

Perspectives

Understanding Ecological Complexity in a Chemical Stress Context: A Reflection on Recolonization, Recovery, and Adaptation of Aquatic Populations and Communities

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Abstract: Recovery, recolonization, and adaptation in a chemical stress context are processes that regenerate local populations and communities as well as the functions these communities perform. *Recolonization*, either by species previously present or by new species able to occupy the niches left empty, refers to a metacommunity process with stressed ecosystems benefiting from the dispersal of organisms from other areas. A potential consequence of recolonization is a limited capacity of local populations to adapt to potentially repeating events of chemical stress exposure when their niches have been effectively occupied by the new colonizers or by new genetic lineages of the taxa previously present. *Recovery*, instead, is an internal process occurring within stressed ecosystems. More specifically, the impact of a stressor on a community benefits less sensitive individuals of a local population as well as less sensitive taxa within a community. Finally, *adaptation* refers to phenotypic and, sometimes, genetic changes at the individual and population levels, allowing the permanence of individuals of previously existing taxa without necessarily changing the community taxonomic composition (i.e., not replacing sensitive species). Because these processes are usually operating in parallel in nature, though at different degrees, it seems relevant to try to understand their relative importance for the regeneration of community structure and ecosystem functioning after chemical exposure. In the present critical perspective, we employed case studies supporting our understanding of the underlying processes with the hope to provide a theoretical framework to disentangle the relevance of the three processes for the regeneration of a biological community after chemical exposure. Finally, we provide some recommendations to experimentally compare their relative importance so that the net effects of these processes can be used to parameterize risk-assessment models and inform ecosystem management. *Environ Toxicol Chem* 2023;42:1857–1866. © 2023 The Authors. *Environmental Toxicology and Chemistry* published by Wiley Periodicals LLC on behalf of SETAC.

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INTRODUCTION

Studies of the ecological impact of chemical stressors have mostly evaluated the sensitivity of individuals under laboratory conditions and, to a much lower extent, of populations and communities under field or semifield conditions (micro-, mesocosms; sensu Beketov & Liess, 2012)—a fact that has concerned the scientific community for decades (Cairns, 1986; Chapman,

2002). Under (semi-)field conditions, the overall impact of chemicals on ecosystems over time depends primarily on their direct effects, which are a function of the toxic potency of the chemicals and the sensitivity of each organism. In addition, processes such as recolonization, recovery from, and adaptation to the stressors (see Figure 1), which underlay the regeneration of the affected communities, complicate a reliable estimation of the impacts caused by individual chemicals or their mixtures on the structure and function of communities and ecosystems. Such ecological processes are usually not considered by the most commonly used prospective or retrospective tools applied for the risk assessment of chemicals, such as the toxic unit approach (Liess & von der Ohe, 2005) or the multisubstance potentially affected fraction of species in a community (De Zwart &

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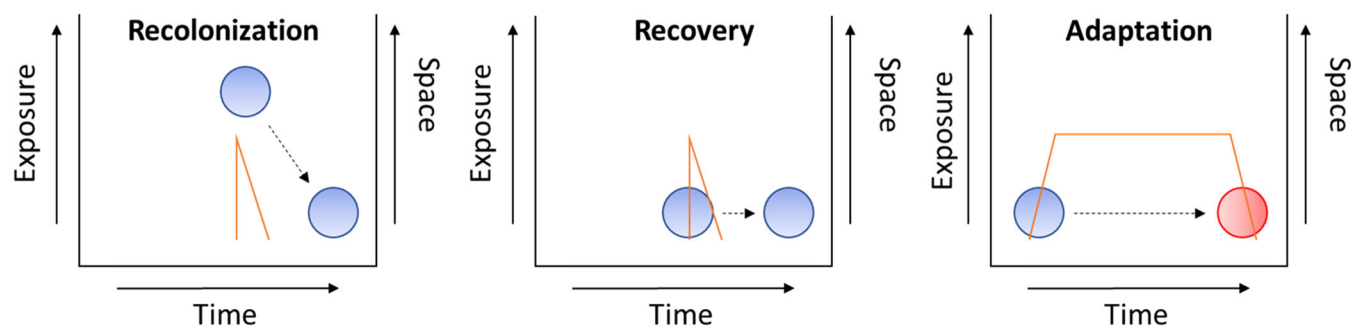


