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Verdonschot, Piet F.M.; Lee, Gea H.

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# Perspectives on the functional assessment of multi-stressed stream ecosystems

Piet F. M. Verdonschot<sup>1,2,3</sup> and Gea H. van der Lee<sup>1,2,4</sup>

<sup>1</sup>Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94240, 1090 GE Amsterdam, The Netherlands

<sup>2</sup>Wageningen Environmental Research, Wageningen University and Research, P.O. Box 47, 6700 AA Wageningen, The Netherlands

**Abstract:** Past research has examined how anthropogenic stressors affect both structural and functional attributes of stream ecosystems. Nevertheless, biomonitoring programs rely mostly on structural metrics for surface-water quality and status assessments, and few studies have examined the extent to which functional metrics can strengthen these structure-based assessments. We reviewed studies that combined the response of stream-ecosystem structural and functional measures to single and multiple stressors. These studies illustrate that structural and functional measures can respond in similar, complementary, or even contradictory magnitude and direction to different stressors. Because of this complexity, we suggest that a combination of structural and functional measures may provide added information on surface-water quality and status, especially when ecosystems are affected by multiple stressors. Better knowledge about trophic and non-trophic roles of dominant taxa and the effects of changes in species diversity on stream ecosystem processes could improve understanding of the relationships among structural and functional measures. Based on our review, we suggest that future research should be designed to: 1) increase understanding of the roles of individual species and communities in the functioning of stream ecosystems, and 2) quantify the responses of individual species and communities to individual stressors and combinations of multiple stressors. We propose that increasing the knowledge base about the suites of traits that occur in different species, how these traits coevolved under local environmental abiotic and biotic conditions, and how they interact is needed to understand how multiple stressors affect ecosystem structure and function. This trait-based knowledge is essential to understanding the relationship between structure and function in multi-stressed stream ecosystems and could help managers to make stronger inferences about the combined effects of multiple stressors on water quality and status. **Key words:** process, structure, primary production, respiration, decomposition, species composition, invertebrates, microbes, algae, fungi, disturbance, stressor

In 1960, Hynes (1960) used measures of several biological groups and biological-oxygen demand to describe patterns of structural and functional responses to a point discharge of organic waste into a river. Since then, the effects of anthropogenic stressors on both structural and functional attributes of stream ecosystems have been increasingly studied (Dale and Beyeler 2001, Giller et al. 2004, Young et al. 2008, von Schiller et al. 2017). Nevertheless, most water-quality assessment strategies rely on structural metrics like indicator species, species diversity, and species composition (e.g., Rosenberg and Resh 1993, Bailey et al. 2004). For example, the United States Clean Water Act and the European Union Water Framework Directive use biological

indicators, mostly consisting of structural metrics based on species composition and ecosystem structure, to assess ecosystem integrity or ecological status, respectively (USEPA 2002, Birk et al. 2012). Communities, especially those including macroinvertebrates, are frequently used for assessment because they can be diverse and because species replacement or losses can occur in response to a variety of anthropogenic stressors (e.g., Clapcott et al. 2012). Although structural metrics are assumed to measure deviation from a desired ecological condition, they provide limited information on how ecosystems function or how those functions are affected by stressors in tandem with structural measures (Dale and Beyeler 2001, Tilman 2001). A large body

E-mail addresses: <sup>3</sup>piet.verdonschot@wur.nl; <sup>4</sup>gea.vanderlee@wur.nl

of evidence now shows that stressors may affect the structure and function of ecosystems differently, indicating that assessments should not only be based on what organisms are present but should also directly measure ecosystem processes or functions (Boulton 1999, Karr 1999, Loreau 2002, Gücker et al. 2006, Bergfur et al. 2007, Palmer and Febria 2012). A primary goal of many biomonitoring programs is to detect whether anthropogenic stressors affect ecosystem integrity, and using a combination of ecosystem structural and functional measures could help water managers to make stronger inferences about the effects of stressors on ecosystem integrity (Young et al. 2008, Feio et al. 2010).

