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Critical Review

RESILIENCE IN ECOTOXICOLOGY: TOWARD A MULTIPLE EQUILIBRIUM CONCEPT

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Abstract: The term resilience describes stress–response patterns across scientific disciplines. In ecology, advances have been made to clearly define resilience based on underlying mechanistic assumptions. Engineering resilience (rebound) is used to describe the ability of organisms to recover from adverse conditions (disturbances), which is termed the rate of recovery. By contrast, the ecological resilience definition considers a systemic change, that is, when ecosystems reorganize into a new regime following disturbance. Under this new regime, structural and functional aspects change considerably relative to the previous regime, without recovery. In this context, resilience is an emergent property of complex systems. In the present study, we argue that both definitions and uses are appropriate in ecotoxicology, and although the differences are subtle, the implications and uses are profoundly different. We discuss resilience concepts in ecotoxicology, where the prevailing view of resilience is engineering resilience from chemical stress. Ecological resilience may also be useful for describing systemic ecological changes because of chemical stress. We present quantitative methods that allow ecotoxicologists and risk managers to assess whether an ecosystem faces an impending regime shift or whether it has already undergone such a shift. We contend that engineering and ecological resilience help to distinguish ecotoxicological responses to chemical stressors mechanistically and thus have implications for theory, policy, and application. *Environ Toxicol Chem* 2017;9999:1–7. © 2017 SETAC

Keywords: Engineering resilience Ecological resilience Ecosystem response Communities Risk assessment

INTRODUCTION

The field of ecotoxicology plays an important role in understanding how chemical stressors, such as those used in the production of food and fiber (e.g., textiles), affect the environment [1]. Reduced individual growth and survival, altered community structure, abundance, and food webs, and impaired ecosystem processes resulting from chemical stressors have all been documented [2,3]. These effects are evident in ecosystems across continents [4] and might be the result of a broad range of substances. The present study, however, mainly uses the impact of pesticides as a model scenario.

Obvious environmental impacts of chemical stressors highlight the shortcomings of current legislation. For instance, the ecological risk assessment (ERA) of pesticides in the European Union requires that “no unacceptable effects occur in the environment.” Although the protection goals are still debated, the requirement to safeguard ecosystem services has been recognized by the European Food Safety Authority [5]. The harmlessness (i.e., aiming to achieve acceptable risks) of pesticide application for nontarget environments is an important requirement for their authorization, particularly because pesticides are applied to agricultural land to protect crops from pests. The exceedances of regulatory thresholds, as defined during the ERA of insecticides, in 50% of global surface waters or sediments [6] point either to a deficiency of the exposure or effect assessment [7] or misuses of the insecticides.

Ecologists increasingly recognize that ecosystems can undergo *regime shifts* (technical terms in italic are defined in Table 1 on first use) [8,9]. Such regime shifts imply substantial

abiotic and biotic change [10]. These changes are often perceived as negative because of the frequent loss of ecosystem services [11] and the need for costly restoration and management efforts to sustain these services [12]. It is uncertain how the widespread occurrence of pesticides above regulatory threshold, with associated species loss [6], affects ecosystem integrity from local to regional to global scales. This uncertainty further increases when pesticide impacts on ecosystems recur (pulse disturbances) and interact with other stressors [13]. That is, the interaction of multiple pesticides or other chemicals of anthropogenic origin, but also other forms of environmental stress (e.g., global warming, introduction and spread of non-native organisms, land-use change, alteration of biogeochemical cycles), combined with increasing demands for food as a result of growing human populations, may accelerate ecological and social system change [1].

Because of the complex interaction between people and nature, ecosystems may be unable to cope with the impact of chemical stressors or landscape changes in terms of long-term provision of ecosystem services. Although there are some promising results from soil microorganisms that show adaptation to zinc increases with increasing exposure [14] and elevated community stability under additional stress [15], it is unclear to what degree these results can be generalized to other organism groups or whole ecosystem responses. An understanding of the resilience of ecosystems to ongoing environmental change is therefore needed.