FIGURE 1: Main processes supporting the regeneration of a community and ecosystem functions after exposure to chemical stress. *Recolonization* describes the arrival of a species to a habitat and its successful establishment in the form of a flourishing population after exposure (orange line). In a chemical stress-related context, we also find the term *external recovery*, which is a special case of recolonization because it also includes the expectation to reach a community that is comparable to the situation before exposure supported by subsidy from surrounding unexposed habitats. *Recovery* is usually described as the capacity of affected populations to reach, after exposure to chemical stress (orange line), the abundance or biomass shown by the normal operating range of the unexposed population without external support. In some cases, this is also referred to as *internal recovery*. *Adaptation* involves changes at the individual and population levels. This includes the appearance of newly tolerant phenotypic, with or without genotypic, modifications as a consequence of exposure (orange line) and selection of individuals in the population with advantageous traits. We expand on this classical definition toward the end of the chapter to cover the effects of adaptation at the community level, meaning the functions these communities performed. This process may also be referred to as *increased resistance*.

Posthuma, 2005). Considering the complexity of data and their interpretation in a risk-assessment context (Taub, 1997), we argue that it is important to investigate the ecological mechanisms that support the regeneration of a biological community after chemical exposure through recolonization, recovery, and adaptation, as well as by their interplay, to narrow the gap between chemical risk predictions and biomonitoring results (see also Clements & Rohr, 2009).

Recolonization refers to a metacommunity process through which stressed ecosystems are subsidized by dispersing organisms from other source areas, restoring community complexity and ecosystem processes. Consequently, species recolonizing habitats, and by doing so occupying empty ecological niches, may act as additional filters obscuring or amplifying the effects of chemicals on communities (Caquet et al., 2007). However, recolonization is highly dependent on the connectivity of an exposed ecosystem to surrounding habitats serving as a source of organisms, with river connectivity being a major challenge worldwide (Grill et al., 2019). Whereas recolonization describes a flux of organisms into an ecosystem, *recovery* refers to an ecosystem inherent process during which generally less sensitive organisms (species or individuals) remain in the stressed community. This process may lead over the long run to a local adaptation of individuals of certain species. In fact, *adaptation* involves changes at the individual level spanning from the appearance of new tolerant genotypic capacities, with either changes in the gene sequence or epigenetic changes that activate or inactivate genes without changing the DNA sequence. Thus, individual changes from adaptation can result in a higher metabolic activity and a higher efficiency to transform chemicals and in phenotypic trait modifications such as higher ability to escape exposure through an earlier emergence (see Kolbenschlager et al., 2023).

Because these processes (i.e., recolonization, recovery, and adaptation) are usually operating in parallel—though at variable effectivity—in nature, it seems relevant to understand their

relative importance as well as their potential interplay. In this critical perspective, we reflected on them and showed several case studies that provide evidence of the mechanisms described above to build a theoretical framework allowing us to disentangle the relevance of the three processes and their interaction. Finally, we provide recommendations on how to assess the relative relevance of these three processes under (semi-)field experimental conditions, which is key to improving our ability to project ecosystem-level responses to (chemical) stressors over time and for environmental management in general.

RECOLONIZATION

A colonization process describes the arrival of a species to a habitat and its successful establishment in the form of a flourishing population (Lomolino et al., 2017). Studying the colonization of habitats, often with newly available ecological niches created through the extirpation of species by (natural or anthropogenic) disturbances, has a long tradition in ecology. In fact, it has been the focus of an entire research field related to island biogeography theory (see the classic publication of MacArthur & Wilson, 1967). One of the most recognized tests of this theory regarding the effects of size and distance between isolated habitats on colonization and community regeneration was carried out by experimental defaunation eliminating arthropod communities from a set of mangrove islets of Florida Bay with pesticides (Simberloff & Wilson, 1970). (Re-)Colonization—also following exposure to chemicals—will depend, according to the island biogeography theory, on habitat isolation and size, as well as on the traits of the potential colonizers and ecosystem properties and dynamics (Hortal et al., 2014; Whittaker & Fernández-Palacios, 2007).

