

# Perspectives on the context-dependency of stream community responses to contaminants

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## SUMMARY

1. Natural variation in the structure and function of aquatic communities along environmental or spatiotemporal gradients can influence how systems respond to biotic and abiotic disturbances. Although these context-dependent responses are a well-established element of basic ecology, they have received little attention from an ecotoxicological perspective.
2. As the scope of freshwater bioassessment expands from single catchments to broad-scale, regional surveys, it has become apparent that community responses to contaminants can vary significantly among locations. This variability is generally considered a nuisance and an impediment to recognising ecological patterns; however, natural spatiotemporal variation in communities also provides opportunities to test hypotheses about context-dependent responses to contaminants in aquatic ecosystems.
3. This study presents three examples of context-dependent responses of benthic stream communities to contaminants. We show how longitudinal variation in community composition, the development of tolerance to contaminants and exposure to multiple stressors influence the historical context of a community and hence may determine community responses to contaminants.
4. Aquatic ecotoxicologists have made significant progress identifying abiotic factors that influence contaminant bioavailability and toxicity. A similar effort could be undertaken to identify specific ecological factors (e.g. community composition, natural disturbance regimes and life-history characteristics) that contribute to variation in susceptibility of communities to contaminants. Understanding the nature of context-dependent responses and the mechanisms responsible for variation among communities should be a key element of ecological risk assessment and a research priority in ecotoxicology.

*Keywords:* benthic macroinvertebrates, contaminants, context-dependent responses, ecotoxicology, streams

## Introduction

The relative importance of biotic and abiotic factors in structuring biological communities varies among locations and along environmental gradients, often resulting in context-dependent responses of communities. The basic hypothesis motivating research on context dependency is that the relative importance of factors structuring communities, such as physical disturbance or species interactions, will be greater in some communities

than in others. Recognising the importance of context-dependent responses has improved our understanding of ecological patterns and processes (Sousa, 1979; Cardinale, Nelson & Palmer, 2000). For example, knowing that the importance of a species can vary longitudinally along a stream continuum (Wellnitz & Poff, 2001), along disturbance gradients (Menge & Sutherland, 1987), across its distribution range (Power *et al.*, 1996) or with trophic structure (Hooper *et al.*, 2005) can help explain spatial variation in the strength of species interactions.

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While the idea of context-dependent responses is well established in ecology (Cardinale *et al.*, 2000; Nowlin & Drenner, 2000), it has received little attention in ecotoxicology (Clements, Hickey & Kidd, 2012; Dinh Van *et al.*, 2013; Merriam *et al.*, 2013). Previous studies have shown that the effects of pesticides on aquatic communities may depend on the types of predators present (Relyea, Schoeppner & Hoverman, 2005) and initial community composition (Rohr & Crumrine, 2005), suggesting that the concept of context dependency can be extended to include variation in responses of communities to contaminants and other anthropogenic stressors (Table 1). Here, we provide a perspective on how an understanding of natural variation in stream benthic communities can improve our ability to predict impacts of contaminants.

### Context-dependent responses and ecotoxicology

Stream communities are structured by a combination of local, regional, historical, climatic and biogeographic factors that operate across broad landscapes (Poff, 1997; Finn & Poff, 2005). Because of the traditional emphasis on individual streams in bioassessment, our understanding of the relative importance of regional factors is relatively poor, and therefore, our ability to predict variation in effects of contaminants among communities is limited. As the focus of these studies shifts from individual catchments to broad-scale regional surveys (Clements *et al.*, 2000; Walsh *et al.*, 2005; Stoddard *et al.*, 2006; Chinnayakanahalli *et al.*, 2011; Beketov *et al.*, 2013), it has become increasingly apparent that effects of contaminants can also vary among locations (Schmidt *et al.*, 2012). Although some of this variation is due to abiotic factors that determine contaminant bioavailability,

natural differences in community composition may also influence responses. Our basic tenet is that many of the ecological factors which structure communities (e.g. food-web structure, disturbance regime, life-history characteristics and contaminant exposure history) will also determine responses to contaminants.

