

Critical Review

COMMUNITY RESPONSES TO CONTAMINANTS: USING BASIC ECOLOGICAL PRINCIPLES TO PREDICT ECOTOXICOLOGICAL EFFECTS

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Abstract—Community ecotoxicology is defined as the study of the effects of contaminants on patterns of species abundance, diversity, community composition, and species interactions. Recent discoveries that species diversity is positively associated with ecosystem stability, recovery, and services have made a community-level perspective on ecotoxicology more important than ever. Community ecotoxicology must explicitly consider both present and impending global change and shift from a purely descriptive to a more predictive science. Greater consideration of the ecological factors and threshold responses that determine community resistance and resilience should improve our ability to predict how and when communities will respond to, and recover from, xenobiotics. A better understanding of pollution-induced community tolerance, and of the costs of this tolerance, should facilitate identifying contaminant-impacted communities, thus forecasting the ecological consequences of contaminant exposure and determining the restoration effectiveness. Given the vast complexity of community ecotoxicology, simplifying assumptions, such as the possibility that the approximately 100,000 registered chemicals could be reduced to a more manageable number of contaminant classes with similar modes of action, must be identified and validated. In addition to providing a framework for predicting contaminant fate and effects, food-web ecology can help to identify communities that are sensitive to contaminants, contaminants that are particularly insidious to communities, and species that are crucial for transmitting adverse effects across trophic levels. Integration of basic ecological principles into the design and implementation of ecotoxicological research is essential for predicting contaminant effects within the context of rapidly changing, global environmental conditions.

Keywords—Community ecotoxicology Contaminant transport Global change Indirect effects Resistance/resilience

INTRODUCTION

More than 20 years ago, John Cairns, Jr., expressed frustration with the lack of a sound ecological foundation in the newly emerging field of ecotoxicology [1]. Several decades after the term *ecotoxicology* was introduced, many of the questions in aquatic toxicology and the techniques employed to address these questions remain solidly entrenched in a reductionist philosophy. Although the implementation of more sophisticated monitoring, analytical, experimental, and statistical techniques has greatly improved our ability to quantify the effects of contaminants on communities, environmental scientists still struggle with the often-bewildering complexity and variability of natural ecological systems. Therefore, this seems like an opportune time to evaluate progress within the field of ecotoxicology and highlight some of the recent developments that have improved our ability to predict responses to xenobiotics at higher levels of organization.

The present review focuses on community ecotoxicology, defined as the study of the effects of contaminants on patterns of species abundance, diversity, community composition, and species interactions [2,3]. Most of the significant paradigms in basic ecology were developed by researchers studying communities, and these hypotheses have direct applicability to community ecotoxicology (Table 1). From the descriptions of successional changes in plant associations to the theoretical treatment of island biogeography and the classic experimental studies conducted in the rocky intertidal zone, communities

have been a source of inspiration to ecologists. Improved understanding of basic ecological concepts, such as the importance of species interactions, the role of disturbance, stability–diversity relationships, and food-web structure, has enhanced the ability to predict effects of contaminants in aquatic and terrestrial ecosystems. If communities are defined by the strength of interactions among species [4], it follows that ecotoxicologists should account for these interactions when predicting responses to xenobiotics. Although species interactions will not be the major structuring force in all communities, in those situations where factors such as competition and predation are important, the relative strength of these interactions will likely influence how communities respond to anthropogenic disturbance.

For several reasons, communities are an appropriate level of biological organization in which to investigate contaminant effects. Because communities represent the midpoint between populations and ecosystems in the hierarchy of biological organization, they offer important insights regarding mechanisms of contaminant effects at lower levels and are intimately connected to socially relevant endpoints (e.g., ecosystem services) at higher levels. Furthermore, protecting community-level endpoints, such as species richness and diversity, is critical for maintaining ecological integrity. Because species richness is intimately linked to ecosystem function (e.g., primary production, energy flow, and nutrient cycling), maintaining a diverse community is essential for protecting ecosystem services, defined here as benefits received from ecosystems that contribute to the well-being of all organisms, including humans. Furthermore, species-rich communities often are more stable and recover from disturbance more

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Table 1. Significant theoretical advances in basic community ecology and their potential applications in ecotoxicology

Community paradigm	References	Ecotoxicological applications	References
Food-web theory	[108–110]	Contaminant transport models	[82,90–92,96,97,111]
Trophic cascade hypothesis		Biomagnification	
Ecological gradients	[112–114]	Biomonitoring	[115,116]
Information theory		Application of diversity indices	
Habitat template model		Species traits	
Theory of island biogeography	[117–119]	Community resilience	[33,34,36,39,119]
Ecological succession		Restoration ecology	
Competitive exclusion principle	[120,121]	Indirect effects of contaminants	[2,3,6,9,13,18,53]
Predator–prey theory			
Disturbance theory	[122,123]	Pollution-induced community tolerance	[52,55–57,69–72]
		Community conditioning hypothesis	
Hierarchy theory	[124]	Endpoint selection in ecological risk assessment	[125,126]
Intermediate disturbance hypothesis	[127–129]	Subsidy-stress gradients	[9,102,130–132]
Environmental stress gradients		Hormesis in toxicology	
Ecological thresholds	[42,43]	Contaminant-induced shifts in stable states	[47,48,51]
Species richness and ecosystem function	[74–79]	Measurement and assessment endpoints in ecological risk assessment	[125,133–136]
		Valuation of ecosystem services	

quickly than depauperate communities. Finally, the study of aquatic communities has played a prominent role in the recent expansion of state and federal biomonitoring programs in the United States. Community-level endpoints for algae, macro-invertebrates and fish are routinely included in the U.S. Geological Survey National Water-Quality Assessment Program (NAWQA; <http://water.usgs.gov/nawqa/>) and the U.S. Environmental Protection Agency (EPA) Environmental Monitoring and Assessment Program (<http://www.epa.gov/emap/>).

Several recent publications have provided comprehensive reviews or critiques of community ecotoxicology [2,3,5–9]. The objective of the present review is not simply to expand on these previous reviews but, rather, to highlight some of the emerging paradigms in the field. This review will emphasize those basic ecological principles that have the greatest potential to improve our ability to predict community responses to, and recovery from, contaminants and other anthropogenic stressors.