Recolonization is a process that describes how empty niches left after a disturbance (such as chemical stress) are reoccupied and which may be realized by previously present species or by newcomers. The latter results in a shift in the community

composition. Hence, recolonization refers to a metacommunity process, allowing stressed ecosystems and the functions they perform to benefit from the dispersal of organisms from other areas. Which species arrive in a relatively short time will strongly depend not only on their dispersal abilities but also on their availability in nearby habitats (Trekels et al., 2011). Restoring local populations by the same species from connected habitats is one form of recolonization (sometimes referred to as *external recovery*), which may or may not introduce organisms that exhibit a different chemical sensitivity relative to the original population. In addition, the term *recolonization*, as used in our review in a wider sense, may cover the occupation of ecological niches by species new to the local community. While this process is more easily traceable by a before–after comparison, it may have consequences for the sensitivity and the functions the local community performs and is determined by the proportion of empty niches in relation to the traits of the newcomers. If the chemical stress level remains higher than the pre-exposure conditions (e.g., after the activation of a wastewater-treatment plant discharging into a pristine ecosystem), species that are faster dispersers than the previously existing species may replace the former, by effectively occupying ecological niches as a function of their lower sensitivity to the current stress levels at the respective site. In other words, recolonization may facilitate the resistance, that is, the capacity to essentially remain as it was, and resilience, that is, the capacity of regeneration, of local communities to potentially repeat events of chemical stress exposure when their niches have been effectively occupied by new colonizers. These new colonizers may take advantage of the lack of priority effects (De Meester et al., 2016) by the demised previous residents and replace them in the long run, if they are largely redundant and the regional pool includes strong competitors in a heterogeneous space. In any case, the contingency of the colonization process may drive different reassembly pathways, ending with a community structure that differs from the original one (Fukami, 2015) and is perhaps even greatly divergent functionally if some new residents have ecological roles that were not present in the past (e.g., new predators, pathogens, ecosystem engineers), organizing at an alternative but stable state (Bundschuh et al., 2017). The early new colonizers are expected to include species with traits supporting dispersal. According to metacommunity studies, these would include small passive dispersers (e.g., prokaryotic organisms, microscopic algae, microinvertebrates) and large active dispersers, especially those able to fly, like birds and insects (De Bie et al., 2012), with the exact processes being strongly context-dependent (Galvez et al., 2022). For instance, flying insects may take a few weeks or months to restore their populations (or replace others) through immigration and colonization of ponds after pesticide treatments (Caquet et al., 2007). Passive dispersers may arrive by wind, water, or animal and human vectors (Frisch et al., 2007; Valls et al., 2016; Vanschoenwinkel et al., 2008). But the potential arrival of any of these organisms will be affected by the isolation of the water body. The regeneration of highly connected aquatic ecosystems, such as running waters, may be faster because they could benefit, for instance, from

downstream drift of a variety of organisms, including bacteria, algae, invertebrates, and amphibians (Mackay, 1992), and even upstream migration in the case of swimmers like fish or amphipods. In contrast to streams and rivers, isolated ponds and lakes are, by definition, less well connected to other freshwater habitats and therefore show lower recolonization rates, particularly for organisms without nonaquatic stages (Trekels et al., 2011) and especially for organisms with low dispersal abilities, such as benthic invertebrates without flying phases or resting eggs (e.g., mollusks, amphipods, shrimps; Keller et al., 1992). The recolonization of a water body can appear as a very random process. It depends on spatial context, as well as on contingent effects on potential species present in the regional pool (ontogenetic stages, population growth state) or on the occurrence and direction of vectors (wind, wandering mammals), so that it can look largely neutral in metacommunity terms (Kolasa & Romanuk, 2005; Leibold et al., 2004), especially under homogeneous landscapes or mild ecological conditions. However, species sorting effects can also determine which taxa can, after arrival, establish a population. Local environmental conditions select which colonizers survive and reproduce, and this may be related not only to the pre-exposure conditions (e.g., salinity, pH, temperature, light) but also to chemicals being constantly or repeatedly released. Therefore, there might be a progressive change in the potential successful immigrants depending on their (life stage-dependent) sensitivity to local (chemical) stressors. Consequently, local communities are subjected to a dynamic (re-)assembly process. Thereby the interplay (or feedback) between (re-)colonizers and local species shapes the development of the community. These processes may sometimes result in a restructured food web and taxa dominance, an observation that is very illustrative in the context of invasive species (Davis, 2009; Sax & Brown, 2000).