Some studies have inferred function from a structural perspective using food webs (Hladyz et al. 2011b), functional feeding groups (Cummins and Klug 1979), or other adaptive and 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 and McKie 2015, Raffard et al. 2017, Truchy et al. 2019). Adaptive and functional traits refer to organismal processes (e.g., the ability to assimilate nutrients) that may influence processes at higher organizational levels. True ecosystem processes are complex and dynamic operations among interacting abiotic and biotic components, such as leaf-litter breakdown (Gessner and Chauvet 2002), ecosystem metabolism (Fellows et al. 2006), primary and secondary production (Wallace et al. 1996, Udy et al. 2006), and nutrient cycling (Niyogi et al. 2004, Bukaveckas 2007, Marcarelli et al. 2011). Measurements of functional metrics that provide insights into these true ecosystem processes are relatively inexpensive, straightforward to carry out, and, in the case of metabolism, amenable to automation (Collier et al. 2013). Several review papers discuss how these ecosystem processes relate to specific stressors (e.g., Webster and Benfield 1986, Young et al. 2008, Tank et al. 2010) but do not explicitly compare the use of functional and structural metrics for water-quality and status assessments. Moreover, streams and rivers commonly experience multiple, co-occurring anthropogenic stressors (Ormerod et al. 2010, Schäfer et al. 2016), which can complicate structural and functional responses. A key question, thus, remains as to what extent including functional measures of stream ecosystems, in addition to more traditional structural measures, can strengthen the ability of water-quality and status assessments to make inferences about the effects of stressors on ecosystem integrity, particularly when assessed ecosystems are affected by multiple stressors.

To shed light on this question, we first review studies that assessed the effects of a single stressor on both structural and functional measures, discuss the similarities and differences between structural and functional responses within and among studies, and pinpoint potential causes for these differences. We then expand our review to studies on the effects of multiple stressors on combined structural and functional measures. Next, we explore ideas about how

mechanistic understanding of structure and related processes (i.e., functional roles of species) can improve assessment of stream ecosystems. Finally, we provide perspectives on future directions for assessment of multiple stressors on stream ecosystems. It should be noted that we did not include all papers published on this topic; rather, we included a relevant subset to provide insights and perspectives into what current research can offer toward informing water managers about stressor effects on water-quality and status-assessment measures.

## COMPARING STRUCTURAL AND FUNCTIONAL ASSESSMENTS OF SINGLE STRESSORS

Responses by structural and functional measures to different stressors can be similar, complementary, or even contradictory in magnitude and direction, both within and between studies. Here, we define stressor as an environmental factor that acts as a debilitating agent to create degradation in an ecosystem (Odum et al. 1979). A selection of studies that assessed the effects of stressors on combined structural and functional response measures is listed in Table 1. Below, we highlight several studies to exemplify the different types of structural and functional responses.

### Similar responses in magnitude and direction

There is consensus on several structural and functional indicators that respond in obvious and unidirectional ways to specific stressors, supporting the idea that changes in structural measures are indicative of changes in function. Such generalizations can be made, for example, for the response of structural measures based on algae and macrophytes and functional measures based on primary productivity. Nutrients, light, and sufficiently warm temperatures are required for photosynthesis. An increase in these factors generally favors fast-growing, dominant species of algae (Smucker et al. 2014, Burson et al. 2018) and macrophytes (Barko et al. 1986), which, in turn, stimulate higher primary production (e.g., Phinney and McIntire 1965, Steinman and McIntire 1987, Bott et al. 2006, Dodds 2006, Bernot et al. 2010, Rasmussen et al. 2011). Cyanobacteria thrive under high temperature and nutrient conditions, and they can outcompete green algae that, in turn, outcompete diatoms (Patrick et al. 1969, Vermaat and Hootsmans 1994, Allan et al. 2006). Increased nutrient loads also cause changes in phytoplankton species composition, even if the N:P ratio of the nutrient loads remains constant, by shifting species interactions from competition for nutrients to competition for light (Burson et al. 2018). As nutrients increase, either through eutrophication or organic pollution, the growth and survival prospects of particular species of primary producers causes increases in their biomass. Increased biomass then leads to more nutrient recycling and energy flow, which subsequently causes changes in species composition, dominance,

Table 1. A selection of studies providing mechanistic (structure-based) drivers of functional responses to anthropogenic stressors.

Structural measure	Functional 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. 2011a
Fungi			Suberkropp and Chauvet 1995, Bärlocher and Corkum 2003, Gulis and Suberkropp 2003, Ferreira et al. 2006b, Gulis et al. 2006, 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. 2011a, 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
Macroinvertebrates (general)	Clapcott et al. 2010, Savoy et al. 2019	Clapcott et al. 2010	Robinson et al. 1998, Jonsson and Malmqvist 2000, Loreau 2002, Woodcock and Huryn 2004, Acuña et al. 2005, Gücker et al. 2006, Hagen et al. 2006, Bergfur et al. 2007, Dang et al. 2009, Death et al. 2009, Gücker et al. 2009, McKie et al. 2009, Riipinen et al. 2009, Clapcott et al. 2010, Hladyz et al. 2011a, Schäfer et al. 2012b, Collier et al. 2013, Smeti et al. 2019, Truchy et al. 2019
Shredders			Dangles and Guerold 2001, Pascoal et al. 2001, Huryn et al. 2002, Jonsson et al. 2002, Jonsson and Malmqvist 2003, Dangles et al. 2004, Woodcock and Huryn 2004, Carlisle and Clements 2005, Gulis et al. 2006, Lecerf et al. 2006, McKie 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. 2011a		
Filter-feeders	Cardinale and Palmer 2002, Friberg et al. 2009		Cardinale and Palmer 2002, Cardinale et al. 2002

abundance, and secondary production of higher trophic levels (Smucker et al. 2014).