INDIRECT EFFECTS OF CONTAMINANTS ON COMMUNITIES

Indirect effects of xenobiotics are defined as a change in species interactions caused by a chemical, and recent evidence suggests that such effects might be more common than direct chemical effects [5–9]. Indirect effects can be transmitted within or across trophic levels of species-interaction webs by chemicals that cause sublethal effects (trait changes), lethal effects (density changes), or both (Fig. 1). Community ecologists are beginning to appreciate indirect effects that are mediated by changes in species traits rather than densities. In fact, trait-mediated indirect effects of consumers can have impacts on communities equal to or greater than those of density-mediated indirect effects [10]. The same is probably true for contaminants, because at concentrations commonly found in nature, xenobiotics almost certainly cause more trait changes than direct mortality does [11,12]. Indeed, the trait-mediated effects of pesticides on a host–parasite interaction were estimated to be larger than the density-mediated effects of the chemicals [13]. Unfortunately, trait-mediated indirect effects often are missed because of their subtlety. For instance, xenobiotics can alter species abundances merely by interfering with information transfer among organisms [14,15]. A single

chemical also can cause simultaneous trait- and density-mediated indirect effects. For example, atrazine was reported to immunosuppress frogs and increase snail densities (the first intermediate host for trematodes), both of which increased trematode infections in the frogs [13]. Although ecotoxicologists have long recognized the potential importance of indirect effects, these effects have remained understudied and not thoroughly incorporated into ecological risk assessment.

Recently, community ecology theory has been proposed as a framework for predicting indirect effects of contaminants to facilitate their integration into risk assessment [9]. By loosely treating contaminants as *predators* in species-interaction modules (Fig. 1), it was argued that scientists could forecast the direction and magnitude of pollution-induced indirect effects. Coupling this information with knowledge of direct toxicity, species richness, species-interaction strengths and trophic links and their distributions would then facilitate identifying *key species* whose loss (or, possibly, decline) could trigger secondary extinctions as well as fragile communities where the loss of a species, on average, could cause considerable reduction in system stability [16]. One value of this approach is that it adapts with changes in communities through time and space, an important feature given that the direction and magnitude of indirect effects of pollution can be dependent on community composition [8].

This community ecology, or pesticide-as-predator, approach to understanding indirect effects offers several insights for ecotoxicology [9]. For example, it becomes apparent that pollution can have both positive and negative indirect effects, that the direction of indirect effects often might alternate with consecutive trophic levels (Fig. 1a), and that certain chemicals occasionally can even increase diversity by directly reducing the abundance of competitive dominants (i.e., keystone chemicals) (Fig. 1b). Consequently, factors that determine the strength of top-down and bottom-up effects of organisms also might dictate the strength of contaminant-induced trophic cascades. Given that contaminants have many similarities to predators, multiple-predator theory [17] also might provide a framework for predicting indirect effects of contaminant mixtures on communities (Fig. 1c), an intimidating problem given the extraordinary number of possible mixtures and community compositions.

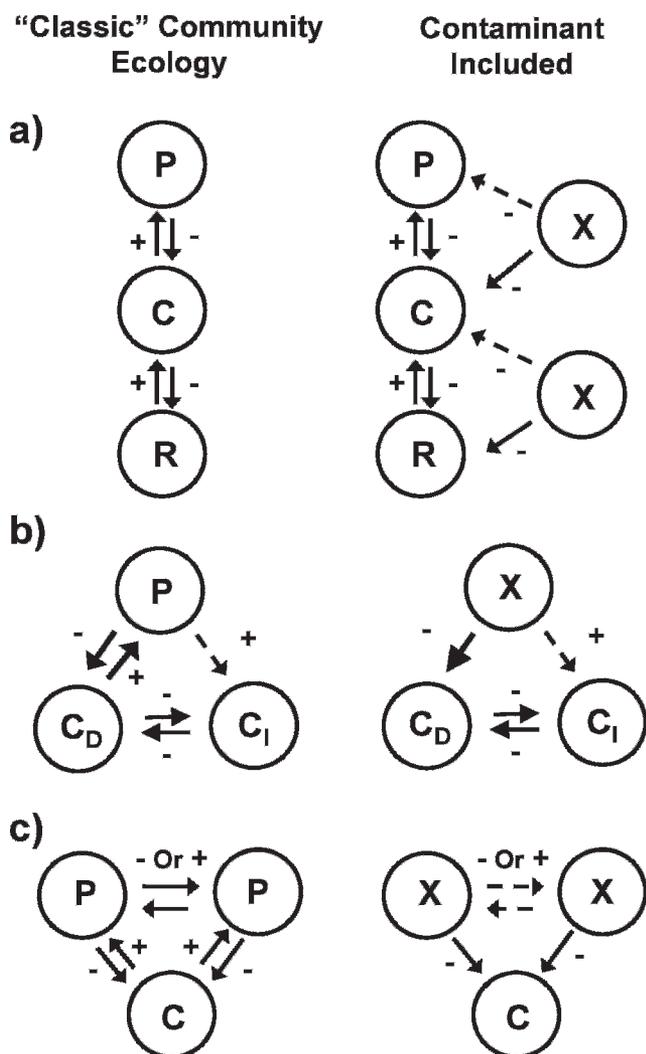


Fig. 1. Species-interaction modules depicting the hypothesized indirect effects of xenobiotics relative to the classic community ecology scenario. In these interaction modules, density-mediated interactions can be replaced by trait-mediated interactions to obtain the analogous trait-mediated indirect effects: (a) tritrophic interactions: Contaminants can have direct and indirect effects at three (and, sometimes, more) trophic levels, and the direction of the effects can often alternate with consecutive trophic levels; (b) keystone predation: Contaminant impacts on competitive dominant species (C_D) enable competitive inferior species (C_I) to persist, which can even result in increases in biodiversity; (c) multiple predators: Contaminants can interact additively, synergistically, or antagonistically with one another, similar to intraguild predators. Predators, consumers, resources, and xenobiotics are depicted by the letters P, C, R, and X, respectively. Dashed lines represent indirect effects; solid lines are direct effects. Positive and negative effects are signified by + and -, respectively.

