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

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Integrating measures of ecosystem structure and function to improve assessments of stream integrity

Piet F. M. Verdonschot^{1,2,3}, Gea H. van der Lee^{1,2,4}, and Ralf C. M. Verdonschot^{2,5}

¹Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94240, 1090 GE Amsterdam, The Netherlands ²Wageningen Environmental Research, Wageningen UR, P.O. Box 47, 6700 AA Wageningen, The Netherlands

Abstract: Freshwater ecosystems have been degraded by multiple stressors. To mitigate the effects of multiple stressors on freshwater ecosystems, we must assess the current ecological condition of these systems, diagnose the cause of the environmental impact, and predict how they will respond to future changes in anthropogenic pressures. Most biomonitoring programs use metrics of community structure to quantify ecological condition; however, they do not assess the overall ecological integrity of an ecosystem, including ecosystem function. This series of papers explores how structural and functional aspects of stream ecosystems can respond to different stressors. The use of a combination of structural and functional measures increases the ability to assess degradation of stream ecosystem integrity. We suggest that future studies should focus on development of measures that integrate ecosystem structure and function, such as the identification and refinement of species traits that are clearly associated with important functional properties of species and whose responses to different anthropogenic pressures can aid in informing the specific management activities likely to be most effective in restoring degraded stream ecosystems. **Keywords:** community structure, ecosystem function, assessment, monitoring, traits, multiple stressors

We are facing a global ecological crisis with accelerating biodiversity loss and accompanying changes in ecosystem processes and their services. Spatial and temporal patterns of species occurrences are being altered across all major ecosystems (Butchart et al. 2010, Dirzo et al. 2014). In parallel, human activities are having detrimental impacts on essential ecosystem processes, such as primary production, fluxes of energy and nutrients, and decomposition (Von Schiller et al. 2017). Biodiversity loss and the disruption of natural ecosystem processes are particularly evident in freshwater ecosystems, where human activities have resulted in multiple stressors (Dudgeon et al. 2006, Dudgeon 2010).

To mitigate the effects of these multiple stressors on freshwater ecosystems, we must assess their current ecological condition, diagnose the causes of observed environmental impact, and predict how they will respond to future changes in anthropogenic pressures (Cairns et al. 1993). To make assessments of ecological condition, we need ecological indicators that can be used to assess the status and trends of ecosystem integrity (Karr 1999). In general, values of these indicators at assessed sites are compared with those

at reference sites to quantify the extent of alteration. A great variety of environmental characteristics can be measured for this purpose; however, the number of measures typically included in biomonitoring programs is restricted by logistical constraints (e.g., time, cost; Landres 1992, Cairns et al. 1993, Dale and Beyeler 2001). Most biomonitoring programs rely on taxonomic inventories of the macroinvertebrate, fish, algae, or macrophyte assemblage structure based on one or more measures of presence/absence, abundance, dominance, indicative value, richness, or diversity (Rosenberg and Resh 1993, Barbour et al. 1999, Boulton 1999, O'Brien et al. 2016). Ecologists often try to infer the functional state of freshwater ecosystems from structural attributes (by using functional traits of species) as well as how changes in assemblage composition, especially the replacement or loss of species, will alter rates of ecological processes (Boulton 1999, Karr 1999, Dale and Beyeler 2001, Tilman 2001, Bergfur et al. 2007, Palmer and Febria 2012). However, direct measurements of ecosystem function are needed to capture the complex and dynamic biophysical processes that result from interacting abiotic and biotic components (Palmer and Febria 2012),

 $E-mail\ addresses:\ ^3piet.verdonschot @wur.nl,\ equal\ contribution;\ ^4gea.vanderlee @wur.nl,\ equal\ contribution;\ ^5ralf.verdonschot @wur.nl,\ equal\ co$

such as leaf-litter breakdown (Gessner and Chauvet 2002) and ecosystem metabolism (Fellows et al. 2006).