RECOVERY

Population recovery is usually described as the capacity of affected populations to return to the abundance or biomass within the normal operating range of the unexposed population (Vighi & Rico, 2018). Recovery is intrinsically related to the life-cycle traits of the organisms that form the population, including the degree of voltinism, the quantity and quality of offspring produced, and the capacity to develop dormant or resistant life stages (Barnthouse, 2004; Kattwinkel et al., 2012). The capacity of populations to recover from chemical stress has been studied in field and semifield experiments with pulsed exposure regimes (see Barnthouse, 2004; Gergs et al., 2016). Gergs et al. (2016) provided a comprehensive evaluation of the recovery time observed for different taxonomic groups, showing that, on average, it can span from days or weeks (for algae and some microcrustaceans) to several months or more than 1 year (for some macrocrustaceans, bi- and univoltine insects, mollusks, and macrophytes). These authors also observed that the recovery time of aquatic macroinvertebrates is closely related to the type and persistence of stressors in the

ecosystem, with pesticides having a smaller impact on recovery rates as compared, for example, to metals. The recovery time of aquatic populations is also influenced by the magnitude of impact and thus the share of the initial population size that can contribute to reproduction after exposure (Barthouse, 2004). In this regard, it is common to observe dose-dependent effects on the recovery time of many aquatic populations (e.g., macrocrustaceans, snails; Roessink et al., 2005). Resistant individuals that remain after the exposure, as well as resting stages, can contribute to the recovery of populations. Many groups of aquatic organisms are able to produce dormant stages during their life cycle, such as the spores of prokaryotes, fungi or phytoplankton algae, plant seeds and turions, or invertebrate diapausing eggs and cysts (Alekseev & Vinogradova, 2019; Brock et al., 2003). These resting stages are especially adapted to withstand stressful conditions (e.g., freezing, drought) so that they are more common in temporary than in permanent water bodies (Caceres, 1997; Williams, 1998). Tolerance to extreme environments is widely known for tardigrades and many other propagules of aquatic organisms (Guidetti et al., 2011). However, their capacity to survive chemical stress events has been less studied (Arenas-Sanchez et al., 2016). Vandekerckhove et al. (2013) showed an extreme tolerance of ostracod eggs to a variety of stressors, including insecticides; and Zadereev et al. (2019) also found a high tolerance of cladoceran resting eggs to toxic substances. On the other hand, Navis et al. (2013) found that some pesticides can affect hatching rates of dormant eggs of *Daphnia magna*, as well as the survival and performance of the hatched individuals (either affecting embryos or hatchlings), thus having implications for the evolutionary potential of a population. Dormancy is, however, relatively uncommon in some key organisms in aquatic environments, including many insects, although these may be more efficient at recolonizing impacted environments thanks to their higher dispersal abilities (see previous section on recolonization).

Other factors that affect population recovery include changes in environmental conditions, food availability, or species interactions. For example, extreme weather events, such as droughts or heat waves, have been proposed as key factors influencing the pace of population recovery to chemical stress events (Arenas-Sanchez et al., 2019; Polazzo, Roth, et al., 2022). dos Anjos et al. (2021) showed that food availability, expressed as the biomass of primary producers in eutrophic and mesotrophic mesocosms, can affect the recovery capacity of *D. magna* exposed to pesticides. On the other hand, several studies have demonstrated that interspecific competition or the presence of efficient predators significantly delays recovery of microcrustacea and insect populations following pesticide exposure (Foit et al., 2012; Knillmann et al., 2012), while in some cases such interference can be obscured by other “less common” ecological interactions such as intraguild predation (Van den Brink et al., 2017).