Changes in flow can also affect algal and macrophyte community structure and primary productivity. Low flows generally enhance primary production through increased light availability and nutrient concentrations because of decreased dilution and increased substrate stability, as well as because of reduced shear stress on periphyton and enhanced macrophyte establishment (e.g., Acuña et al. 2010, Marcarelli et al. 2010, Val et al. 2016). In the opposite response direction, floods generally result in decreased primary production because substrate stability decreases, causing higher turbidity that may reduce light conditions (e.g., Uehlinger 2000, Morgan et al. 2006, Roberts et al. 2007,

Leggieri et al. 2013, Val et al. 2016). Furthermore, scouring reduces the abundance, biomass, and diversity of macrophytes and algae, especially periphyton (Riis and Biggs 2003, Wellnitz and Rader 2003, Vilches and Giorgi 2010). Toxicants and other forms of chemical pollution may also inhibit primary production if the algal and macrophyte taxa present are sensitive to the particular substance (Peters et al. 2013). For example, acid mining was related to both a decline in species diversity of algal-dominated periphyton (structural measure) and decreased productivity (functional measure) (Smucker et al. 2014).

Other generalizations can be drawn for the responses of structural measures based on macroinvertebrates and functional measures based on organic-matter breakdown.

Historically, benthic macroinvertebrate species composition has constituted the basis for most biomonitoring programs worldwide because of their indicative value for assessing oxygen depletion resulting from organic pollution (Wiederholm 1980, Rosenberg and Resh 1993). It is well established that lowered dissolved oxygen alters macroinvertebrate assemblage composition through a loss of oxygen-sensitive species like key shredders (Gelroth and Marzolf 1978, Schlief and Mutz 2009), which tends to slow down organic-matter breakdown rates (Chauvet 1997, Pascoal and Cássio 2004). Similar responses in both magnitude and direction are observed for other stressors that have a large impact on macroinvertebrate assemblages and subsequently influence organic-matter breakdown, such as metal pollution (Carlisle and Clements 2005, Chaffin et al. 2005), pesticides (Schäfer et al. 2007), and salinity (Schäfer et al. 2012b). Likewise, macroinvertebrate communities are also sensitive to low flows and droughts (Dewson et al. 2007), and as conditions become unfavorable for key shredder species, the organic-matter breakdown rates tend to lower uniformly (Gelroth and Marzolf 1978, Schlief and Mutz 2009, Mendoza-Lera et al. 2012, González et al. 2013, Monroy et al. 2016).

### Complementary responses

Various studies have found that structural and functional measures were complementary and should be used in concert to capture a broader range of potential effects and provide insights into the functional consequences of changes in community structure (e.g., Pascoal et al. 2001, Friberg et al. 2009, Collier et al. 2013). For example, Pascoal et al. (2001) found that macroinvertebrates increased in density but decreased in taxon diversity in response to an increase in nutrient concentrations, while leaf breakdown rates increased substantially. Friberg et al. (2009) also found an increase in density and a decrease in diversity of invertebrates, as well as a subsequent increase in organic-matter breakdown rates, in response to higher temperatures. In contrast, some other structural (macrophyte and fish assemblage composition) and functional (algal productivity) measures did not respond to changes in temperature (Friberg et al. 2009). The difference in structural- and functional-measure response sensitivity to reach-scale pressures and local habitat conditions, and their differences in response at multiple spatial scales, may strengthen their complementarity (Collier et al. 2013) in informing stream assessments.

Several studies have argued that functional measures are more sensitive than structural measures to changes in stressors (e.g., Dangles et al. 2004, Gulis et al. 2006, Riipinen et al. 2009). Gulis et al. (2006) showed that in study streams classified by a macroinvertebrate index as having very good ecological conditions, organic-matter breakdown rates responded to low levels of eutrophication. In other studies, leaf-litter breakdown responded more strongly than total abundance, biomass, and species diversity of detritivores

to acidification (Dangles et al. 2004, Riipinen et al. 2009). Moreover, it has been argued that functional measures have added value when included in assessments because they vary less among bioregions than structural measures do (e.g., Clapcott et al. 2010).

Other studies have found higher variability in functional vs structural measures (e.g., Crossey and La Point 1988, Bergfur et al. 2007, Death et al. 2009). Crossey and La Point (1988) looked at the effectiveness of community production and respiration measurements as biomonitoring tools for environmental impacts, and their results indicated that inherent variability may limit the use of these community-level functional measures in routine environmental monitoring. Similarly, Bergfur et al. (2007) and Death et al. (2009) concluded that macroinvertebrate metrics performed much better than leaf-litter breakdown rates along nutrient enrichment and water abstraction gradients, respectively. In the case of Death et al. (2009), the lack of functional response to water abstraction could only be explained by more thorough investigation of the individual responses of each of their study streams, which did not add to the efficiency of assessment.