By generating testable predictions regarding which communities will be sensitive to contaminants, which contaminants will be particularly insidious to communities, and which species are crucial for transmitting adverse contaminant effects, the interaction-web framework should help to direct research, management, and policy toward chemicals and chemical mixtures that are particularly insidious and toward communities and species that are particularly fragile. This approach has successfully predicted community-level contaminant effects where it has been adopted [18–23] (<http://www.epa.gov/waterscience/models/aquatox/validation/validation.pdf>), indicating that it holds great promise for moving community ecotoxicology closer to a predictive science.

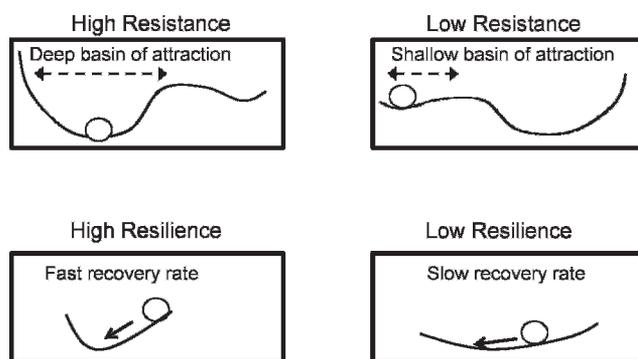


Fig. 2. Schematic demonstrating characteristics of resistance and resilience in communities [50]. The depth of the basin of attraction reflects the amount of disturbance a community can withstand before shifting to an alternative stable state, defined here as ecological resistance. The recovery rate is an indication of the resilience of the community.

However, considerable advances in our understanding of fundamental community ecology might still be necessary for this approach to have widespread and consistent predictive abilities.

RESISTANCE AND RESILIENCE OF COMMUNITIES

The theoretical concepts of resistance and resilience have figured prominently in the ecological literature for several decades [24] and have important practical applications in community ecotoxicology. *Resistance* is defined here as the ability of a community to maintain equilibrium conditions following exposure to a contaminant. In contrast, *resilience* is defined as the ability of a community to return to pre-disturbance conditions after a contaminant is removed (Fig. 2). A better understanding of the ecological factors that determine resistance and resilience will improve the ability to predict how communities respond to and recover from xenobiotics [2]. For example, the loss of resistance or resilience caused by chronic exposure to a stressor will increase the likelihood that communities will shift to alternative stable states [25,26]. Because of lower species diversity, communities recovering from chemical perturbations may be more vulnerable to other anthropogenic stressors, including climate change, ultraviolet (UV)-B radiation, and invasive species [27,28]. In one of the earliest investigations of resistance and resilience to contaminants, Kaufman [29] reported that communities obtained from high stress environments were more tolerant than those from stable environments. Support also exists for the hypothesis that communities in *naturally* disturbed habitats are preadapted to disturbance and actually more resistant to anthropogenic stressors [30]. Reconciling these different perspectives on stressor interactions will be necessary to predict how communities will respond to multiple stressors. It is well established that effects of multiple perturbations often are not additive [31]; therefore, superimposing disturbance on a community already subject to a chemical stressor may cause unexpected “ecological surprises” [26,32].

Resilience and recovery from disturbance

Improvements in water or sediment quality following remediation at contaminated sites are expected to produce improvements in aquatic communities. Predicting recovery trajectories after remediation is difficult, however, primarily because resilience is influenced by a wide array of biotic and

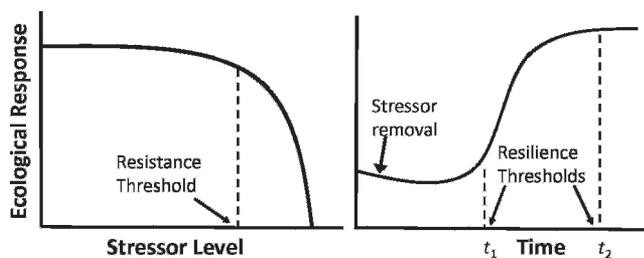


Fig. 3. Resistance and resilience thresholds in community ecotoxicology. A resistance threshold is the contaminant concentration at which we see an abrupt change in the community response. Resilience thresholds are the two points in time where recovery is initiated (t_1) and completed (t_2) after stressor removal.

abiotic factors that operate across landscape scales [33–37]. Failure to account for local and regional factors may explain why some studies were unable to document recovery following restoration [38]. Community recovery following improvements in water quality also may be delayed by the establishment of tolerant species that outcompete and impede recolonization by sensitive species, a phenomenon reported in acid-polluted lakes [39]. In addition, the specific nature of the disturbance (e.g., physical vs chemical) [40], the amount of natural variation that a community experiences [30], the presence of other stressors [31], and functional redundancy [26] determine recovery rates in aquatic communities.

In addition to identifying local and regional factors that influence recovery, appropriate experimental designs are essential for demonstrating cause-and-effect relationships between restoration and community responses. In a long-term assessment of recovery from acidification, McClurg et al. [36] noted the lack of consistent pre- and posttreatment data in most restoration studies. If contaminant remediation were conducted like a true experiment, requiring consistent pre- and posttreatment data, or at least employed principles of adaptive management, then the ability to demonstrate recovery would be greatly improved. For some classes of stressors, particularly recalcitrant compounds (e.g., polychlorinated biphenyls [PCBs] or dioxins) or sediment contaminants that require removal, a long-term perspective is necessary to separate responses to restoration from those associated with other anthropogenic stressors. The lack of pretreatment data and the limited number of long-term studies investigating recovery after contaminant removal have important practical implications. In a critical review of dredging programs at U.S. EPA Superfund megasites (defined as sites where cleanup costs are expected to exceed \$50 million), the National Research Council concluded that inadequate study designs and lack of pretreatment data have seriously hindered the ability to evaluate restoration effectiveness [41].