Complete community regeneration (also termed *community recovery*) is usually determined by the absence of significant differences between the stressed community and a reference community (or control) on the basis of multivariate statistics

(Vighi & Rico, 2018). From a theoretical perspective, the capacity of communities to regenerate after chemical stress may be influenced by the type and magnitude of effects caused by chemical stressors on each of the populations that form the community. But, as described above for recolonization, the prediction of community reassembly, including the formation of alternative configurations or ecological states, has been considered an arduous task, which is influenced by the availability of niches created by the disappearance of sensitive species, priority effects driven by tolerant organisms, and a myriad of reassembly pathways guided by species interactions (Carpenter et al., 2011; Persson et al., 2007; Polazzo, Marina, et al., 2022). Recent experimental studies have assessed the influence of topological characteristics of community interaction networks (i.e., number of nodes and connectivity among them) on their resilience to different disturbances, suggesting that species richness and food web complexity (i.e., interspecies dependence) tend to make aquatic communities more resilient to disturbance (Pennekamp et al., 2018; Yuan et al., 2021). Zhao et al. (2019) tested this hypothesis with pesticides using model communities under laboratory conditions and showed that horizontal diversity (higher number of species in the same trophic level) tends to increase the community regeneration capacity to pesticide stress, while vertical diversity (higher number of trophic levels) yields an opposite pattern. Experiments that can effectively quantify the regeneration capacity of complex aquatic communities are limited in the literature as a result of, among other factors, the interlinked nature of recovery and recolonization. Among the few studies that attempted to separate these two processes are Caquet et al. (2007) and Hanson et al. (2007), who compared the regeneration time of aquatic communities to the insecticide deltamethrin in mesocosms that were or were not isolated with a fine mesh impeding aerial colonization. These authors found that the regeneration period of macroinvertebrate communities from isolated mesocosms was significantly larger (months) than the time nonisolated mesocosms required to reach pre-exposure conditions, likely through the combination of species recovery and recolonization. At the same time, less evident results were found for the zooplankton community or functional parameters such as organic matter decomposition rates.

The tolerance of dormant stages to chemical stress makes them especially suited to allowing the regeneration of communities after an episode of disturbance by nonpersistent pollutants. Indeed, metacommunity dynamics can be strongly influenced by the role of dormant stages, by their survival in comparison to active life stages, and by their emergence patterns (Brendonck et al., 2017; Williams, 1998; Wisnoski et al., 2019). Resting stages can therefore be considered as an insurance against disturbances, as well as a dispersal in time (Brendonck et al., 2017), so that the higher the abundance in the egg or seed bank, the higher the probability of a (fast) regeneration of the community (i.e., its resilience) after pulsed disturbances. Furthermore, this accumulation of long-lived, dormant stages may be essential to facilitate evolution-mediated priority effects (Wisnoski et al., 2019), which can be instrumental for the adaptation of local populations to chemical

stress (see next section). In this sense, the monopolization hypothesis (De Meester et al., 2002) states that local adaptation may hamper the establishment of new colonizers of the same species because locally adapted individuals can monopolize resources and consequently avoid their use by newcomers, which will not be able to grow as fast as their conspecific counterparts adapted to local conditions. This hypothesis can be expanded to a community context in which species compete for the same resources so that the locally adapted species will monopolize the environment faster than potential new immigrants, which will in that way have a lower ability to reproduce in the occupied environment (Urban & De Meester, 2009). Contrarily, when the newcomers have advantages to confront the remaining effects of exposure, either direct or indirect, better than the remainders, the new colonizers might displace the previously well-established taxa.

ADAPTATION

Adaptation involves changes at the individual and population levels, including the appearance of newly tolerant genotypic capacities and phenotypic trait modifications. While the latter covers the ability to escape exposure (e.g., through an earlier emergence; Kolbenschlager et al., 2023), genotypic modifications refer to changes in the gene sequence or to epigenetic alterations. Individuals with these new adaptive traits will have higher fitness than other individuals in the same population so that through selection the new trait will eventually dominate in the population. As a consequence, adaptation is a dynamic process and a cornerstone of evolution. Anthropogenic pressures, which include climate change, shifts in land use, as well as chemicals being released, add yet another layer shaping adaptation. In case of chronic or repeated exposure to chemicals, the more tolerant individuals of a population may replace sensitive members of the same population, leading to a less sensitive local population, which may be explained by genetically manifested more efficient detoxification processes. While adaptation allows for a more efficient reaction to local press or repeated pulse disturbances (Glasby & Underwood, 1996), it might also make the same population more prone to other stressors toward which no adaptation was developed (see Zubrod et al., 2017) partly to be explained by genetic impoverishment (Pedrosa et al., 2017).