Finally, an example by Uehlinger et al. (2003) showed that there may also be differences between the impact and recovery patterns of structural and functional measures. They found that even though metabolism and assemblage composition of periphyton were both changed by a flood event, metabolism recovered relatively quickly, whereas there was a persistent shift in the periphyton structure (Uehlinger et al. 2003). Thus, structural and functional measures may provide complementary information on the assessment of impact and recovery patterns over time.

### Variable and non-linear responses

In some cases, different responses to the same stressor have been reported for structural and functional measures across studies. For example, loss of fungal diversity and lowered organic-matter breakdown rates in nutrient-enriched streams reported by Lecerf and Chauvet (2008) contrasted with the results of other nutrient-enrichment experiments showing either a positive effect on both fungi and organic-matter breakdown (Gulis and Suberkropp 2003) or no effect at all (Ferreira et al. 2006a). 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 were low at both ends of the nutrient gradient. Processing rates may increase in moderately stressed systems, whereas processing rates may be suppressed under the influence of high stress, leading to a non-linear functional response (Niyogi et al. 2002, Young and Collier 2009, Clapcott et al. 2010, Woodward et al. 2010). Similarly, moderate degrees of eutrophication may result in a more diverse community of producers and consumers (Rosenzweig 1995, Townsend



et al. 1998, Thompson and Townsend 2005), but a further increase of eutrophication can cause algal blooms. The associated low dissolved oxygen and poor habitat conditions generally decrease species diversity (e.g., Dodds 2006, Niyogi et al. 2007, Dunck et al. 2015). These examples illustrate the importance of assessing a sufficiently long stressor gradient to capture the range of possible structural and functional responses (Woodward et al. 2012, Feld et al. 2016).

Environmental conditions specific to different locations and points in time may also alter assessment results. Conditions related to climate or season, such as temperature oscillations (e.g., Dang et al. 2009), flow velocity (e.g., Ferreira et al. 2006b), and the quantity of organic matter in the stream (e.g., Roberts et al. 2007), may elicit different structural and functional responses, with detection of responses depending on where and when stressor impacts are assessed. For example, temperature can strongly affect toxicant bioavailability and subsequently strengthen or weaken its effects on structural and functional measures (Peters et al. 2013, Ferreira et al. 2016). Moreover, habitat heterogeneity can lead to different structural and functional responses at different sites (Robinson et al. 1998). For example, Collier et al. (2013) showed the influence of small-scale spatial variation in physical conditions on macroinvertebrate abundances and organic-matter breakdown rates. Characteristics of site-specific organic matter may also influence assessment outcomes. The plant species used in litter-decomposition studies may, for example, affect the relationship observed between structure and function (e.g., LeRoy et al. 2006, Bruder et al. 2014, 2016) because the chemical composition of natural plant material varies within and among both biogeographic regions and leaf species (Lecerf and Chauvet 2008, Graça and Poquet 2014) and can even vary within individual trees (Sariyildiz and Anderson 2003). Variance partitioning analysis could be a valuable approach to partition the influence of these environmental conditions between structural and functional measures in space and time (e.g., Truchy et al. 2019).

### CHALLENGES OF COMPARING STRUCTURAL AND FUNCTIONAL RESPONSES IN MULTI-STRESSED ECOSYSTEMS

Stressors do not usually occur in isolation because most anthropogenic activities cause a multitude of stressors. Focusing on 1 stressor in multi-stressed ecosystems could mean missing other, more important drivers of structural and functional responses (Clapcott et al. 2010). Moreover, interacting stressors may enhance (synergism), lessen (antagonism), or be neutral (additive) in terms of the effects of each individual stressor (Piggott et al. 2015b). To investigate the extent to which multiple stressors affect ecosystem structure and function in comparable ways, we discuss 3 examples of anthropogenic activities that contribute multiple stressors to stream ecosystems: land-use change (e.g., Allan

2004), wastewater-effluent discharge (e.g., Walsh et al. 2005), and hydromorphological alteration (Feld 2004).