Ecological thresholds

Theoretical and empirical studies suggest that some communities show abrupt, nonlinear changes in structure or function in response to perturbations [42–44]. These thresholds, or ecological discontinuities, are defined as significant changes in an ecological state variable as a consequence of continuous changes in an independent variable [45]. The threshold is defined as the point at which rapid change initially occurs. The concept of an ecological threshold is closely related to the concepts of resistance and resilience described

above (Fig. 3). Thresholds of resistance represent contaminant concentrations at which abrupt alterations in community structure are observed. Thresholds of resilience represent the points in time where recovery is first initiated and eventually completed after stressor removal. Threshold responses, which may be triggered by either natural or anthropogenic disturbances, have been reported in lake, coral reef, pelagic, and desert communities [32,46]. As described above, loss of natural resistance caused by long-term exposure to a chronic stressor may trigger a threshold response and shift the community to an alternative state. Depending on the nature of the stressor, these alternative states may remain stable long after stressors are removed [31,32].

Threshold responses also may occur along contaminant gradients [47,48], but quantifying the specific location of a breakpoint often is difficult [49,50]. More importantly, if a state shift occurs after a threshold is exceeded, recovery may not take place until contaminant concentrations are reduced significantly below levels that triggered the initial shift. Thus, knowing if a community is approaching a threshold has important management implications. Sondergerger et al. [51] developed a new analytical method to detect ecological thresholds based on significant changes in the slope (first derivative) of a stressor–response relationship. The significant zero crossings (SiZer) model applies a nonparametric smoother to the stressor–response data and then examines the derivatives of the smoothed curve to identify an ecological threshold (Fig. 4). Significant changes in the first derivative, operationally defined as a threshold, are displayed as a function of a bandwidth (h) that controls the smoothness of the curve (Fig. 4a and b). The SiZer model has been applied to examine both resistance and recovery thresholds [51]. As an example, long-term data regarding abundance of metal-sensitive mayflies (Heptageniidae) following restoration of a metal-contaminated stream were analyzed using SiZer. Quantitative benthic macroinvertebrate samples were collected before (1989–1991) and after (1992–2006) completion of a water-treatment facility on this stream. Using a bandwidth of 1.5 ($\log h = 0.18$), a recovery threshold, defined as the point at which the first derivative changed from significantly positive to zero (shown as t_2 in Fig. 3), was observed in 1997 (Fig. 4c). These results indicate that abundance of metal-sensitive mayflies peaked approximately five years after completion of the water-treatment facility and remained stable for the duration of the present study. Note that at this bandwidth, the threshold where recovery first began (i.e., where the first derivative changed from zero to significantly positive; shown as t_1 in Fig. 3) could not be detected. By selecting a smaller value for the bandwidth ($\log h = -0.30$), the slope changed significantly on several occasions in the early 1990s; however, inspection of Figure 4a indicates that the model is likely *overfitting* (undersmoothing) these data.

The existence of threshold responses and alternative stable states in community ecotoxicology has important consequences for ecological restoration. Identifying threshold responses along contaminant gradients will require that ecotoxicologists consider alternative statistical approaches for analyzing concentration–response relationships. For example, lakes and coral reefs are particularly sensitive to nutrient enrichment and have shown distinct threshold responses [26,47]. Elimination of macrophytes in lakes or loss of dominant hermatypic (e.g., reef building) species in coral reefs are examples of significant state shifts. Recovery

