Young et al., 2008) or by a reduction in grazers (Niyogi et al., 2002).

Respiration is primarily driven by the availability of labile organic matter and temperature, and to a lesser extent nutrients (Bernot et al., 2010). Both organic pollution and increased nutrient loading form a subsidy for microbial processes and thus generally result in increased respiration (e.g. Mulholland et al., 2001; Roberts et al., 2007; Aristi et al., 2015). Warming is also often related to enhanced respiration as temperature is an important regulator of metabolic activity (Phinney & McIntire, 1965; Sinsabaugh, 1997; Acuña et al., 2008; Rasmussen et al., 2011). The sensitivity of respiration to temperature may, however, be obscured by the quantity and quality of organic matter in the stream (Mulholland et al., 2001; Acuña et al., 2004; Jankowski et al., 2014). For example, in the study of Roberts et al. (2007) high temperatures coincided with low organic matter availability during summer and thus resulted in reduced respiration. No impact of light availability on respiration is expected, as processes that contribute to respiration are not necessarily dependent on light (McTammany et al., 2007; Young et al., 2008). Light availability could, however, be related to respiration if algae are responsible for a large portion of respiration in the stream (e.g. Benson et al., 2013). Little is known to what extent hydro-morphological changes impact ecosystem respiration (Elosegi & Sabater, 2013). Increased flow may enhance respiration through the input of organic matter, while the transport capacity of organic matter decreases during low flow events (e.g. Roberts et al., 2007; Val et al., 2016). In other streams, a small reduction in respiration was observed after floods and an increase after droughts (Acuña et al., 2004; Uehlinger et al., 2003; Uehlinger, 2006). This difference is presumably related to the differences in stability of the bed sediment between streams (Uehlinger & Naegeli, 1998). The effects on respiration from scouring during flooding may be restricted, as microbes are protected from abrasion in the hyporheic zone (Uehlinger & Naegeli, 1998; Chester & Norris, 2006; Benson et al., 2013). Like primary production, the effect of toxicants and other chemical pollution on respiration is dependent on whether a shift in community can compensate for toxicant induced species losses or whether other stressors cancel out the effect of toxicants (Schäfer et al., 2012a).

DECOMPOSITION UNDER ANTHROPOGENIC STRESS

Decomposition, the loss of detrital mass over time, takes place through several interacting processes, including leaching, microbial (fungal and bacterial) and macroinvertebrate activities and abrasion (Figure 1; Webster & Benfield, 1986; Graça, 2001). These processes are subject to the chemical and physical properties of organic matter, the microbial and macroinvertebrate community present and the environmental factors (Webster & Benfield, 1986). Estimates of decomposition rates are mostly based on the measurement of mass loss of leaves incubated over a certain period in the stream (Meyer, 1980; Boulton & Boon,

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1991). Decomposition in coarse-mesh bags is affected both by physical fragmentation, invertebrate and microbial activity, while in fine mesh bags it is mainly affected by microbial activity (Gessner & Chauvet, 2002). These litter-bag studies may, however, overestimate the importance of macroinvertebrates to decomposition rates as losses of incompletely decayed fragments from physical and biological fragmentation are included in the estimates (Brinson et al., 1981; Heard et al., 1999; Lepori et al., 2005; Friberg et al., 2009) and shredders may aggregate on experimental leaf packs when litter resources in streams are rare (Tiegs et al., 2008). Other factors causing variation in the results are, for example, the intra- and interspecific variability in quality (e.g. nutrients ratios) of the incubated leaves (Gessner & Chauvet, 1994; Suberkropp & Chauvet, 1995; Lecerf & Chauvet, 2008), incubation time (Bergfur et al., 2007) and natural variation in external factors, like seasonality (Frainer et al., 2014; Frainer & McKie, 2015) and inter-annual variability (Yeung et al., 2018).