Indeed, adaptation of populations has been reported from agricultural streams using *Gammarus pulex* as a model species (Shahid et al., 2018). These authors showed that gammarids from stream sections within an agricultural landscape were more tolerant to an insecticide than those from a forested unpolluted area. The change in sensitivity was positively correlated with an increasing ecotoxicological potential (using the toxic unit concept, which normalizes the concentrations of chemicals to their ecotoxicological potential determined under laboratory conditions, often involving standard test organisms) of local pesticide exposure and distance from uncontaminated upstream sections. The latter points to the possibility for recolonization (see above) by nonadapted specimens attenuating the adaptation at the population level. In yet another study by the same research

group (Becker & Liess, 2017), species collected from agricultural streams were also less sensitive to the same model insecticide. However, this increased tolerance was only apparent for populations sampled from communities characterized by a low diversity. Hence, adaptation of populations to chemical stress is not a simple function of their history of exposure inducing selection. The ecological context, with species interactions being one factor (Becker & Liess, 2015) to which a population has to respond, plays a significant role in selecting for specimens with a specific set of traits.

Species traits may indeed be a significant factor determining species sensitivity and may hence be seen as constraining or favoring adaptation. For instance, the pace of life, which is linked to the metabolic activity of populations (Reale et al., 2010), has been significantly related to tolerance toward chemicals (Janssens et al., 2021). Janssens et al. (2021) showed a higher tolerance of fast-paced populations of the damselfly larva *Ischnura elegans* than slow-paced populations. This observation was explained by a quicker detoxification or elimination of the pesticide, due to an anticipated elevated metabolic rate, relative to slow-paced populations. Besides the metabolic activity of *Ischnura* populations, their ability to lose external gills (i.e., gill autotomy) as an antipredator strategy was shown to have significant impacts on the damselflies' ability to tolerate chemical stress by reducing the surface-to-volume ratio of the species and thus chemical uptake (Janssens et al., 2021). Gill autotomy had opposite impacts on *Ischnura* tolerance in slow- versus fast-paced populations. While the loss of gills in slow-paced populations increased tolerance, the opposite was observed for their fast-paced counterparts. The authors suggested that this pattern is a consequence of a double-edged sword—Gill autotomy reduces uptake of chemicals, which was likely positively reflected by a slow-paced population; but it also limits oxygen uptake, which potentially scaled metabolic activity and ultimately detoxification or elimination (Janssens et al., 2021).

Although adaptation is defined as a process that is effective on the individual level, whose consequences are ultimately mirrored at the population level, also communities may become less sensitive to stress supported by recovery and (re) colonization. This aspect is considered further in our review, while it is formally to be termed *resistance* instead of *adaptation*. Against this background, the traits of the species forming a community can also help to develop a link between chemical contamination and community vulnerability. One example among many (see also Arenas-Sanchez et al., 2021; Berger et al., 2018; Rico et al., 2016) is the Species at Risk index, which divides the species within a community between those at risk from, for example, pesticide exposure and those not at risk. Thereby, the index considers the sensitivity, generation time, presence of aquatic life stages during pesticide application periods, as well as potential of the species to recover and recolonize a system (Liess & von der Ohe, 2005). Long-term changes in this index can hence point to a structural decreasing sensitivity at the community level, which is sketched by the pollution-induced community tolerance (PICT) concept (Blanck et al., 1988). A higher tolerance, often measured as short-term physiological responses (e.g., photosynthetic activity for