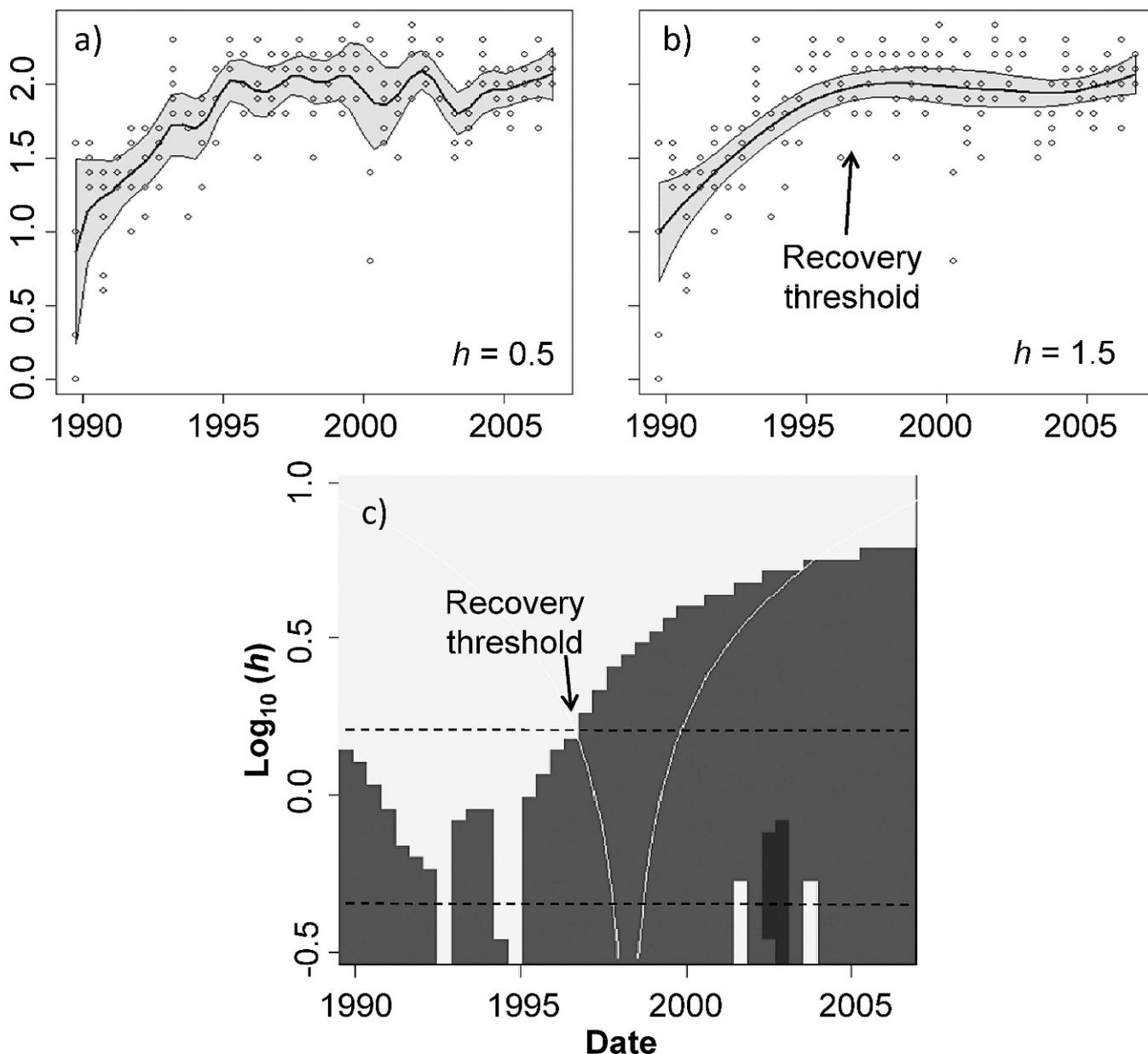


Fig. 4. Application of the significant zero crossings (SiZer) model to identify threshold responses of mayflies in a metal contaminated stream before (1989–1991) and after (1992–2006) completion of a water treatment facility. Results of locally weighted polynomial regression at two different bandwidths (h) are shown (a and b). A narrow bandwidth of $h = 0.5$ ($\log_{10} h = -0.30$) is clearly overfitting (or undersmoothing) the data (a), whereas a bandwidth of $h = 1.5$ ($\log_{10} h = 0.18$) provides a more realistic representation of these patterns (b). The SiZer map (c) shows changes in the first derivative as a function of time at different bandwidths. Reading from left to right at any given value of h , a significantly increasing derivative is shown in white, a significantly decreasing derivative is shown in black, and a derivative of possibly zero is shown in gray. The horizontal distance between the white lines is equal to $2h$ and represents the effective width of the locally weighted polynomial. The two horizontal dashed lines show bandwidths corresponding to the two smoothing functions in a and b. At a bandwidth of $\log_{10} h = -0.30$, the first derivative changes significantly on several occasions; however, because we are overfitting the data, these changes likely reflect random variation. At a more realistic bandwidth (e.g., $\log_{10} h = 0.18$), the first derivative changes from significantly increasing to zero in about 1997. This point is defined as the recovery threshold.

in these communities is unlikely until stressor levels are reduced well below those that triggered the initial response [32]. Because of the inherent uncertainty in predicting threshold concentrations for many contaminants, and because of the consequences of state shifts if a threshold is exceeded, a more conservative approach is to identify a range of stressor values at which threshold responses are likely to occur [45]. By selecting the most appropriate bandwidth, SiZer allows an investigator to consider a range of potential threshold values based on the inherent uncertainty in the data.

COMPARATIVE COMMUNITY ECOTOXICOLOGY

It is well established that responses of communities to contaminants vary among chemicals and chemical classes. Considerably less information is available regarding how communities from different locations respond to the same contaminant. The responses of communities to chemicals are influenced by their inherent resistance and structural characteristics, which in turn are a function of species interactions, successional stage, and previous history of exposure. Because of significant spatial and temporal variations in community structure, the ability to predict effects of contaminants is

greatly improved by studies that compare the responses of different communities to the same stressor or class of stressors [8]. In this section, two examples will be described in which investigators have used experimental approaches to gain insights regarding how responses vary among communities. First, researchers testing the pollution-induced community tolerance (PICT) hypothesis have employed increased tolerance at contaminated sites as a direct indicator of contaminant effects [52]. Second, studies comparing responses of communities from reference and contaminated locations have demonstrated that increased community tolerance has a cost that increases susceptibility to other stressors [53].

Pollution-induced community tolerance

Increased tolerance of populations to contaminants often is a result of strong selection pressure and may provide a direct measure of contaminant effects [54]. Similarly, increased tolerance at the community level, resulting from either population-level changes or the elimination of sensitive species, provides evidence that community restructuring was caused by the pollutant [52,55]. Pollution-induced community tolerance is tested by collecting intact communities from contaminated and reference sites and then exposing them to contaminants under controlled conditions, with the expectation that the reference community will experience a greater reduction in species abundance and diversity. Assuming that development of tolerance is not linked to other species traits, increased tolerance observed at polluted sites relative to reference sites provides a direct measure of contaminant effects [56]. Unlike traditional measures of community structure, community tolerance is less affected by natural environmental variation; therefore, locating identical reference and contaminated sites is less critical [57]. Furthermore, assuming that stressor interactions and the establishment of cotolerance are relatively unimportant, PICT could be used to quantify effects of individual chemicals in systems receiving multiple stressors [58]. For example, assume that field surveys show alterations in community composition in a stream exposed to several different xenobiotics. If PICT experiments demonstrated increased tolerance to only one stressor, this chemical most likely is responsible for changes in community structure observed in the field. The assumptions that chemicals will not interact or that populations will not develop cotolerance must be carefully examined and likely will not apply when modes of action and detoxification mechanisms are similar among chemicals [59].

Despite the appeal of the PICT approach, it has some practical limitations. Pollution-induced community tolerance is based on the assumptions that sensitivity to contaminants varies among species, sensitive species are replaced by tolerant species at contaminated sites, and differences in tolerance can be detected using short-term experiments [60]. The first two assumptions are well established in the community ecotoxicology literature. However, the third assumption is more problematic, because it requires direct experimentation. Unlike population-level tolerance, which can be assessed on a variety of species, logistical considerations will limit the types of communities where tolerance can be investigated experimentally. Consequently, most PICT experiments have been conducted using small organisms with relatively fast life cycles, including bacteria, algae, meiofauna, and benthic macroinvertebrates (see Table 25.6 in Newman and Clements [3]).