#### Example 1: Land-use change

Changes in land use can result in the removal of riparian vegetation, nutrient enrichment, sediment addition, flow reduction, and warming (Allan 2004). Each of these stressors may have a different effect on ecosystem structure and function. For example, the removal of riparian vegetation leads to more available light, from which an increase in primary production might be expected. However, removal of vegetation can also decrease primary production through an increase in sediment runoff (Young and Huryn 1999, Frankforter et al. 2010). Sediment loads may limit the growth of primary producers through enhanced movement of sediment (Biggs et al. 1999, Schofield et al. 2004) and increased turbidity, resulting in light limitation (Ryan 1991). The resulting change in algal assemblage may, in turn, reduce the amount and quality of food for herbivorous macroinvertebrates (Townsend and Riley 1999). The removal of riparian vegetation may also limit the distribution of shredders both directly by, for example, removal of egg deposition structures or indirectly by altering the quality of allochthonous inputs with the ultimate result of influencing leaf breakdown rates (Sponseller and Benfield 2001).

Multiple stressors resulting from land-use change can also lead to combinations of interactive effects (i.e., synergistic, additive, and neutral) that complicate our ability to disentangle stressor effects on structural and functional metrics. For example, one study found that sediment addition had mostly negative effects on algal biomass production, leaf-litter decomposition, and invertebrate abundance, and these effects were synergistically enhanced by reduced flow (Matthaei et al. 2010). Two cases of antagonism in agricultural streams were shown by Gücker et al. (2009), where physical stress counteracted the effects of eutrophication by diminishing respiration, and eutrophication counteracted the effects of physical stress by enhancing primary production. In another study, fine sediments weakened the subsidy effect of increased nutrients on algal and invertebrate taxa and communities (Wagenhoff et al. 2011). Additive effects associated with stressors from agricultural land use (i.e., nutrients, a nitrification inhibitor, sedimentation, and flow-velocity reduction) on organic-matter breakdown rates were more common than stressor interactions in a study by Bruder et al. (2016). However, in some cases the synergistic interactive effects of fine-sediment deposition and flow reduction were of the same magnitude as the main stressor effects, here fine-sediment deposition. In other studies, the combined effects of nutrient enrichment and increased temperature were shown to enhance organic-matter breakdown either additively (Piggott et al. 2015a) or synergistically (Ferreira and Chauvet 2011). Nutrient enrichment and fine-sediment input interacted antagonistically to reduce

organic-matter breakdown, potentially because of reduced microbial access to nutrients and oxygen in the water column (Pascoal et al. 2005, Piggott et al. 2015a).

### Example 2: Wastewater treatment plant effluent

Wastewater treatment plants (WWTPs) generally discharge dissolved nutrients and organic waste along with a suite of toxic substances, like pharmaceuticals and personal care products (Paul and Meyer 2001). Moreover, WWTP effluents may alter the hydrological and thermal regimes of receiving streams with periodic high-flow events and warmer water temperatures, respectively (e.g., Carey and Migliaccio 2009, Burdon et al. 2020). Depending on the nature of the WWTP effluent, structural and functional measures can be affected positively or negatively. WWTP effluents have been shown to alter the composition of primary producer, microbial heterotroph, and macroinvertebrate assemblages (Hart and Robinson 1990). For example, effluent discharge can cause a decline in macroinvertebrate taxon diversity (Cabrini et al. 2013), whereas the biomass and abundance of certain groups of invertebrates can increase (Muñoz et al. 2009, Alexander et al. 2013) or decrease (Alexander et al. 2013). Likewise, rates of ecosystem processes (e.g., organic-matter breakdown) can also increase (Bundschuh et al. 2009) or decrease (Moreirinha et al. 2011).

The overall impact of WWTPs on structure and function is complex. Dissolved nutrients, organic matter, and warmer water temperatures can subsidize biological activity, whereas toxic substances can be deleterious to organisms and suppress biological activity (Izagirre et al. 2008, Aristi et al. 2015, Burdon et al. 2020). Moreover, the subsidizing effect of enhanced nutrient supply may also be suppressed by reduced light availability caused by the accompanying sediment input, suggesting a stress effect on the activity of primary producers but not the microbial assemblage (Aristi et al. 2015). How these toxic contaminants affect structural and functional measures also depends on local flow conditions. For example, Corcoll et al. (2015) found that long-term exposure to a mixture of pharmaceutical compounds in combination with flow intermittency negatively influenced the structure and metabolism of algal and bacterial communities in biofilms. Algae suffered cumulative effects whereas bacteria showed higher resistance to both stressors, and subsequent production was affected to a greater degree than organic-matter breakdown (Corcoll et al. 2015). A comparable effect was shown by Smeti et al. (2019) where diatom diversity increased across fine-sediment pollution (including persistent organic pollutants, pesticides, and phenolic compounds) and flow-intermittency gradients, whereas both macroinvertebrate diversity and ecosystem functions (resource-use efficiency of primary producers in biofilms and organic-matter breakdown by macroinvertebrates) were negatively affected.