Consideration of context-dependent responses could improve our ability to establish quantitative relationships between contaminants and community structure. Unlike effects of anthropogenic stressors at lower levels of ecological organisation (e.g. organs, individuals, populations), which are relatively consistent, effects at the level of whole communities and ecosystems are more variable and often not well understood (Clements & Rohr, 2009). This is partly a result of a poor understanding of the underlying mechanisms. However, differences in the responses of communities from different locations may also contribute significant variation, particularly in studies conducted at regional scales. Failure to account for context-dependent responses impedes our ability to distinguish between reference and contaminated sites. Variation in the responses of communities to contaminants also contributes significant uncertainty to site characterisation during ecological risk assessment. By simply assuming that communities from different locations respond similarly to contaminants, effects can easily be either underestimated or overestimated.

Aquatic ecotoxicologists generally have a very good appreciation for how abiotic factors [e.g. temperature, pH, water hardness and dissolved organic carbon (DOC)] influence contaminant bioavailability. In fact, these factors are routinely included in the development of site-specific water quality criteria. In contrast, our understanding of how community structure affects responses to contaminants is quite limited. Although it

**Table 1** Examples of context-dependent responses of benthic communities to contaminants

System	Stressors	Response	References
Marine periphyton	Arsenate, Tributyltin	Effects varied with history of contaminant exposure	Blanck & Wangberg (1988), Blanck & Dahl (1996)
Freshwater diatoms	Metals	Sensitivity varied longitudinally	Medley & Clements (1998)
Freshwater macroinvertebrates	Metals	Sensitivity varied longitudinally	Kiffney & Clements (1996)
Freshwater macroinvertebrates	Metals, acidic pH, UV-B	Sensitivity to acidic pH or UV-B radiation depended on exposure history to metals	Courtney & Clements (2000), Kashian <i>et al.</i> (2007)
Freshwater macroinvertebrates	Metals and predation	Effects of predation greater in metal-contaminated systems	Kiffney (1996), Clements (1999)
Damselfly populations	Metals and climate change	Local thermal adaptation determined responses to Zn	Dinh Van <i>et al.</i> (2013)
Mountain streams	Mining and conductivity	Effects depended on land use	Merriam <i>et al.</i> (2013)

is unlikely that natural variation in community composition along environmental gradients could be used to develop water quality criteria, an improved understanding of how communities from different locations respond to contaminants could improve our ability to predict effects. For example, regional surveys have demonstrated that the composition of stream fish and invertebrate communities is strongly influenced by landscape features such as latitude, drainage area, flow and temperature regime (de Zwart *et al.*, 2006; Chinnayakanahalli *et al.*, 2011). These differences in the habitat template could be accompanied by different responses to contaminants. We believe that a critical first step in the development of context-dependent assessments will be to link landscape-level predictors of aquatic communities to contaminant responses (Fig. 1). Below, we present three examples where variation in community composition influenced responses of benthic communities to contaminants. Although we do not suggest these are universal patterns, we contend that longitudinal variation in community composition, the development of tolerance to contaminants and the exposure of communities to multiple stressors provide opportunities to test specific hypotheses about context-dependent responses in aquatic ecosystems.

### Longitudinal variation and context-dependent responses

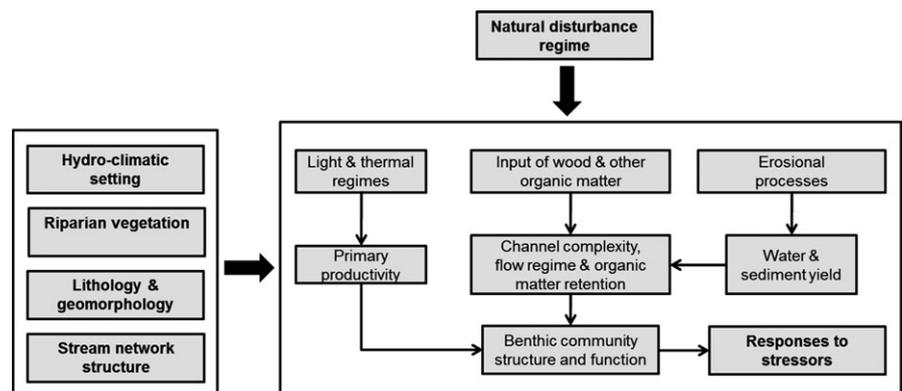
Stream ecologists have long appreciated the importance of longitudinal variation in determining the structure of benthic communities and rates of ecosystem processes. This relationship is conceptualised in two broad categories of models: (i) a linear model embodied in the river continuum concept (RCC) (Vannote *et al.*, 1980), which posits gradual downstream changes in hydrologic and geomorphic processes that are paralleled by modifications in community structure and ecosystem processes;

and (ii) nonlinear models which suggest that river ecosystems exhibit significant physical discontinuities (e.g. sediment size, wood abundance, channel complexity) from headwaters to river mouths (Rice, Greenwood & Joyce, 2001; Benda *et al.*, 2004; Kiffney *et al.*, 2006). Common to both models is the prediction that natural variation in the physical habitat template (*sensu* Southwood, 1977) results in concomitant changes in life-history traits, species abundance, community composition, trophic structure, functional feeding groups and species interactions (e.g. Rice *et al.*, 2001).