A systematic quantitative assessment of litter decomposition across a gradient of nutrient enrichment at the continental scale by Woodward et al. (2012) showed that breakdown rates are low at both ends of the nutrient gradient. Microorganisms can assimilate nutrients from the water column, resulting in higher rates of decomposition when there is external nutrient loading, with the largest effects when background nutrient concentrations are low (Suberkropp & Chauvet, 1995; Woodward et al., 2012; Ferreira et al., 2015; Jabiol et al., 2019). This positive effect on decomposition rates by microbes may, however, be counteracted by a reduction in shredder abundance when elevated nutrient concentrations result in low dissolved oxygen levels (Hagen et al., 2006) or other stressors deteriorating the environmental conditions (Woodward et al., 2012). Similarly, organic pollution can lead to a rapid decline of dissolved oxygen, which frequently coincided with slower decomposition rates (Chauvet, 1997; Pascoal & Cássio, 2004). Both field and laboratory studies demonstrated that warming results in faster breakdown rates, particularly related to microbial processes (see review by Webster & Benfield, 1986). High flows are generally associated with increased decomposition rates, which may relate to enhanced physical fragmentation (Heard et al., 1999; Lepori et al., 2005; Paul et al., 2006) and changes in the consumer community (Gaudes et al., 2009). Especially in autumn, enhanced decomposition rates may be related to increased sediment transport and high current velocities (Ferreira et al., 2006b). Low flows, droughts and morphological alterations generally resulted in lower decomposition rates, because conditions became unfavorable for key shredders species (Gelroth & Marzolf, 1978; Schlief & Mutz, 2009; Mendoza-Lera et al., 2012; González et al., 2013) and fungal performance decreased or ceased (Bruder et al., 2011). The sensitivity of macroinvertebrates to reduced flow depends on the species and the amount of flow reduction (Dewson et al., 2007a) and in some cases no change in macroinvertebrate composition and decomposition was observed after flow reduction (e.g.

Dewson et al., 2007b). Furthermore, decomposition of organic substrates in intermittent and ephemeral streams is affected by drying-rewetting cycles (Fierer & Schimel, 2002) resulting in higher leaching effects (Shumilova et al., 2019). Decomposition was usually slower in streams impacted by toxic pollution and other chemical stressors, such as metal pollution (Carlisle & Clements, 2005; Chaffin et al., 2005), pesticides (Schäfer et al., 2007), acidification (Dangles et al., 2004) and salinity (Schäfer et al., 2012b). Meta-analyses by Peters et al. (2013) and Ferreira et al. (2016) showed that the effect of pesticides and metals was more evident in the presence of macroinvertebrate decomposers than when only microbes were involved in decomposition. Tolerant microorganisms may be able to replace sensitive species, maintaining their function (Blanck, 2002; Feckler et al., 2018).

CONTEXT DEPENDENCE OF FUNCTIONAL PARAMETERS

Although some general trends of anthropogenic stressors on ecosystem functioning were identified, the overall response is complex as the processes largely depend on site-specific factors (Tank et al., 2010). First, site-specific abiotic factors may impact how anthropogenic stressors affect ecosystem processes, e.g. temperature and pH can strongly affect toxicant bioavailability and subsequently cause high variability in the effect on ecosystem functioning (Peters et al., 2013; Ferreira et al., 2016). These abiotic factors may also vary in time and space. For example, Frainer & McKie (2015) found that the changes in decomposition along a land-use gradient with increasing nutrients became less obvious due to the loss of detritivore functional diversity along the gradient in autumn and effects were completely offset by a shift in functional trait composition in spring. Beside temporal and spatial scale, habitat heterogeneity can lead to different functional responses (Collier et al., 2013). Second, the presence of dominant taxa can influence the effect of a stressor on process rates (Dangles & Malmqvist, 2004). This is particular evident in decomposition studies where the impact of stressors on specific species of amphipods (Dangles & Guerold, 2001; Dangles et al., 2004; Lecerf et al., 2006; Piscart et al., 2009; Rasmussen et al., 2012b), isopods (Bergfur et al., 2007), caddisflies (Robinson et al., 1998; McKie et al., 2006) and stoneflies (Carlisle & Clements, 2005) caused significant differences in decomposition rates. Furthermore, dominant functional feeding groups may change along a stressor gradient, as was shown for an acidification gradient by Layer et al. (2013). The authors showed that the resistance of a dominant generalist herbivore-detritivore delayed the recovery of specialist grazers along the acidification gradient, and thereby may delay functional recovery. Third, the impact on functioning depends on the length and position of the studied stressor gradient. In moderately stressed systems process rates may increase, while process rates may be suppressed under influence of high stress, which can lead to a non-monotonic response (Niyogi et al., 2002; Hagen et al., 2006; Young & Collier, 2009; Clapcott et al., 2010; Woodward et al., 2010). Studies comparing process rates in reference streams to one level