### Example 3: Hydromorphological alterations

One of the most obvious examples of complex multiple-stress responses is related to hydromorphological deterioration. Hydromorphological alterations of natural streams are diverse, ranging from the removal of large instream wood to the construction of new artificial channels (Elosegi and Sabater 2013), and bring about a variety of changes in flow and alterations to habitat structure and availability. Changes in primary production due to morphological alteration are dependent on whether the channel's cross-sectional area is increased or decreased, resulting in different patterns in flow velocity, shear stress, and sediment transport (Gücker et al. 2009). These 3 factors are also important determinants of algal and benthic assemblage structure (Poff et al. 1990, Schofield et al. 2004). Increased flow may enhance respiration through the input of organic matter, whereas 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 has been observed after floods, and an increase has been observed after droughts (Uehlinger et al. 2003, Acuña et al. 2004, Uehlinger 2006). This difference in respiration response is presumably related to differences in bed substrate stability among streams (Uehlinger and Naegeli 1998). Some researchers have found that the effects of flood-induced scouring on respiration may be limited because microbes are protected from abrasion in the hyporheic zone (Uehlinger and Naegeli 1998, Chester and Norris 2006, Benson et al. 2013). Other authors have reported, however, that after a flood, epiphyton was more productive because of the greater availability of nutrients (Stevenson 1990). In another study, synergistically combined effects of contamination with flow reduction after river damming reduced fungal biomass and taxon diversity, which, in turn, led to reduced shredder performance and leaf-litter decomposition (Colas et al. 2016).

### Strategies for assessing multi-stressed ecosystems

The examples above show that structural and functional responses to multiple anthropogenic stressors can be complex and multidirectional. Anthropogenic effects of 1 stressor can be confounded by changes in another stressor, and both can, in turn, be changed by a 3<sup>rd</sup> stressor, depending on effects to individual organisms. Thus, quantification of interacting multiple-stressor effects is needed when assessing anthropogenic impacts on ecosystem structure and function. By projecting the contribution of each specific stressor to a multi-stressor space and linking these to the presence and abundance of taxa and ecosystem functions, the drivers of ecosystem response may be elucidated. In addition to considering multiple stressors, it is prudent to consider multiple processes simultaneously because different processes can interact or respond in opposite directions, thereby influencing overall ecosystem function (Giling et al. 2019).

There are several potential approaches to better understand the effects of multiple stressors on ecosystem structure and function. One approach is an experimental design proposed by Giller et al. (2004) that incorporates a control and 4 different sequences of stressors (stressors A and B) with several sampling dates: before application of the stressors, after the 1<sup>st</sup> application of stressors (e.g., 1<sup>st</sup> treatment 1–5 with application of stressors A, B, A, B, control, respectively), after the 2<sup>nd</sup> application of stressors (e.g., 2<sup>nd</sup> treatment 1–5 with application of stressors B, A, A, B, control, respectively), and on additional occasions after the 2<sup>nd</sup> application. This experimental design allows testing how different species assemblages and associated ecological processes respond to 2 sequences of different types of stress (AB, BA) and 2 sequences of the same types of stress (AA, BB), as well as their subsequent recovery patterns. Another approach for disentangling the effects of multiple stressors on ecosystem structure and function is the use of extensive statistical analysis on large datasets. For instance, Feld et al. (2016) presented a protocol that describes how to rank multiple stressors' importance (e.g., using random forest analysis), detect relevant interactions (e.g., using boosted regression tree analysis), and estimate their standardized effect size (e.g., using generalized linear modeling) from a dataset with a minimum of 150 independent observations that cover the most relevant stressors' gradients. A 3<sup>rd</sup> approach is the use of ecological network theory as described by Bruder et al. (2019). Rather than measuring the direct effects of stressors on structural and functional measures as independent endpoints, ecological networks focus on the biotic (trophic and non-trophic) and environmental interactions. They proposed that quantifying these network characteristics using structural equation modeling can show the direct and indirect impacts of multiple stressors on organisms, communities, and ecosystem processes.

### FUNCTIONAL ROLES OF SPECIES

The effects of stressors on ecosystem processes are often dictated by effects on structural measures, such as community composition (Truchy et al. 2019). In general, environmental stressors can mediate structure–function relationships by either suppressing the role of a dominant taxon or by decreasing species diversity (Cardinale and Palmer 2002). Understanding species' roles in ecosystem processes is, therefore, critical for assessing ecological consequences of anthropogenic stressors (Dangles and Guerold 2001, Carlisle and Clements 2005).