Resilience theory, which focuses on the ability of systems to absorb stressors, has recently gained traction for studying ecological responses to disturbances. Unfortunately, the increased popularity of resilience and related concepts has resulted in the loss of clarity of the concept, introduced by Holling more than 40 yr ago in ecology [16]. Multiple definitions of resilience have been put forward [10], and the

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Table 1. Glossary of technical terms

Term	Definition
Alternative regimes	An alternative regime is defined by stable structures, functions, processes, and feedbacks.
Ecological resilience	This describes the amount of alteration needed to change a set of processes and structures to a different set in an ecosystem. High resilience would mean that a considerable amount of energy is needed to induce such changes.
Engineering resilience	This assesses the recovery time of structural or functional variables in an ecosystem to predisturbance conditions. High resilience is interpreted as fast return times.
Feedback loops	These are circuits in complex systems that reinvest some of the yield to the input of a system to allow for self-correction and adjustment to internal and external variables. Feedback loops can be balancing (or negative) and occur when the expected magnitude of change will lessen in the future. Reinforcing (or positive) feedback loops, in contrast, occur when the expected magnitude of changes will increase in future.
Functional group	A group of species shares a set of traits determining their role in ecosystem processes (e.g., shredders contributing to leaf litter decomposition).
Functional trait	A characteristic or property of a species determines its role in ecosystem processes (e.g., mouthparts of invertebrates such as representatives of the functional group shredders determine their feeding on leaf litter).
Multiple equilibria	This is an inherent property of ecological resilience, which allows the existence of alternative stable states governed by different sets of processes and structures. Hence, ecosystems can work at multiple and not just one equilibrium.
Regime shift	Inherent to the ecological resilience definition is that ecological systems can undergo nonlinear change or shift between alternative states, such as, for example, shallow lakes that show clear-water and turbid alternative states.
Response diversity	Different species in the same functional group respond differently (in terms of type or intensity) to disturbance.
Tipping point	This describes the amount of energy/stress put into an ecosystem that exhausts its capacity to adapt to and cope with additional disturbances. Hence the system abruptly reorganizes in a new regime with new structures, functions, and processes.

term is often used in a normative context [17]. In the present study, we discuss resilience concepts in terms of their relevance and application to ecotoxicological research. We also highlight the implications for predictive and retrospective ERAs. Retrospective ERA, which is predominantly based on field studies and monitoring, may particularly benefit from the consideration of these concepts, which can help to identify systems that are vulnerable to regime shifts [18]. The prevailing view of resilience in ecotoxicology is the ability of organisms to resist or rebound from chemical stress [19,20], and thus ecosystem dynamics can be studied from a single equilibrium focus (i.e., *engineering resilience*). *Ecological resilience*, on the other hand, accounts for the ability of some complex systems to operate and organize in *multiple equilibria*, that is, when systems undergo regime shifts and reorganize in *alternative regimes* [21].

We present an overview of resilience based on recent examples from the ecological literature, introducing statistical tools that provide techniques for quantitative evaluation of the resilience of communities and ecosystems to pesticides and other stressors. Although we contrast these definitions of resilience, we also show that they are not mutually exclusive. We contend that considering ecological and engineering resilience in ecotoxicology allows stress–response relationships to be contextualized mechanistically, both in theory and practice. Such an improved understanding may also provide insight for refining ERA and other chemical stressor–related policies.

RESILIENCE

Adopting concepts in ecotoxicology

The term resilience has very different meanings, depending on the context [10]. Among the most commonly used definitions in ecology are engineering resilience and ecological resilience, which are often poorly differentiated. Engineering resilience (or resiliency, recovery, or bounce-back) defines the ability and time required (and is thus a rate) for structural or functional

attributes in ecosystems to return to their initial condition once released from stress [22] (see point 1 in Figure 1). In ecotoxicology, engineering resilience is often experimentally tested to examine terrestrial and aquatic community trajectories after exposure to pesticides or other chemical stressors [23]. If populations exposed to toxicants recover, in terms of, for instance, their abundances to levels comparable to unexposed controls within an acceptable period (usually 8 wk), the impact of the stressor may be judged acceptable [5].