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of alteration of the stream or a short section of the gradient may lead to different results (Woodward et al., 2012; Feld et al., 2016).

It is thus important to consider the impact of abiotic factors in time and space, the presence of dominant taxa and the length and position of the stressor gradient when studying the impact of anthropogenic stressors on ecosystem functioning. A histogram can, for example, be used to check the range and distribution of stressor values, which can be compared to values reported previously in the targeted ecosystem (Feld et al., 2016). Moreover, Truchy et al. (2019) provided a valuable approach to partition the influence of context dependence, in their case spatial structuring and community composition, from the effect of environmental variables on ecosystem functioning using variance partitioning analysis. Such an approach can potentially increase the explanatory power in studies on ecosystem processes (Truchy et al., 2019).

MULTIPLE STRESSOR EFFECTS ON FUNCTIONAL PARAMETERS

Anthropogenic activities commonly result in changes in multiple stressors (Ormerod et al., 2010), e.g. agricultural activities can result in increased nutrient loading, decreased oxygen concentration, increased concentration of pesticides, sedimentation and removal of riparian vegetation. However, frequently studies focus on the effect of a single stressor in isolation, even though this stressor may not be limiting or influencing the functional response (Clapcott et al., 2010). For instance, the removal of riparian vegetation results in more available light for which one would expect an increase in primary production, but removal of vegetation can also increase turbidity through sediment runoff decreasing primary production (Young & Huryn, 1999; Frankforter et al., 2010). The removal of riparian vegetation may also limit the distribution of shredders, e.g. directly by removal of egg deposition structures or indirectly by altering the quality of allochthonous inputs and thus influence leaf breakdown rates (Sponseller & Benfield, 2001). Further, interacting stressors may lessen (antagonism) or amplify (synergism) the effects of each individual stressor (Piggott et al., 2015). Synergism was, for example, observed by Matthaei et al. (2010) when the negative effects of fine sediment inputs on algal production were stronger at reduced flow. In the study of Bruder et al. (2016) stressor interactions associated with agricultural land use were less common than additive effects, but in some cases the synergistic interactive effects on decomposition were of the same magnitude as the main stressor effects. Gücker et al. (2009) showed two cases of antagonism in agricultural streams, namely physical stress counteracted the effects of eutrophication diminishing respiration, whereas eutrophication counteracted the effects of physical stress enhancing primary production.

Quantification of multiple stressor effects need thus be accounted for when assessing anthropogenic impacts on ecosystem functioning. Potential approaches include

an experimental design incorporating different sequences of naturally occurring stressors with several sampling dates: before application of the stressors, after the first application of stressors (e.g. treatment: A, B, A, B and control), after the second application of stressors (e.g. treatment: B, A, A, B and control) and on additional occasions after the second application to follow recovery of the system (see Giller et al., 2004). The effect of multiple stressors on ecosystem functioning may also be disentangled using extensive statistical analysis on large datasets (see protocol presented by Feld et al., 2016). Another promising perspective was provided by Bruder et al. (2019) who advocated ecological network theory as a way forward. Ecological networks include both biotic (trophic and non-trophic) and environmental interactions and can show the direct and indirect impacts of multiple stressors on organisms, communities and ecosystem processes. Beside the need to include multiple stressors, it is recommended to use similar methods to consider multiple processes simultaneously, as different processes can interact or respond in opposite direction and thereby influence the overall functioning of ecosystems (Gilling et al., 2018).