Natural disturbance events, including floods, fires and landslides, which dynamically create and maintain certain habitat attributes, are major drivers of spatial and temporal variation in structure and function of stream ecosystems. Thus, just as habitat patches create discontinuities in space, disturbances create habitat discontinuities in time (Benda *et al.*, 2004). Moreover, the natural disturbance regime (e.g. intensity, frequency and predictability of large floods relative to baseline conditions) likely differs among locations within a catchment, among catchments and over time according to regional biogeoclimatic constraints (Poff & Ward, 1990; Benda *et al.*, 2004). These differences in disturbance regime modify the intensity and temporal distribution of selective forces acting on populations that partly determine their response to environmental stressors (Fisher, 1977; Poff & Ward, 1990). A potential consequence of natural variation in the physical habitat template across a river network is differential sensitivity of communities to environmental stressors, including contaminants.

Remarkably few studies have explicitly tested the hypothesis that effects of environmental stressors on benthic communities vary longitudinally along a river network, although such research has been recommended for decades (Poff & Ward, 1990). Medley & Clements (1998) reported that benthic diatom communities collected from

**Fig. 1** Conceptual model showing the hypothesised influence of landscape-level characteristics (regional climate, riparian vegetation, geomorphology and river network structure) and disturbance regime on catchment-level processes. We predict that responses of benthic communities to contaminants and other anthropogenic stressors will vary among streams and be determined by both landscape- and catchment-level processes.



a relatively pristine, high-altitude site in Colorado were less sensitive to metals than communities from a lower altitude site. These differences were attributed to natural longitudinal variation in community composition as diatoms from the upstream site were dominated by metal-tolerant, early-successional species, whereas downstream communities were dominated by sensitive, late-successional taxa. Differential sensitivity to contaminants may also result from differences in natural disturbance regimes that vary longitudinally. Although few studies have considered the effects of natural variability on sensitivity of stream communities to contaminants (Kiffney & Clements, 1996), research conducted in marine ecosystems showed that communities from highly variable systems were more tolerant to chemical stressors (Fisher, 1977; Hyland, Hoffman & Phelps, 1985). Consequently, researchers have speculated that communities from these naturally variable ecosystems may be 'pre-adapted' to anthropogenic stressors (Rapport, Regier & Hutchinson, 1985). Longitudinal variation in stream temperature, which influences body size and other key life-history characteristics of species, may also influence responses to contaminants. For example, populations of the mayfly *Rhithrogena hageni* were more sensitive to metals when they were dominated by smaller, early instars (Clark & Clements, 2006).

Although longitudinal position within a river network determines disturbance regime, community composition and life-history characteristics of the resident populations, the mechanisms responsible for context-dependent responses of communities to contaminants remain largely elusive. A better understanding of variation in responses among communities can be achieved by conducting comparative studies across a range of catchments and by viewing river systems from a dynamic network perspective (Fisher, 1997; Benda *et al.*, 2004). Empirical studies have generally confirmed the importance of network structure in determining physical habitat heterogeneity (Rice *et al.*, 2001; Benda *et al.*, 2004), water chemistry (Kiffney *et al.*, 2006) and invertebrate and fish diversity (Osborne & Wiley, 1992; Rice *et al.*, 2001; Kiffney *et al.*, 2006). For example, the network dynamic hypothesis (NDH) predicts that disturbance frequency and intensity will be higher near or immediately downstream of tributary confluences, especially if the tributary basin was recently disturbed (Benda *et al.*, 2004). At present, there are no published studies that explicitly test predictions of the NDH as they relate to species responses to environmental stressors, but natural differences in community composition provide obvious opportunities to test for context-dependent responses. Benthic communities at