photoautotrophs or respiration for heterotrophs) of microorganisms to stress, results not exclusively from a shift in species composition but also from adaptation of populations (see above) resulting from constant or repeated exposure to (chemical) stressors that act as a selection pressure forcing adaptation. Thereby, PICT builds on several ecological hypotheses, namely the redundancy (i.e., the loss of species will be compensated functionally by more tolerant species) and the insurance (i.e., biodiversity buffers impacts in ecosystem functions) hypotheses (Tlili et al., 2016). In a study targeting micropollutant adaptation of periphyton communities in streams receiving wastewater input, Tlili et al. (2017) documented at downstream sites a change in bacterial and algal communities. This change toward less sensitive species resulted in changes in secondary production and in primary production and photosynthetic activity, respectively, at substantially higher levels of stress. The magnitude of this change in tolerance at down- relative to upstream sites was finally correlated to the load of micropollutants among four studied streams in Switzerland. Similarly, leaf-associated fungal communities from streams within an agriculturally dominated catchment were less sensitive to increasing fungicide stress in a laboratory experiment relative to communities from a stream with a forest-dominated catchment. This functional stability was linked to shifts toward less sensitive fungal species characterized by a high efficiency to decompose leaf litter (Fleckler et al., 2018).

Consequently, the effects of adaptation at the population level and increased resistance at the community level are highly relevant, but difficult to quantify, and may or may not be manifested in a shift in physiological (e.g., growth, energy reserves, reproduction) or functional (e.g., contribution of ecosystem-level processes such as organic matter decomposition or primary production) responses, respectively. Quantifying the relevance of these processes in complex ecosystems requires, however, a sophisticated experimental design under more controlled conditions (e.g., in the laboratory). Nonetheless, the insights generated by following some of the above-described approaches can enrich our understanding of risks posed by chemical and nonchemical stressors, helping us also to understand ecological boundaries when it comes to the amount of pressure an ecosystem can cope with.

AN ATTEMPT TO QUANTIFY RECOLONIZATION, RECOVERY, AND ADAPTATION

When dealing with each of these three processes (i.e., quantify recolonization, recovery, and adaptation), we would need to understand how they interact. For instance, recolonization would differ if the potentially colonizing species were differentially adapted to the high levels of stress because this would limit the availability of ecological niches, aggravating the establishment of new colonizers. Nevertheless, we acknowledge that quantifying each potential parameter relevant to determining the strength of recolonization, recovery, and adaptation may not be possible. This is particularly true because all three processes are dynamic and thus require a time-dependent assessment (i.e., repeated quantification; Figure 2). Nonetheless, we summarize below some approaches that could be relevant to understanding their relative contribution in the framework of chemical stress in freshwaters.

Recolonization by macroinvertebrates within a stream network could be assessed by deploying drift nets (Elliott, 1970), which should be monitored regularly. Thereby, the drift-related influx from upstream reaches and the efflux to downstream reaches can be quantified, helping to determine the potential retention of organisms in the stressed stream section. So far, several experiments have characterized impacts of chemicals on invertebrate drift (see Berghahn et al., 2012; Magbanua et al., 2013), while the net influence of incoming individuals on population or community regeneration has been less explored. Few modeling studies, however, have allowed a quantitative assessment of habitat connectivity and landscape permeability on the recolonization and recovery of aquatic populations partially exposed to pesticides in agricultural landscapes (Galic et al., 2012, 2013).

Enclosures containing the local macroinvertebrate community before an exposure—but still connected to the surrounding environment—could support our understanding of how the community would develop excluding recolonization. In other words, this would allow us to assess the potential of the local community to recover without external subsidy. However, it should be considered that enclosures will