MECHANISMS BETWEEN STRUCTURAL AND FUNCTIONAL RESPONSES

A selection of studies that combined structural and functional measures when studying the effect of anthropogenic stressors are listed in Table 1. Several studies focused on the combination of decomposition as functional measure and diversity and/or abundance of macroinvertebrates and/or microbes as structural measures, yielding various outcomes. For example, the loss of fungal diversity in eutrophied streams reported by Lecerf & Chauvet (2008) contrasted with the results of other eutrophication experiments showing either a positive effect on both fungi and decomposition (Gulis & Suberkropp, 2003) or no effect at all (Ferreira et al., 2006a). Lecerf & Chauvet (2008) suggested that oxygen depletion on the surface of leaves, caused by intense deposition of fine sediments and oxidation of organic matter by other microorganisms, was detrimental to aquatic hyphomycetes. Despite the increase of fungal spores and mycelial biomass due to nutrient enrichment, the oxygen regime could strongly determine the observed effect on decomposition (see also Bruder et al., 2016). The relation between microbial and invertebrate structure and decomposition may also change with environmental conditions, like temperature oscillations related to, amongst others, climate or season (Dang et al., 2009) or site-specific differences in habitat (Robinson et al., 1998). Even the plant species used in litter decomposition studies may affect the relation observed between structure and function, e.g. in the study by Bruder et al. (2016) fungi appeared important for birch litter decomposition but played a minor role for mahoe litter decomposition.

Apart from environmental conditions, the functional roles of individual species are important in affecting the relation between ecosystem structure and function (Dangles & Guerold, 2001), as the effects of anthropogenic stressors on ecosystem processes is often

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mediated through effects on the community composition (Truchy et al., 2019). Currently this knowledge is mainly associated with the role shredders play in decomposition under different types of stressors. Shredder species can differ substantially in the degree that they decompose litter (Dangles & Guerold, 2001). Dangles & Guerold (2000) demonstrated that acidification changed the shredder community structure which in turn changed the litter breakdown process and impact upland stream functioning. Specifically, the difference in acid-tolerance between *Protonemura* sp. (Plecoptera: Nemouridae) and *Gammarus fossarum* determined the breakdown rate (Dangles & Guerold, 2001). Also liming caused negative effects on both macroinvertebrate assemblages, in terms of evenness and abundance of shredders and litter decomposition due to a change in relative occurrence of limnephilid caddisflies versus stoneflies (Mckie et al., 2006). Contrary, Jonsson & Malmqvist (2003) in experiments showed that increase in shredder richness enhanced leaf breakdown rates.

Even minor changes in community composition, such as the loss of a single species, can thus lead to disproportionate changes in decomposition (e.g. Carlisle & Clements, 2005; Lecerf et al., 2006; Bergfur et al., 2007). Others have, however, observed that taxonomic richness of shredders has greater effect on litter processing than shredder biomass (e.g. Huryn et al., 2002; Jonsonn et al., 2002). Frainer et al. (2014) observed a variation in detritivore functional diversity (i.e. a combination of feeding strategy, biomass, emergence period and substrate and current velocity preference) between seasons in stream pools and riffles, indicating the importance of fluctuations in the relative abundances not of species, but of species functional roles for ecosystem process rates. Furthermore, the functional roles appear not only to be driven by environmental conditions but also by geographical position which suggests that spatial structuring in ecosystem functioning beyond that attributable to species sorting along environmental gradients can be important (Truchy et al., 2019). Species richness could enhance decomposition rates in experiments, even when all species belonged to the same guild (Jonsson & Malmqvist, 2000). Three potential mechanisms could explain the increase in decomposition rates with increasing species richness, namely 1) facilitation between species (i.e. niche partitioning), 2) less negative interactions (i.e. behavioral interactions might be less in diverse communities, so more time can be spent on feeding) (Jonsson & Malmqvist, 2000), and 3) the insurance effect (i.e. diverse communities are more likely to include tolerant species, which are able to compensate for those negatively affected by a given stressor) (Loreau et al., 2002; McKie et al., 2009). In general, environmental conditions can thus moderate structure - function relationships either by suppressing the role of a dominant taxon or by degrading diversity (Cardinale & Palmer, 2002), which underlies the importance of understanding species roles in ecosystem processes when assessing ecological consequences of anthropogenic stressors (Carlisle & Clements, 2005).