recently disturbed confluences are likely to be dominated by species that possess life-history traits (e.g. high dispersal ability, semi-voltinism) allowing them to colonise and persist in stressful environments (Poff & Ward, 1990). These traits may also confer greater tolerance or persistence to novel stresses such as contaminant exposure (Fisher, 1977; Poff & Ward, 1990). Furthermore, we can scale up from potential reach-level differences in community sensitivity to the subcatchment or catchment scale because of the hierarchical nature of river habitats (Frissell *et al.*, 1986). For example, network shape (trellis versus dendritic) partly determines the importance of tributary confluences on physical heterogeneity, with dendritic networks promoting confluence effects throughout the catchment. In other words, the potential difference in community tolerance may depend on whether a tributary junction is part of a dendritic network, where relative geomorphic effects on the main stem are greater than for a similar-sized tributary in a trellis-shaped network. Thus, we would hypothesise that benthic communities in dendritic river networks are more tolerant of novel environmental stressors because species making up these communities have evolved traits conferring greater tolerance relative to species assembled in trellis-shaped networks.

In conclusion, this section emphasises the key roles of river network structure, disturbance regime, geology and climate in determining benthic community structure and function in river networks. There is some evidence that the resulting natural variation of benthic communities in space and time can confer differential sensitivity to environmental stress (e.g. Medley & Clements, 1998). Expanding upon these few studies is essential if we are to gain a general understanding of how position within stream networks determines community responses to environmental stressors. The NDH provides a useful conceptual framework to address the context dependency of contaminant effects on river ecosystems.

### Community-level tolerance and context-dependent responses

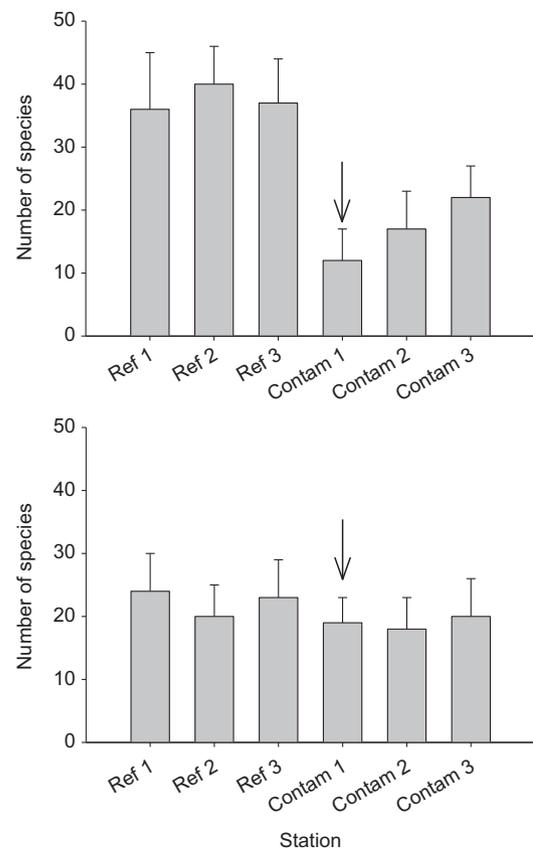
Long-term exposure of populations to contaminants often results in increased tolerance relative to naïve or unexposed populations. The mechanisms responsible for the greater tolerance can be broadly separated into two categories: physiological acclimation and genetic adaptation (Posthuma & Van Straalen, 1993). Although increased tolerance in contaminated environments is generally considered a population-level phenomenon, it has important implications for communities. A shift in

community composition that results from the replacement of sensitive species by tolerant species (termed 'interspecific selection'; Blanck & Wangberg, 1988) is a common response in contaminated ecosystems and a reliable indicator of impacts. Variation in the way that communities from reference and polluted environments are affected by toxicants is another example of a context-dependent response. If exposure to a contaminant results in the loss of sensitive species, then we would expect the restructured community to be more tolerant to this stressor. In addition to improving our basic understanding of how contaminant effects vary among locations, these context-dependent responses have very practical implications for the selection of reference sites in biomonitoring studies. For example, we predict that the elimination of sensitive species from a location, either by natural or by anthropogenic disturbances, would make it more difficult to detect differences between reference and contaminated sites (Fig. 2). This is a common phenomenon in urban, agricultural or other disturbed catchments where communities have been truncated by exposure to a variety of physical or chemical stressors (Stoddard *et al.*, 2006).