Cost of tolerance

The PICT approach described above uses increased tolerance in communities as an indicator of contaminant effects. Comparative ecotoxicology studies also have been used to measure the consequences of enhanced tolerance. The theoretical support for this hypothesis is based on the observation that acclimating or adapting to one set of environmental stressors has a cost and will increase susceptibility to other environmental stressors [53,61–63]. Levinton et al. [64] attributed rapid loss of metal tolerance in oligochaetes following cleanup at a metal-contaminated site to the fitness costs associated with adaptation to Cd. Reduced genetic diversity resulting from low population density, population bottlenecks, and inbreeding depression are other examples of fitness costs in contaminated environments that may have long-term consequences [65–67]. The cost associated with acclimation also may help to explain the slow rate of recovery or enhanced susceptibility to other stressors observed in some populations following improvements in water quality. Although population density eventually may return to pre-disturbance levels following removal of a contaminant, reduced genetic diversity and lower resilience may persist for many generations, thereby increasing the likelihood of a shift to an alternative stable state. It is well established that repeated disturbances in systems recovering from anthropogenic perturbations may have long-lasting and cryptic effects [31,68].

Most research on the cost of tolerance has focused on population-level consequences, but communities from chemically stressed environments also may be more susceptible to novel stressors [53]. In many respects, loss of species diversity is comparable to reduced genetic diversity, with similar implications for ecological resilience. These ideas have been formalized in the community-conditioning hypothesis, which predicts long-term persistence of toxicant effects on communities long after a contaminant has degraded or been removed [69,70]. According to the community-conditioning hypothesis, just as genetic structure reflects the history of populations over evolutionary time, communities also preserve their unique history, including incidences of previous chemical exposure. It has been reported that macroinvertebrate communities from metal-contaminated sites were highly tolerant to metals, as predicted by the PICT hypothesis, but significantly more sensitive to other stressors, including acidification [71], UV-B radiation [72,73], and stonefly predation [53]. Results of microcosm experiments (Fig. 5) showed that benthic communities recovering from metal contamination were more susceptible to UV-B radiation and that UV-B radiation interacted with metals to structure communities [72]. These studies demonstrate that a thorough understanding of exposure history is of fundamental importance for predicting how communities will recover from chemical stressors. Apparent recovery of traditional measures, such as abundance, species richness, or community composition, does not imply that the historical nature of a community has been lost. Similar communities can show very different response trajectories after a stressor has been removed depending on their history of exposure.

RELATIONSHIP BETWEEN DIVERSITY AND ECOSYSTEM FUNCTION

Although the present review has focused primarily on how chemical stressors directly or indirectly affect community structure, contaminant-induced change in species richness also

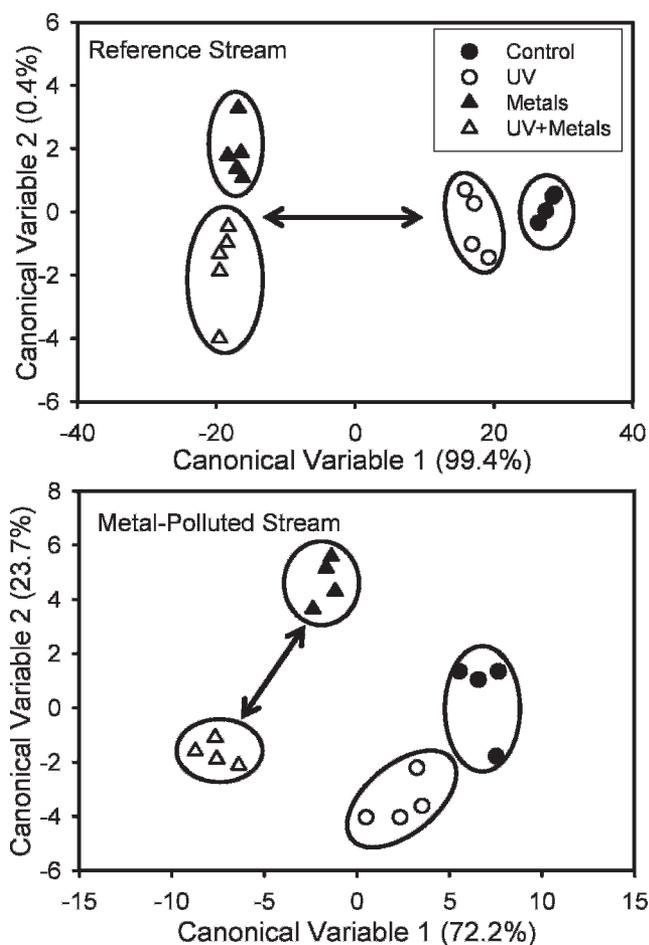


Fig. 5. Results of multivariate analyses based on stream microcosm experiments showing individual and combined effects of metals and ultraviolet (UV)-B radiation on macroinvertebrate community composition. Experiments were conducted using communities collected from a reference site (**top**) and a metal-contaminated site (**bottom**). Communities from the reference site were affected primarily by added metals, as indicated by separation along canonical variable 1. Note that because canonical variable 2 explained only 0.4% of the variation, the observed separation between the metals-only and metals-plus-UV-B treatments was unimportant for reference communities. In contrast, communities from the metal-contaminated site were affected by both metals and UV-B radiation. Furthermore, differences between the metals-only and metals-plus-UV-B treatments were much greater than differences between controls and UV-B-only treatment, suggesting that the effects of UV-B were greater in the presence of metals.

can impact ecosystem processes. The relationship between species richness and ecosystem function is well established in the ecological literature [74]. High species richness maximizes resource acquisition across trophic levels, reduces the risk associated with stochastic changes in environmental conditions, and protects communities from invasion by exotic species [75]. Considerable debate remains over the specific mechanisms responsible for the relationship between species richness and ecosystem function; however, studies have consistently shown that reductions in species richness are associated with the loss of ecosystem function [74]. Recently, these relationships have taken on greater practical significance as policymakers become increasingly aware that species also provide the ecosystem with goods and services that are essential for human welfare.