Table 1: A selection of studies providing mechanistic (structure-based) explanations of the functional response to anthropogenic stressors.

Structural measure	FuncFtional measure		
	Production	**Respiration**	**Decomposition**
Bacteria	Corcoll et al. 2015	Masseret et al. 1998, Carlisle and Clements 2005	Pascoal et al 2001, Lecerf et al. 2006, Hladyz et al. 2011b
Fungi			Suberkropp and Chauvet 1995, Gulis and Suberkropp 2003, Bärlocher and Corkum 2003, Gulis et al. 2006, Ferreira et al. 2006b, Bergfur et al. 2007, Castela et al. 2008, Lecerf and Chauvet 2008, Bruder et al. 2016
Algae	Crossey and La Point 1988, Masseret et al. 1998, Cardinale and Palmer 2002, Uehlinger et al. 2003, Death et al. 2009, Hladyz et al. 2011b, Corcoll et al. 2015, Truchy et al. 2019	Crossey and La Point 1988, Corcoll et al. 2015	Smeti et al. 2019
Macrophytes			Gücker et al. 2006
Invertebrates (general)	Clapcott et al. 2010, Savoy et al. 2019	Clapcott et al. 2010	Robinson et al. 1998, Jonsson and Malmqvist 2000, Loreau et al., 2002, Woodcock and Huryn 2004, Acuña et al. 2005, Hagen et al. 2006, Gücker et al. 2006, Bergfur et al. 2007, McKie et al. 2009, Dang et al. 2009, Death et al. 2009, Gücker et al. 2009, Clapcott et al. 2010, Hladyz et al. 2011b, Riipinen et al. 2009, Schäfer et al. 2012b, Collier et al. 2013, Smeti et al. 2019, Truchy et al. 2019
Shredders			Brown et al. 1983, Dangles and Guerold 2001, Pascoal et al. 2001, Huryn et al. 2002, Jonsson et al. 2002, Jonsson and Malmqvist 2003, Woodcock and Huryn 2004, Dangles et al. 2004, Carlisle and Clements 2005, Gulis et al. 2006, McKie et al. 2006, Lecerf et al. 2006, Bergfur et al. 2007, McKie and Malmqvist 2009, Riipinen et al. 2009, Frainer et al. 2014
Grazers	Hill et al. 2001, Friberg et al. 2009, Hladyz et al. 2011b		
Filter-feeders	Cardinale and Palmer 2002, Friberg et al. 2009		Cardinale and Palmer 2002, Cardinale et al. 2002

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Although most studies focused on explaining the mechanisms between structural parameters and decomposition, some examples exist of studies that focused on the relation between structural parameters and metabolism (Table 1). For example, Uehlinger et al. (2003) showed that floods temporarily reduced periphyton biomass and composition, as well as ecosystem metabolism, although metabolism recovered relatively fast while a persistent shift in the periphyton structure was observed with high inter-annual variation. Other studies reported a lowering of periphyton species richness and diversity, because sensitive species were replaced by resistant species (e.g. green algae and heterotrophs), in combination with increased community metabolism due to heavy metals (Crossey & La Point, 1988), treated waste water (Masseret et al., 1998) and pharmaceuticals (Corcoll et al., 2015). Invertebrate community changes were also shown to affect metabolism, e.g. an increase in grazing snails resulted in an increase in productivity of their food resource (periphyton) (Friberg et al., 2009). Moreover, it has recently been proposed that characterizing productivity regimes can also provide information on the structure of aquatic communities, as the magnitude and timing of primary production can affect primary and secondary consumers (Savoy et al., 2019).