Increased community tolerance following exposure to contaminants has been demonstrated in numerous aquatic ecosystems and is the basis of the pollution-induced community tolerance (PICT) concept (Blanck & Wangberg, 1988; Tlili *et al.*, 2015). Although the majority of such studies have been conducted with microbial communities (Blanck, 2002), analogous responses may occur in stream macroinvertebrate communities. For example, microcosm experiments conducted with macroinvertebrates from a metal-polluted stream showed that communities collected downstream from metal inputs were more tolerant to metals than those from an upstream reference site (Fig. 3). Although the approach in this study is not strictly an example of applying the PICT concept, the observed increase in tolerance to metals was a direct result of community restructuring and the elimination of metal-sensitive species. The key strength of the experimental approach was that observing increased tolerance to metals provided an additional line of evidence that metals were directly responsible for the alteration in community structure observed in the field.

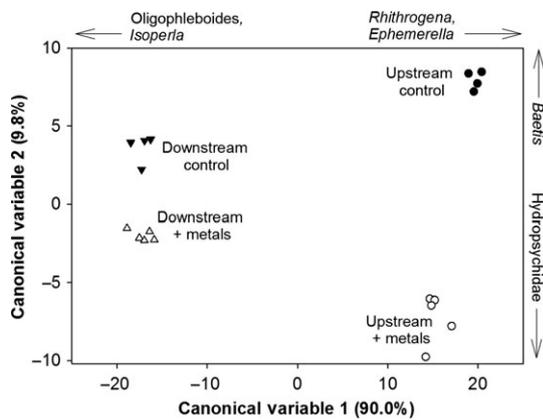
#### Cost of tolerance and context-dependent responses to multiple stressors

Increased tolerance to a particular contaminant may result in a context-dependent response to other contaminants or stressors. Evolutionary theory has long considered the



**Fig. 2** Hypothetical effects of contaminants on communities from undisturbed (upper panel) and disturbed (lower panel) streams. Study designs for both streams include three uncontaminated (reference) sites and three downstream sites along a gradient of contamination (arrows indicate the source of contamination). We predict that elimination of sensitive species truncates the communities in the disturbed streams and reduces effects of contaminants, making it more difficult to detect differences between disturbed and undisturbed sites.

phenomenon of tradeoffs or adaptive costs associated with a variety of natural and anthropogenic factors. A classic example is the co-evolutionary relationship between plants and herbivores, where production of chemical defences to repel herbivores often decreases fitness of plants (Pilson, 2000). Exposure of populations to contaminants can also result in the development of tolerance that may come at a cost to fitness, suggesting a trade-off between the benefit of tolerance to a contaminant and the reduction in fitness associated with tolerance (Durou, Mouneyrac & Amiard-Triquet, 2005; Arnold, Hodson & Langdon, 2008). For example, Marchand *et al.* (2004) observed lower genetic diversity in flounder (*Platichthys flesus*) populations from contaminated sites compared to reference sites. Reduced fecundity and poor condition of fish at the polluted site were associated with the cost of resistance for those genotypes.



**Fig. 3** An example of increased tolerance in macroinvertebrate communities exposed to metals in stream microcosms. Canonical discriminant analysis was used to show responses of communities collected from an upstream reference station (circles) and a downstream contaminated station (triangles). Benthic communities in metal-treated streams from both sites were exposed to a mixture of Cd, Cu and Zn for 10 days (see Clements, Cadmus & Brinkman, 2013, for detailed methods). The separation between control and metal-treated microcosms was much greater for the upstream reference community, indicating greater effects of metals. The amount of variation explained and the taxa responsible for separation along each canonical axis are shown.

Tolerance costs may not be restricted to population-level responses, but can extend to communities. As described above, community tolerance can arise from either increased resistance to a contaminant at the population level or through the elimination of sensitive species. The implications may be significant, but relatively few studies have investigated the cost of tolerance at the community level. Nevertheless, tolerant benthic communities from streams impacted by metals were more susceptible to several chemical, physical and biological stressors than communities collected from reference sites (Clements, 1999; Courtney & Clements, 2000; Kashian *et al.*, 2007). Specifically, communities tolerant to metals were more sensitive to acidic pH than communities from a reference site with no history of previous metal exposure (Courtney & Clements, 2000). Likewise, metal-tolerant benthic communities were more sensitive to ultraviolet radiation (UV-B; Kashian *et al.*, 2007). A similar pattern was observed when stonefly predators were introduced to macroinvertebrate communities from metal-polluted and reference streams; despite greater metal tolerance, communities from the polluted site were significantly more susceptible to stonefly predation (Clements, 1999).