Rapid return times (recovery) can be interpreted as reflecting high engineering resilience, and recovery can be quantified using time as the unit of measurement. However, the definition of rapid is subjective and may depend on the scale of observation. For instance, testing for engineering resilience in short-term experiments may not cover time periods of observable recovery. In contrast, assessing engineering resilience in the field over longer periods is more complex and can be problematic, although successful studies do exist (e.g., insect recovery demonstrated within a single generation following chemical disturbances [24]). Some systems do not appear to recover following disturbance, such as those ecosystems that experienced acidification in the 1970s and 1980s. The sluggish recovery and seeming inability to attain preacidification conditions of many ecosystems have been attributed to a lack of sufficient time for recovery [25]. Similar phenomena may also be observed in landscapes and waterscapes with chronic or repeated exposure to pesticides or complex mixtures of micropollutants from wastewater treatment plants [26]. In the acidification debate, current alternative explanations for the failure to recover invoke the irreversibility of impact, that is, acidification has nudged ecosystems to an alternative stable regime from which it is unlikely to revert to preacidification conditions (see points 2 and 3 in Figure 1 [27]). Recovery may occur in some attributes of the ecological system under scrutiny, whereas other attributes, such as species interactions (including trophic relationships [28]), may be irreversibly changed. Such phenomena have been formalized in the community

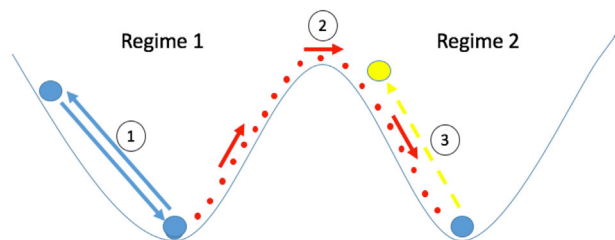


Figure 1. Ball-in-cup heuristic showing theoretical ecosystem regimes and 2 distinct resilience mechanisms. Regime 1 comprises a desirable regime for humans and regime 2 a degraded undesirable regime. 1) Engineering resilience or bounce-back after disturbances/pesticide application within a regime (traditional approach in ecotoxicology). 2) When an ecosystem passes a threshold and shifts to an alternative regime (i.e., ecological resilience; note: there is no bounce-back to regime 1). 3) In such a degraded regime, pesticide application may be necessary to coerce the resilience of this degraded regime to guarantee ecosystem service provisioning (agricultural production).

conditioning hypothesis [29]. For systems and communities that are not static over time, which is nearly all ecological systems, it is frequently unclear to what reference condition or baseline the return time should be measured.

It is sometimes possible to force a return to reference condition/baseline with human intervention. Lakes having reorganized in an acidified regime can release toxic aluminum, which interferes with the production of fish (a desirable ecosystem service). To reduce toxicity and maintain fish production, managers have limed lakes for decades [30]. However, when liming ceases, they return to the acidified regime [31], highlighting the robustness of this regime. Liming merely mitigates the impacts of acidification rather than permanently restoring lakes to a previous circumneutral regime. This illustrates that liming, which is a very costly management approach, is coercing the degraded, acidified regime to maintain ecosystem service production [31].

The acidification example highlights the limitations when engineering resilience is used as the yardstick to measure impact, and also the consequences for management. Like other concepts that fall under the umbrella of ecological stability, variability, resistance, persistence, and robustness [32], engineering resilience assumes that systems are characterized by a single equilibrium, and that structural and functional aspects always recover after disturbance, when given sufficient time [19]. While this is reasonable for some systems, such as streams subject to chemical spills [33], for others this assumption fails to take into account the potential for alternative regimes of the same system, that is, when recovery is curtailed because of threshold responses after disturbances (Figure 1). This possibility of existing in alternative regimes is accounted for in the ecological resilience definition.

Ecological resilience emphasizes the ability of a system to absorb disturbance, responding and adapting to it through the calibration of *feedback loops*. More specifically, Holling [16] defined ecological resilience as a measure of the amount of stress that is required to transform a system from being maintained by one set of reinforcing processes and structures to being maintained by a different set of processes and structures (and is therefore a property of systems). Inherent in this definition of resilience is that ecological systems can undergo nonlinear changes or shifts between alternative regimes (i.e., regime shifts; Figure 1). Ecosystems can operate in multiple equilibria and therefore do not have one single equilibrium regime. Engineering resilience or recovery over time can be a

component of ecological resilience when a threshold is not crossed, and can be used in a predictive way when a system approaches a threshold, which is also referred to as the *tipping point*. Theoretically, as the tipping point is approached (but not exceeded), recovery rates slow down [34,35] and so recovery takes longer [36].