#### Dominant taxa in key functional roles

One way that the presence of dominant taxa can influence the effect of a stressor on ecological processes is via process rates (e.g., Dangles and Malmqvist 2004). This effect is primarily associated with the role shredders play in

determining the rate of litter decomposition under different types of stressors. Shredder species can differ substantially in the rate that they break down organic matter (Dangles and Guerold 2001), which has been shown by multiple leaf-litter decomposition studies where the effects of stressors on specific species of amphipods (Dangles and Guerold 2001, Dangles et al. 2004, Lecerf et al. 2006, Piscart et al. 2009, Rasmussen et al. 2012), isopods (Bergfur et al. 2007), caddisflies (Robinson et al. 1998, McKie et al. 2006), and stoneflies (Carlisle and Clements 2005) led to differences in organic-matter breakdown rates. Even minor changes in community composition, such as the loss or replacement of a single dominant species, can lead to disproportionate changes in organic-matter breakdown rates (e.g., Carlisle and Clements 2005, Lecerf et al. 2006, Bergfur et al. 2007). For example, Dangles and Guerold (2000) demonstrated that acidification significantly changed litter breakdown rates in an upland stream because of the difference in acid tolerance between the stonefly *Protonemura* spp. (low shredding rates) and the amphipod *Gammarus* spp. (high shredding rates).

#### Diversity meets function

Taxonomic diversity of shredders has also been shown to be key in driving organic-matter breakdown rates (e.g., Huryn et al. 2002, Jonsson et al. 2002, Jonsson and Malmqvist 2003). One experimental study showed that increased species diversity enhanced organic-matter breakdown rates, even when all species belonged to the same guild (Jonsson and Malmqvist 2000). Four potential mechanisms have been suggested to explain how increased species diversity can enhance organic-matter breakdown rates and offset the effects of stressors: 1) complementary resource use (e.g., a combination of different feeding strategies, life cycles, and substrate and current-velocity preferences; Frainer et al. 2014), 2) facilitation between species (Tiunov and Schue 2005), 3) fewer negative interactions between species (i.e., behavioral interactions might occur less often in diverse communities, allowing more time to be spent on feeding; Jonsson and Malmqvist 2000), and 4) the insurance effect (i.e., diverse communities are more likely to include tolerant species, which are able to compensate for those species negatively affected by a given stressor; Loreau 2002, McKie et al. 2009). The ability of tolerant species to replace sensitive species in response to stressors while maintaining or even enhancing a particular ecosystem function is particularly evident for microorganisms (Masseret et al. 1998, Blanck 2002, Corcoll et al. 2015, Feckler et al. 2018) but has also been shown for invertebrates (e.g., Woodcock and Huryn 2005).

#### Non-trophic roles

In addition to functional roles based on trophic interactions, there are also non-trophic functional roles that may play an important, but largely unknown, role in ecosystem



function (Jones et al. 1994, Wright and Jones 2006, Kéfi et al. 2012, Dussault 2019). For example, ecosystem engineers (i.e., organisms that directly or indirectly physically modulate the availability of resources to other species and thereby alter environmental and ecological processes) provide non-trophic roles in ecosystem functions (Jones et al. 1994, 2010, Wright and Jones 2006, Gutiérrez et al. 2014). Autogenous ecosystem engineers are organisms that modify the environment with their own living or non-living structures. Macrophytes, for instance, create physical habitat with their tissue, affect light, oxygen, and temperature regimes, and alter sedimentation rates (Jones et al. 1994). Other organisms, allogenuous engineers, change the environment by transforming living and non-living matter from one physical state to another, such as beavers that cut down trees to construct dams and burrowing organisms that actively rework soils (Jones et al. 1994, Anderson and Rosemond 2007). The roles of these ecosystem engineers in ecosystem function have received limited attention in empirical studies compared with trophic interactions (Lévêque 2003, Wright and Jones 2006, Borst et al. 2018). A recent example by Puche et al. (2020) offered preliminary evidence that the inclusion of non-trophic roles in ecological models may be crucial to better understand the functioning of complex communities and their responses to stressors. Specifically, they composed a network model based on mesocosm-experiment data with 3 coupled habitats (pelagic, within-meadow, and benthic) subjected to 3 environmental scenarios (warming, increased ultraviolet radiation, and control). Adding non-trophic roles changed the relevance of habitats and the trophic interactions within them (Puche et al. 2020). Future studies including field data could provide further evidence of the importance of these largely unknown non-trophic roles for ecosystem functioning.

#### **FUTURE PERSPECTIVES ON STREAM ASSESSMENT**

Effective water management requires action and prediction based on diagnostic information. Mechanistic understanding of ecosystem structure and related processes can support managers in making stronger inferences about the effects of stressors on ecosystem integrity (Elosegi et al. 2017). Much is known about single stressors causing reductions in the density of key functional dominant species and causing losses of sensitive indicator species. Less is known about the complex interactions among multiple stressors and their effects on species and, therefore, their trophic and non-trophic contributions to ecosystem functions. Furthermore, there is a great deal more available qualitative than quantitative information about structural and functional responses to multiple-stressor interactions. Because quantitative knowledge is needed for effective, integrated water management, we propose that there is a need 1) to increase understanding of the roles of individual species and communities in stream ecosystem function and 2) to quantify

the responses of individual species and communities to individual stressors and combinations of multiple stressors.