Because of interspecific variation in sensitivity to contaminants, loss of species from a community often is a nonrandom

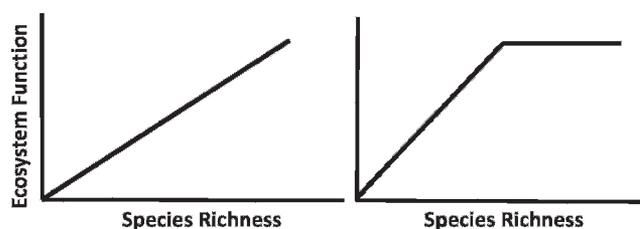


Fig. 6. Two models showing the relationship between species richness and ecosystem function. The diversity-stability model (**left**) predicts a linear relationship, implying that all species in a community contribute equally to ecosystem function. The rivet model (**right**) implies functional redundancy and that elimination of any species may result in the abrupt loss of ecosystem function.

process. Consequently, identifying species that play disproportionately important roles in controlling ecosystem function is a critical step in predicting the effects of species loss [76]. For example, keystone species that modify resource dynamics, trophic structure, and disturbance regimes have the greatest potential to affect ecosystem processes [77]. Thus, protecting these species is essential for preserving ecosystem services. Similarly, because species at higher trophic levels are more susceptible to extinction and more likely to accumulate high levels of contaminants, understanding the relationship between top predators and ecosystem function should be a research priority.

Most of the research addressing the species richness-ecosystem function debate has taken place within the context of basic ecology and conservation biology. In short, protecting ecosystem function has become another important justification for species conservation. Assuming that species loss resulting from exposure to contaminants reduces ecosystem function and impacts ecosystem services, the relationship between species richness and ecosystem function has significant implications for community ecotoxicology. For example, if an ecologically important species also is among the most sensitive to a particular contaminant, its elimination will have disproportionate effects on ecosystem function [9,76]. Thus, in addition to assessing direct effects of contaminants on community structure and ecosystem function, protecting biological integrity requires developing a better understanding of the nature of the relationship between these measures.

To move forward, it is necessary to reconcile the apparent inconsistency between the perspective that all species in an ecosystem are important versus the opinion that ecosystems have functional redundancy and, therefore, the loss of some species will not affect ecosystem processes. In other words, the shape of the species richness-ecosystem function relationship is of fundamental importance (Fig. 6). For example, a linear relationship between ecosystem function and species diversity implies that no functional redundancy exists and that all species in a community contribute equally to ecosystem processes [78]. In contrast, the rivet hypothesis implies functional redundancy within a community. Similar to removing rivets from the wing of an airplane, this model predicts an abrupt decrease in ecosystem function at some critical threshold of species loss [79]. The linear and rivet models have very different toxicological implications. If all species contribute equally to ecosystem function, then differences in contaminant sensitivity among species will have relatively little effect on ecosystem processes. In contrast, the rivet hypothesis predicts that elimination of any species could result in the abrupt loss of ecosystem function.

TROPHIC RELATIONSHIPS AND CONTAMINANT TRANSPORT

Trophic relationships are recognized as a central, unifying theme in ecology [80] that integrate responses across levels of biological organization [81]. An understanding of the structure and dynamics of food webs is essential for predicting fate and effects of contaminants. Because the movement of contaminants through food chains is closely associated with the flow of energy, quantifying trophic relationships provides critical insight regarding contaminant transfer to higher trophic levels. Natural variation in trophic structure among communities may help to explain variation in contaminant levels in top predators [82–85]. For example, the well-documented relationship between food-chain length and biomagnification has important consequences in systems where introduced species lengthen food chains, thereby increasing levels of persistent chemicals in top predators [86–89]. Structural characteristics of food webs (e.g., number of trophic links, connectance, and ratios of predators to prey) also are useful indicators of contaminant effects on communities. One of the most consistent observations at contaminated sites is the loss of larger, longer-lived species and a switch to smaller, more opportunistic taxa [40]. These changes in community structure between reference and contaminated streams alter pathways of energy flow and relative contributions of prey species to predator biomass [81]. Finally, many of the indirect effects of contaminants described above are a result of interspecific differences in sensitivity among trophic levels.

Contaminant transport and biological pumps

Atmospheric deposition of persistent organic pollutants has been measured in remote ecosystems for many years [90]. It is now well established that movement of persistent organic pollutants is facilitated by migratory species and that biological transport of these materials can have a greater influence on contaminant concentrations in Arctic and sub-Arctic food webs compared with direct atmospheric deposition. Migrating salmon and other species that accumulate PCBs in oceans serve as biological pumps and deliver these materials upstream to aquatic and terrestrial food webs. Krummel et al. [91] reported that PCB concentrations in sediments were highly correlated ($r^2 \geq 0.9$) with density of spawning sockeye salmon (*Oncorhynchus nerka*) and were approximately sixfold greater in lakes with fish compared to those in lakes without fish. These marine-derived contaminants also are transported by Arctic seabirds and deposited in sediments. Blais et al. [92] reported that concentrations of Hg, DDT, and hexachlorobenzene were 10- to 60-fold greater in sediments collected from ponds with high petrel (*Fulmarus glacialis*) use as a result of inputs from guano. Energy subsidies across ecosystem boundaries have been the subject of considerable recent attention [93,94], and ecologists are developing a better appreciation for the intimate connection between aquatic and terrestrial habitats [95]. The above-mentioned studies suggest that food-web models of contaminant transport also should account for the movement of persistent chemicals across ecosystem boundaries.

Application of stable isotope techniques to community ecotoxicology

Much of the variability associated with estimating contaminant transfer and biomagnification results from the inherent

uncertainty of assigning organisms to a specific trophic level based on dietary analyses. Routine dietary studies of consumers provide only a snapshot of feeding habits and often omit important seasonal and ontogenetic changes. One of the most significant methodological advances in food-web ecology has been the application of stable isotope techniques to characterize feeding habits. Isotopic analyses of consumers provide a unique signature that is representative of their habitat and feeding habits. By comparing stable isotope ratios of predators and prey across different communities, it is possible to obtain time-integrated estimates of energy flow, trophic position, and carbon sources for major consumers. These techniques have significantly improved the ability to quantify food-chain transport of contaminants in aquatic ecosystems [96]. Trophic magnification factors, defined as the slope of the relationship between contaminant concentration and trophic position, offer considerably more insight regarding the potential transfer of contaminants through food webs compared with conventional biomagnification factors [97,98].