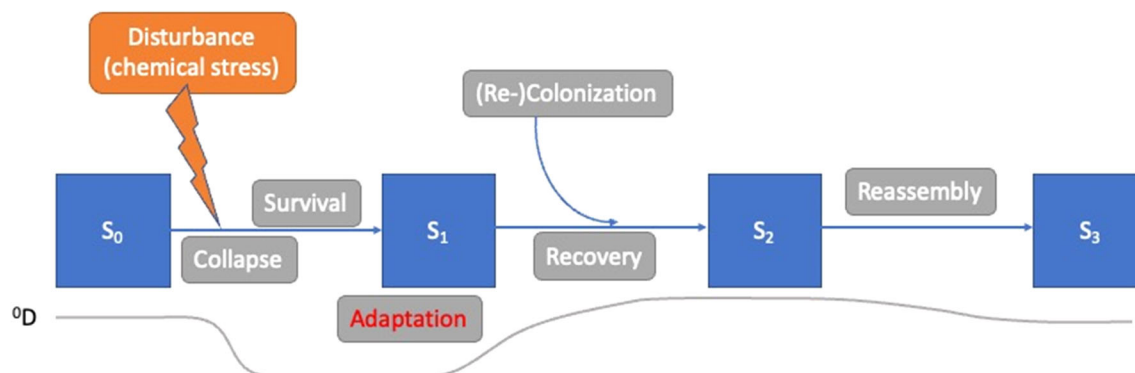


FIGURE 2: Theoretical consideration of the processes and their sequence of appearance after an exposure to chemical stress within local communities. S_0 = preimpact; S_1 = impacted; S_2 = recolonized; S_3 = regenerated/reorganized; D_0 = diversity of order 0 (species richness).

inevitably induce experimental artifacts, such as clogging, which affects flow, or the limited ability of prey escaping from a predator (dos Anjos et al., 2021). Insects with a flying and thus terrestrial life stage represent an additional challenge because this life-history trait will allow organisms to disperse independently of the stream network as such. This effect can be excluded by netting (the inverse of an emergence trap), therefore suppressing oviposition, a strategy that will be difficult to realize in the field; but it could work for seminatural studies employing mesocosm facilities (see Caquet et al., 2007). Alternatively, deploying colonization trays (e.g., buckets of water) next to the field site or the mesocosms may be an indirect measure to quantify aerial recolonization. Quantifying recolonization by microorganisms seems unrealistic under field conditions because the exclusion of recolonizing microorganisms seems less straightforward, not to speak about its quantification, although the mentioned colonization trays may allow some estimation not only of large but also of small organisms. Working with bypass systems may be another elegant way to work around this challenge. Thereby, water from the study site or mesocosm can be actively pumped through an external system prior to and during the exposure period. Following the exposure, a filter that retains any microorganism can be implemented to obtain a subsample of these external systems, prohibiting any further colonization but water, and thus nutrients would still be provided, fostering the assessment of recovery. The remaining external systems may still receive microorganisms from the ecosystem studied, helping us to understand the dynamics of recolonization. Furthermore, the dispersal of microorganisms can be monitored by sampling the stream upward or, for isolated lakes or wetlands, by using active collectors filtering air (Mladenov et al., 2011) displayed at the exposed site. Then, the DNA from collected filters can be extracted and sequenced (Picazo et al., 2019), thus describing the immigration processes and how they provide new potentially colonizing microbes that can be compared with samples collected before and after the exposure.

Quantifying adaptation and derived increased community resistance is even more challenging because they involve evolutionary processes, although the PICT concept as detailed above provides a theoretical framework for microorganisms (for details, see Tlili et al., 2016). In principle, testing adaptation of local populations and increased community resistance could be done by collecting the target taxa in the field and testing their responses (i.e., survival, reproduction, avoidance) to increasing stress levels under laboratory conditions (see Shahid et al., 2018). Transcriptomic analyses hold a rather unexplored possibility to assess the influence of chemical exposure on different genotypes and to identify enriched or suppressed functional pathways (e.g., detoxification) that increase or decrease species tolerance to chemical stress. The analysis of genotypes (prior to and after exposure) could help discern between population recovery and adaptation in multigenerational studies (Leblanc, 1982) or evaluate the adaptation of collected or resurrected individuals (e.g., from diapausing eggs) from locations of

different exposure history (Abdullahi et al., 2022). All of these experimental approaches can help elucidate the mechanisms that are involved in each of these ecological processes at both the population and community levels.

To sum up, an interplay between recolonization, recovery, and adaptation does take place in nature. By taking advantage of the different spatiotemporal dimensions and the genetic and phenotypic analyses of the exposed populations and communities, semifield experiments offer the possibility to separate each individual process, helping to approximate the net effects of the others. This information will help to improve our understanding of the resilience mechanisms of populations and communities to chemical stress and will be pivotal to parameterizing ecological models that help to characterize the impacts of chemical exposure in complex spatiotemporal settings and in scenarios with different environmental conditions, and hence to better understand ecological complexity in a chemical stress context. In the context of chemical risk, policymakers, decision makers, and natural resource managers could attempt to characterize the vulnerability of the ecological scenario they intend to protect by, for example, making a semiquantitative evaluation of the landscape connectivity and species dispersal abilities.

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