It is important to measure both structural and functional properties of ecosystems if we desire to accurately characterize the overall ecological integrity of an ecosystem. However, surprisingly few studies have examined both structural and functional responses to one or more stressors in freshwater ecosystems. We therefore organized a special session entitled "Navigating between ecosystem structure and functioning in research and management: An overview of current knowledge" at the 2018 meeting of the Society for Freshwater Science held in Detroit, Michigan, USA. Participants collectively provided a broad overview of how structural and functional measures of freshwater ecosystems respond to different levels of anthropogenic stress. Our aim was to identify combinations of structural and functional indicators that could help water managers assess the ecological condition of their water bodies, and thereby aid in informing the specific management activities likely to be most effective in restoring degraded stream ecosystems. The contributions to this series of papers include several that were based on presentations made at the special session along with other papers that were submitted in response to a general call for papers we made following the conference.

CONTRIBUTIONS TO THE STATE-OF-THE-SCIENCE ON STRUCTURE-FUNCTION INDICATORS

Three contributions in this series of papers compared structural and functional responses across sites surrounded by different land-use types. Each of these studies was conducted within a different policy context, including New Zealand's National Policy Statement for Freshwater Management (Clapcott et al. 2020), the European Union's Water Framework Directive 2000/60/EC (Van der Lee et al. 2020), and the United States' Clean Water Act (Munn et al. 2020), indicating a global recognition of the desire to use both structural- and functional-based measures of ecological condition to inform water policy and management. Clapcott et al. (2020) applied the New Zealand ecological integrity framework to the Tukituki River catchment, which has been altered by intensive agriculture and exotic forestry. The framework offered insights into how structural attributes (based on plant biomass and both invertebrate and fish species composition) are potentially influenced by environmental factors like water quality, water quantity, and physical habitat. They observed that the ecological processes of metabolism and decomposition of cotton strips were not strongly correlated with the structural metrics they measured. Van der Lee et al. (2020) also compared the response of structural metrics (based on invertebrate composition) and functional metrics (based on decomposition of a standardized organic substrate) to multiple stressors associated with agricultural land use and wastewater treatment plant effluent. In their study, several structural metrics were negatively related to measures of toxic pollution, but decomposition was more complexly related to the measured stressors. Munn et al. (2020) examined the degree to which structural metrics based on invertebrate and fish species composition covaried with metabolism in streams across gradients of agricultural and urban land use. These authors did not observe a relationship between invertebrate structural metrics and stream metabolism, but they did observe a weak relationship between the fish metrics and metabolism. They also pointed out the importance of recognizing landscape-specific context in interpreting metabolism measures by identifying the environmental factors that control stream metabolism. Another contribution in this special series by de Brouwer et al. (2020) documented how invertebrate structural metrics and functional traits responded to the reintroduction of large wood in sand-bed lowland streams. The addition of large wood to the stream channels resulted in major changes in instream environmental conditions as well as structural changes in the invertebrate assemblages. However, the only trait characteristic of the invertebrate assemblages that consistently increased with the addition of large wood was a high affinity for hard substrates.

A major observation in each of these studies was that there may not always be a clear connection between measures of ecological structure and function. These findings are consistent with general trends uncovered from a literature review conducted by Feckler and Bundschuh (2020). They showed that although measures of structure and function were often correlated, the microbially mediated leaflitter decomposition can also remain stable, increase, or exhibit a U-shaped response with changes in the value of structural metrics (e.g., taxonomic diversity). Similarly, Verdonschot and van der Lee (2020) provided other examples from the literature that magnitude and direction of structural and functional measures can respond in a similar, complementary, or even contradictory way depending on the stressor. Weak correlations between measures of structural metrics and ecological processes indicate that ecological processes may also be influenced by other unmeasured factors (e.g., fungi and bacteria), there may be a loss of certain keystone species, or that single, site-based assessments of structure may be mismatched in either time or space with assessments of functional attributes (Clapcott et al. 2020, Feckler and Bundschuh 2020, Munn et al. 2020, Van der Lee et al. 2020). Furthermore, stressors may not affect overall measures of assemblage structure but could alter the functional properties of individual species, which can result in U-shaped or inverted U-shaped functional response patterns (Feckler and Bundschuh 2020).