STRUCTURE AND FUNCTION IN ASSESSMENT OF ANTHROPOGENIC STRESS

Several studies in Table 1 stated specifically that structural and functional measures were complementary and should be used in concert to reflect an integrated assessment of the stream ecosystem. It was proposed that in combination, they capture a broader range of potential effects and provide insights into the functional consequences of changes in community structure (e.g. Crossey & La Point, 1988; Pascoal et al., 2001; Friberg et al., 2009; Collier et al., 2013). For example, in the study by Pascoal et al. (2001) macroinvertebrates increased in density but decreased in taxon richness in relation to an increase in nutrient concentrations from waste water effluent, while leaf breakdown rates were significantly stimulated. That both structural and functional attributes can give complementary information on changes was also shown by Friberg et al. (2009) studying a temperature gradient. Higher temperature related to an increase in density and decrease in diversity of invertebrates, as well as an increase in decomposition rates. While some other structural (i.e. macrophytes and fish community composition) and functional (i.e. algal productivity) measures did not respond to the temperature gradient (Friberg et al., 2009). The difference in response of structural and functional measures to reach-scale pressures and local habitat conditions may strengthen their complementarity (Collier et al., 2013).

Other studies argued that functional measures were even more sensitive than structural measures (e.g. Dangles et al., 2004; Gulis et al., 2006; Riipinen et al., 2009). Gulis et al. (2006) showed that decomposition responded to low levels of eutrophication, while all of the streams were classified as having 'very good' ecological conditions according to

the used macroinvertebrate index. Measurements of leaf litter breakdown also demonstrated a stronger difference in response to acidification in comparison to structural measures, like total abundance, biomass and species richness of detritivores (Dangles et al., 2004; Riipinen et al., 2009). Moreover, it has been argued that functional parameters have added value in assessment because they vary less than structural parameters among bioregions (e.g. Young et al., 2008). In a study including three bioregions of New Zealand, four out of five functional indicators exhibited predictable relationships with land use independent of bioregion (Clapcott et al., 2010).

However, others found high variability in functional measures (see context dependence of functional parameters) and argued that structural measures give a better indication of anthropogenic stressors (e.g. Crossey & La Point, 1988; Hagen et al., 2006; Death et al., 2009). The results of the study of Crossey & La Point (1988) on the effectiveness of community production and respiration measurements as monitoring tools for environmental impact evaluations indicated that inherent variability may limit the use of these community functional measures in routine environmental monitoring. Hagen et al. (2006) concluded that leaf breakdown rates may not be a useful indicator of stream integrity because of the complex effects that agricultural land use had on breakdown rates, while the land use gradient was reflected consistently in the structural invertebrate measures. Similarly, Bergfur et al. (2007) and Death et al. (2009) concluded that macroinvertebrate metrics performed much better than leaf litter breakdown rates along an enrichment and water abstraction gradient, respectively. The functional responses, or lack thereof, to water abstraction could only be explained by more thorough investigation of the individual responses of each of the New Zealand streams, which would not make it a more efficient or complementary than structural measures in assessment (Death et al., 2009).

Taking all these studies into consideration, it may be concluded that data on community composition together with functional measures, such as decomposition rates, greatly contributed to the interpretation of stressor effects and plea for a combined approach (Huryn et al., 2002; McKie et al., 2006; McKie & Malmqvist, 2009).