The observation that tolerance to contaminants may impose some cost is consistent with predictions from physiological ecology and evolutionary theory. In the

light of the evidence that tolerance to a specific stressor may increase the susceptibility to other stressors, it is important to identify the context-dependent mechanisms by which 'cost' operates. However, studies quantifying cost of tolerance are relatively rare so that caution is required when attempting to distinguish life-history changes from the direct effects of contaminants (Posthuma & Van Straalen, 1993). Furthermore, measures of fitness can include large uncertainties, they are difficult to quantify and the relationship between fitness and tolerance is often weak (Tanaka & Tatsuta, 2013). To improve our understanding of context-dependent responses to contaminants, we need to develop better quantitative relationships among contaminant exposure, tolerance and fitness costs. Tanaka & Tatsuta (2013) present a framework based on laboratory estimates to quantify the cost of tolerance at the population level, but additional work is necessary to develop an analogous framework for communities.

An understanding of context dependency could also improve our ability to assess ecological responses to multiple stressors. Co-occurrence of contaminants with other stressors is common in freshwater ecosystems; however, our understanding of the complex and often interactive effects of multiple stressors is limited. Responses of communities to multiple stressors are spatially variable, change temporally and are often difficult to predict. For example, the ecological effects of urbanisation on benthic and fish communities vary regionally (Bryant & Carlisle, 2012). Some of this regional variation is a result of legacy disturbances within a catchment, which can truncate communities and obscure responses to urbanisation or other stressors (Walsh *et al.*, 2005; Cuffney *et al.*, 2010). Similarly, interactions between contaminants and stressors associated with global climate change (e.g. increased temperature, altered hydrology) can result in context-dependent responses (Moe *et al.*, 2013). In addition to the direct effects of climate change on water temperature and hydrology, indirect effects may occur through complex interactions with terrestrial processes. For example, shifts in vegetation from forest to shrub-steppe or grassland-dominated ecosystems are predicted for some mountain basins in the western United States (Davis *et al.*, 2013). These changes in vegetation will likely reduce concentrations of DOC delivered to the stream, resulting in increased bioavailability of contaminants (Brooks, Mcknight & Clements, 2007) and greater flux of harmful UV-B radiation to stream benthos (Kiffney, Clements & Cady, 1997; Zuellig *et al.*, 2007; Clements *et al.*, 2008). Other climate-induced changes that could modify the effects of contaminants on benthic

food webs include increased water temperature and altered precipitation patterns. Similarly, populations adapted to long-term pollution or other stressors may show greater susceptibility to effects of climate change (Moe *et al.*, 2013). Regardless of the combinations of co-occurring stressors, differences in environmental conditions and exposure history will likely influence ecological responses to contaminants and other disturbances (Paine, Tegner & Johnson, 1998), even in well-studied systems (Hecky *et al.*, 2010).

In summary, over the past 20 years aquatic toxicologists have made significant progress identifying biogeochemical factors that influence contaminant bioavailability and toxicity. A similar effort undertaken by ecotoxicologists is likely to identify ecological factors that contribute to variation in susceptibility of communities to contaminants. Although variability in the responses to contaminants is often considered a nuisance and an impediment to the development of predictive models (Clements *et al.*, 2012), research on context-dependent responses could also be quite informative. Just as ecologists would not expect all communities to respond to disturbance in the same way, aquatic toxicologists should not expect communities from different locations to respond similarly to contaminants. Understanding the nature of context-dependent responses and factors that contribute to variation among communities should be a key element of ecosystem characterisation during ecological risk assessment and a research priority in ecotoxicology.

## Acknowledgments

Funding to support our research on context-dependent responses of benthic communities was provided by the U.S. Environmental Protection Agency, the U.S. Geological Survey and the NIEHS Basic Superfund Research Program. Comments by Ahmed Tlili, Mark Gessner and two anonymous reviewers significantly improved this manuscript. We are especially grateful to Drs. Tlili and Gessner for their invitation to contribute to this special issue on the interface between ecology and ecotoxicology.

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(Manuscript accepted 26 April 2015)