When structural and functional metrics differ in how they respond to stressors, they provide different information and relying on just structural metrics can lead to incorrect inferences regarding the overall integrity of an ecosystem (Clapcott et al. 2020, Feckler and Bundschuh 2020, Munn et al. 2020). However, despite previous efforts to provide criteria for interpreting functional measures (e.g., Young et al. 2008), it is still difficult to provide interpretable and robust insights regarding the ecological condition of stream ecosystems based on functional attributes because of the complexity of functional responses to stressors. It is therefore important to provide guidance to freshwater managers regarding which measures are most useful in producing information relevant to management goals, as was done by Evans-White et al. (2020). These authors aimed to inform USA assessment and regulatory agencies about which measures of detrital processes are responsive to nutrient stress. They concluded that litter stoichiometry and decomposition rates are good candidate metrics for detrital processes because they are predictable over time and are sensitive to P enrichment. In particular, measuring litter stoichiometry may require less human and monetary resources to assess nutrient stress than traditional metrics based on algal assemblage structure and would be greatly beneficial to stream managers (Evans-White et al. 2020).

FUTURE DIRECTIONS

Overall, it appears that the high number of potential stressors together with high environmental variability may complicate our ability to integrate measures of ecosystem structure and function to improve assessments of stream ecological condition. Changes in species assemblages, such as the disappearance of a single key species caused by certain stressors, could imply the loss of certain functions, resulting a change in ecosystem functioning. To better integrate measures of ecosystem structure and function, both Feckler and Bundschuh (2020) and Verdonschot and van der Lee (2020) concluded that future studies should focus on the development of species traits because traits shape species' responses to environmental factors and how species influence ecosystem functions (e.g., Violle et al. 2007). For example, the trait-based SPEAR approach as applied by van der Lee et al. (2020) seems promising in diagnosing potential causes of adverse effects. Also, important functions of ecosystem components could be identified from structural attributes by using traits as shown by the study of de Brouwer et al. (2020). On the other hand, more complete knowledge is required of the functional performance of organisms. For example, the ability of microbial species to establish on leaf litter along with measures of their decomposing efficiency could provide a metric that integrates microbial assemblage structure and the function of leaf-litter decomposition (Feckler and Bundschuh 2020).

The integration of structural and functional measures will also require more knowledge on how multiple stressors interact to affect individual species and their trophic and non-trophic (e.g., ecosystem engineering) contributions to functions. Also, stressors do not act independently on single

traits but rather on the suite of multiple, and likely interacting, traits that occur within species (Pilière et al. 2016). For example, the adaptive value of a particular trait, the complementarity or reinforcement in a suite of traits, and a species' plasticity in resource requirements determine the functional role of a species in a community. Therefore, a better understanding and quantification of the role of individual species and species combinations in the functioning of stream ecosystems could help improve the diagnosis of what stressors are most influencing ecosystems and our ability to predict the effects of stressors in freshwater ecosystems (Verdonschot and van der Lee 2020). Potentially, the development of molecular technology that allows for identification and characterization of the functional traits of aquatic biota, especially microbial species (Sims et al. 2013), could improve our understanding of ecosystem functioning and, thus, further improve the assessment of ecological integrity (Feckler and Bundschuh 2020, Verdonschot and van der Lee 2020).

CONCLUDING REMARKS

This series of papers represents an important step toward the understanding of how structural and functional attributes of stream ecosystems respond to different levels and combinations of anthropogenic stress. The varying response of structural and functional metrics to stressors suggests that including functional metrics would result in a more complete assessment of the overall ecological integrity of a stream ecosystem. However, the complexity of functional responses to stressors and the influence of landscape-specific context on this response may still hamper the interpretability of functional measures regarding the ecological condition of stream ecosystems. Therefore, we suggest that future research should focus on the measures that integrate ecosystem structure and function, such as the identification and refinement of species traits that are clearly associated with important functional properties of species and whose responses to different anthropogenic pressures can aid in informing the specific management activities likely to be most effective in restoring degraded stream ecosystems.

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