FUTURE PERSPECTIVES ON STREAM ASSESSMENT

Good water management requires action and prediction based on diagnostic information. Mechanistic understanding of the structure and related processes can support more accurate management (Elosegi et al., 2017). Therefore, a way forward could be 1) to increase understanding of the role of individual species in the functioning of stream ecosystems, and 2) to quantify the response of individual species to stressors and combinations thereof. To understand the role of individual species in the functioning of stream ecosystems single trait approaches have been advocated in the past, but appeared

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unsuccessful. Potentially, the use of the evolutionary perspective of how functional traits have coevolved in response to natural selection could improve this knowledge (Southwood, 1977; Grime, 1979; Winemiller, 1992). Selection pressures do not act independently on single traits but rather on species with a suite of multiple interacting traits (Pilière et al., 2016). The adaptive value of a particular trait may differ within and across species, depending on the life stage, other traits possessed by the species and the prevailing environmental conditions (Statzner & Běche, 2010; Rubach et al., 2011; Wilkes et al., 2017). Species plasticity in resource requirement enlarges its fundamental niche and plasticity in the proportional resource uptake results in expansion of the realized niche (Berg & Ellers, 2010). Both enlarge the adaptive value of a trait and thereby strengthen the functional role of a species in a community. Local environmental (abiotic and biotic) conditions thus determine the structure and function of a local community (Leibold et al., 2004). Knowledge on suites of interacting traits that evolved under local environmental abiotic and biotic conditions (including multiple stressor effects) would help to better understand ecosystem structure and function (Leibold et al., 2004; Hamilton et al., 2019). Furthermore, the tolerance of species traits to one environmental factor (or stressor) can affect the response of communities and functional groups to other stressors. An environmental factor (or stressor) induced shift in a certain trait adaptation by natural selection will strengthening positive co-tolerance among taxa, but a lack of such exposure and adaptation can be expected to decrease co-tolerance and reduce resistance (Vinebrooke et al., 2004). This reasoning does not only account for macroinvertebrates but can be projected on many organism groups, including microbes (e.g. McGee, 2011; Winnemiller et al., 2015). Development of molecular technology that allows for identification and characterization of the functional traits of microbial communities may thereby add to a better understanding of ecosystem functioning (Sims et al., 2013). However, most response and effect traits are based on several interacting genes that are difficult to understand in combination. Moreover, many genes indicative of a trait might not be expressed and therefore be irrelevant for measurable traits but picked up by DNA-mining approaches.

To quantify the response of individual species to stressors and combinations thereof, the development of multiple trait-based species or species assemblage quantified sensitivities to specific stressors could offer potential. Such approach requires a more targeted selection of physiological, behavioural or life-cycle traits, i.e., ones that have a clear mechanistic relationship to single stressors (fundamental determinants of intrinsic sensitivity) and the processes induced by the stressor (e.g. Rubach et al., 2010; Ippolito et al., 2012). Several recent studies have addressed multiple important traits (e.g. Poff & Allan, 1995; Lamouroux et al., 2004). But there has been rather little distinction made between the traits or trait combinations that are truly functional in terms of ecosystem functioning and those that portray other life history characteristics. Yet, a direct emphasis on the

(quantified) relationships between traits, groups of traits or interconnected trait types (functional types) and ecosystem functioning might further increase our understanding of ecosystem functioning (e.g. Harvey et al., 2017; Seibold et al., 2018; Delmas et al., 2019). Knowledge on functional types of all members of a species assemblage (functional categorization) and their interspecies connections could portray local environmental characteristics and constraints set by habitat templates (Goedkoop & Johnson, 1996; Heino, 2005). Changes in species assemblages, such as the disappearance of a single species due to an environmental change, could imply a loss of a functional type which would cause a change in ecosystem functioning or could change the functioning of other species in the same assemblage. Knowledge on the functional roles of dominant, foundation or key species would strongly strengthen the understanding of ecosystem functioning. Knowledge on the effects of losses of individual species or the introduction of novel species whom possess different functional characters can, for example, be extracted from studies on alien and invasive species (e.g. Carlsson et al., 2004; Anderson & Rosemond, 2007; Gutiérrez et al., 2014). Changes of species composition that change the relative share of functional characters would make it possible to study, assess and predict single stressor and multiple stressors effects on ecological assemblages.

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