#### **Understanding suites of interacting traits**

Single-trait approaches to understanding the roles of individual species in stream-ecosystem function have been largely unsuccessful (Hamilton et al. 2020). Potentially, using an evolutionary perspective on the coevolution of functional traits in response to natural selection could improve our understanding of species' functional roles (Southwood 1977, Grime 1979, Winemiller 1992). Selection pressures do not act independently on single traits but, rather, act 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 its life stage, other traits possessed by the species, and the prevailing environmental conditions (Statzner and Bêche 2010, Rubach et al. 2011, Wilkes et al. 2017). A species' plasticity in resource requirements enlarges its fundamental niche, and plasticity in the proportional resource uptake results in expansion of the realized niche (Berg and Ellers 2010). Both enlarge the adaptive value of a trait and thereby strengthen the functional role of a species within a community. Local environmental (abiotic and biotic) conditions, thus, determine the structure and function of a local community (Leibold et al. 2004). Knowledge about suites of interacting traits that evolved under local environmental conditions (including multiple-stressor effects) would help us better understand ecosystem structure and function (Leibold et al. 2004, Hamilton et al. 2020).

The tolerance of species traits to 1 environmental factor (or stressor) can affect the response of communities and functional groups to other stressors. An environmental-factor-induced shift in a single or multiple trait adaptation by natural selection will strengthen positive co-tolerance among taxa, and a lack of such exposure and adaptation can be expected to decrease co-tolerance and reduce resistance (Vinebrooke et al. 2004). This reasoning applies not only to macroinvertebrates but can be projected on many organism groups, including microbes (e.g., McGhee 2011, Winemiller et al. 2015). Development of molecular technology that allows for identification and characterization of the functional traits of microbial assemblages may add to a better understanding of ecosystem function (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; therefore, although they might be identified by DNA-mining approaches, they may be irrelevant for determining local ecosystem structure and function.

#### **Using multiple traits to assess ecosystem function**

Improved knowledge on multiple trait-based species or species-assemblage sensitivities to specific stressors would

help quantify the response of individual species and communities to individual stressors and combinations of multiple stressors. A quantitative approach requires a targeted selection of physiological, behavioral, or life-cycle traits, i.e., traits that have a clear mechanistic relationship with different stressors (fundamental determinants of intrinsic sensitivity) and the processes induced by the stressors (e.g., Rubach et al. 2010, Ippolito et al. 2012). Several recent studies have addressed multiple important traits (e.g., Poff and Allan 1995, Lamouroux et al. 2004), but there has been little emphasis on the traits or trait combinations that are relevant for ecosystem function. A direct emphasis on the quantitative relationships between traits, groups of traits, or multiple interconnected trait types (functional types) and ecosystem processes might further increase our understanding of ecosystem function (e.g., Harvey et al. 2017, Seibold et al. 2018, Delmas et al. 2019). Changes in species assemblages, such as the disappearance of a single species resulting from an environmental change, could cause the loss of a functional type, which would lead to a change in ecosystem function or could affect the functioning of other species in the same assemblage.

The influence of evolutionary history, or phylogeny, on suites of functional traits that shape key ecosystem processes is another area of research that could further strengthen functional assessment in multi-stressed stream ecosystems. Leroy et al. (2020) demonstrated that plant phylogeny was a critically important predictor of litter decomposition rates in rivers and streams, explaining more of the variance in decomposition than was explained by site or climatic regime. In another study the relationship between phylogenetic diversity and productivity appeared to be strong for ancestral microbial lineages but weakened for the evolved lineages (Gravel et al. 2012). Both studies emphasized the potential of using species' evolutionary histories to evaluate ecosystem function. Saito et al. (2015) went a step further by including phylogenetic constraints to functional assessment. They reasoned that a community with species from different taxonomical lineages will be more ecologically diverse than an assemblage composed of phylogenetically close neighbors because the latter is likely to have evolved similar phenotypes and traits through niche conservatism (Saito et al. 2016). Webb et al. (2002) proposed integrating phylogenetic information into future studies by examining the phylogenetic structure of assemblages and exploring the phylogenetic basis of assemblage niche structure.

We conclude that structural and functional responses can be similar or contradictory in magnitude and direction both within and between studies in stream ecosystems. Moreover, impacts from a combination of multiple interacting stressors on ecosystem structure and function are often complex. In these cases structural and functional measures can be considered complementary and should be used in concert to capture a broad range of potential effects and to provide insights into the functional consequences of changes in community structure. Trait-based knowledge

is further needed to understand the relationship between structure and function in multi-stressed stream ecosystems and could help managers to make stronger inferences about the effects of these stressors on water quality and status.

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