FUTURE RESEARCH DIRECTIONS

Mesocosm experiments

One of the reasons that community ecotoxicology might be slow to attract proponents is the extreme level of complexity associated with the discipline. Overlaid on the enormous complexity of ecology are approximately 100,000 registered chemicals [99] (<http://www.eeb.org/activities/chemicals/COM%20Chemicals%20WP%20EN.pdf>), their feasible mixtures, and the impacts of these lone and mixed chemicals on individuals, populations, and species interactions. In fact, complexity probably peaks at the level of community ecotoxicology, because functional redundancies of species may reduce complexity at higher levels of biological organization, such as at the level of ecosystem ecotoxicology.

Given this vast complexity, community ecotoxicology must identify some simplifying assumptions. Indeed, a glaring omission from community ecotoxicology are generalities that define the discipline. Many species show consistent sensitivity to contaminant types [53], suggesting that grouping contaminants with similar modes of action, analogous to guilds in community ecology, might represent an important, simplifying assumption that could lead to generalities. Conducting studies in which individual chemicals (e.g., malathion vs atrazine) are nested within chemical classes (e.g., organophosphate insecticide vs triazine herbicide), which are then nested within chemical types (e.g., insecticide vs herbicide), and in which all treatments are random factors in a statistical model would allow researchers to ascertain the level at which simplifying assumptions can be made. For instance, if an experiment was designed in this manner and revealed that standardized concentrations (perhaps the expected environmental concentrations) of chemicals within a single chemical class all had statistically indistinguishable effects on standardized communities, then the identity of chemicals within the class might be superfluous. Hence, this approach might reduce the 100,000 individual chemicals to a more manageable number of chemical guilds, and it might even allow us to predict the effects of new or untested chemicals that fall within tested chemical classes or types.

This approach emphasizes simultaneously testing multiple chemicals at standardized concentrations rather than the more traditional toxicological approach of quantifying dose re-

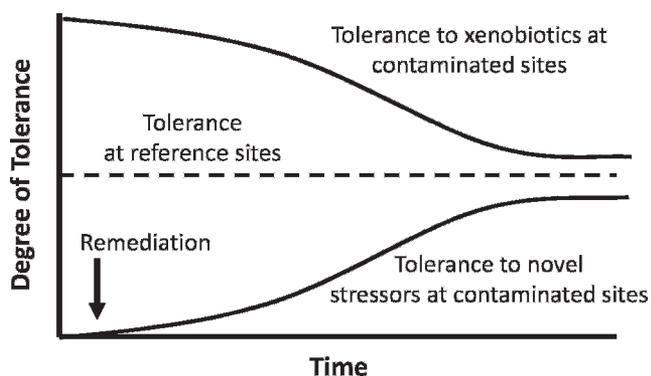


Fig. 7. Conceptual model showing the hypothesized, long-term changes in tolerance to xenobiotics and novel stressors at reference sites (dashed line) and at contaminated sites following remediation (solid line). As communities recover after remediation, we hypothesize that their tolerance to xenobiotics will decrease and their tolerance to novel stressors will increase.

sponses to one or a small number of chemicals [100]. Given the number of chemicals already registered and the high rate at which new chemicals are being registered, this proposed approach might be one of the only ways of realistically and efficiently unveiling generalities that will substantially advance community ecotoxicology. An assumption underlying this single, standardized concentration approach is that concentration or dose responses to chemicals often are positively monotonic. This assumption likely is safe for most chemicals; however, because some chemicals can regularly produce nonmonotonic dose responses [101] and many substances can have hormetic effects at low concentrations [102], this assumption might be problematic for some xenobiotics.

Global change and stressor interactions

Abrupt shifts to alternative stable states are likely to occur in contaminated systems that are simultaneously subjected to effects of global change. Detecting these shifts will require that ecotoxicologists develop broader spatial and temporal perspectives for assessing effects of contaminants. Jackson and Fureder [103] reported that the median duration of long-term freshwater macroinvertebrate studies was nine years and that 85% of these studies had a duration of less than 15 years. Because of the relatively short duration of these studies, ecologists generally are unable to characterize the influence of important climatic cycles, such as El Niño/La Niña or North Atlantic Oscillation events. Distinguishing direct or indirect effects of contaminants from those associated with global change also will require that community ecotoxicologists consider responses at larger spatial scales. The emerging field of landscape ecotoxicology provides an important opportunity to employ new geospatial tools, such as remote sensing and geographic information systems, to address questions at spatial scales that are appropriate for separating contaminant effects from those associated with global change.

Considerable research has been devoted to understanding direct effects of climate change, acidification, N deposition, and UV radiation on communities, but much less is known about how stressors associated with global change interact with contaminants to structure communities. In a 25-year study of acidified streams in Wales, Durance and Ormerod [104] speculated that climate change would enhance effects of acidification on macroinvertebrate communities. Similarly, Clements et al. [73] reported that hydrological and geochem-

ical alterations associated with global change are likely to increase toxicity and bioavailability of metals in streams of the western United States. These findings highlight the importance of assessing ecological resistance and resilience within the context of long-term changes in regional climate.

Susceptibility to novel stressors as an indicator of restoration effectiveness

In addition to the traditional biological metrics, such as species richness and diversity, the ability of communities to withstand or recover from novel perturbations is a potential indicator of restoration effectiveness [50,105]. Although rarely quantified in restoration studies, community resistance and resilience are integral components of ecological integrity [106,107]. If long-term exposure of communities to chemical stressors affects resilience or resistance, then it should be possible to detect these changes over time. As described above, increased tolerance is a common observation in communities exposed to chemical stressors. Assuming there is a cost of this tolerance [53,64,72], communities from previously contaminated sites likely would become less tolerant over time as contaminant concentrations decrease (Fig. 7). Similar to the PICT approach that uses tolerance as an indicator of toxicological effects, *loss* of tolerance in communities is a potential indicator of restoration effectiveness. Furthermore, tolerance to novel stressors likely would increase gradually as communities recover following restoration. Because of their fundamental importance in ecological integrity, measures of community resistance and resilience should be considered when evaluating restoration effectiveness.

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