The practical implications of engineering versus ecological resilience are important. In the next section, we illustrate the necessity to distinguish between these concepts using a hypothetical example of an agricultural lake exposed to nutrient or pesticide stressors.

Ecotoxicology, resilience, and potential management implications

Alternative regimes have been documented for terrestrial, freshwater (streams and lakes), and marine ecosystems [8,37]. Shallow lakes are well-known models of regime shifts and alternative regimes in aquatic ecology [38]. Lakes shift from a clear-water state dominated by submerged macrophytes (desired state) to a new, degraded, and undesired state with turbid water, frequent algal blooms that are often toxic, and reduced ecosystem service provisioning [39]. The driver(s) of this change are often related to agricultural practices, including exposure to excessive nutrient enrichment or pesticides, and the interactions of both or additional stressors. Both regimes are stable, meaning that a threshold of disturbance has been passed and the system has reorganized in a new regime with a new set of feedbacks and mechanisms. Even intensive management intervention is unlikely to disrupt the mechanisms that maintain the system structure and function of the new regime and to reverse the regime shift, as illustrated previously with the liming example (see *Adopting concepts in ecotoxicology*). Engineering resilience does not account for such alternative stable regimes, and incorrectly implies that an undesirable regime would inevitably revert to a desired state without management interaction, if given sufficient time.

Although engineering resilience can be studied in all ecosystems if the initial regime in undisturbed conditions is defined, the broader and more relevant definition is ecological resilience. The possibility of ecological systems to shift between regimes accounts realistically for the dynamic and complex behavior of nature, although the number of possible regime shifts may vary between systems. Lentic systems may have a higher tendency for multiple regime shifts than lotic systems because of their high interconnectedness and spatial integration. This differentiation also suggests that lentic systems allow for the assessment of resilience with a temporal focus, while lotic systems could support resilience research with a spatial and temporal perspective, as lotic systems could benefit from self-cleaning processes that modify the impact of chemical stress downstream of their release. Ultimately, accounting for this complexity has the potential to inform policy and environmental laws (e.g., retrospective ERA), which are often too rigid and view ecosystems as static entities, ignoring the complexity of interactions [28] and their dynamic and often abrupt changes [40].

In ecotoxicology, adopting ecological resilience theory may stimulate debate about regulatory decision-making. It could be applied during retrospective (but also to predictive) risk assessments based, for instance, on monitoring data [sensu 4,41,42]. A better understanding of temporal dynamics may help identify when the potential of ecosystems to recover from disturbances is exhausted (engineering resilience slowing down) and a regime shift is imminent. To this end, scientists, risk managers, and politicians need quantitative metrics to be

able to assess the vulnerabilities of ecosystems, to guarantee the sustainable use of pesticides in the environment [18]. There are several attributes of ecological resilience that form the foundation for the implementation of such quantitative approaches in ecotoxicology, which we review in the present study.

Attributes of ecological resilience

Essential to our understanding of ecological resilience is the notion that ecosystem processes (e.g., flux of matter and energy, primary productivity) depend on functional attributes of species within ecosystems [43], and species' responses to disturbance. As suggested by many studies in the context of biodiversity and ecosystem functioning research [44], this idea departs from the idea that ecosystem processes are mainly determined by structural community attributes like species richness [11]. Building on this argument, systemic vulnerabilities to pesticide exposure instead depend on *functional traits* of species [45], which are used in various indices such as the saprobic index or the species at risk (SPEAR) concept [46]. Here, traits aid in the assessment of whether a species is sensitive or tolerant to a stressor. Collectively, these sensitivities or tolerances mediate the community responses to stress, although additional traits or trait combinations govern the overall response [47]. For instance, a species with a higher physiological ability to cope with a stressor is more tolerant than a species with low physiological tolerance [48]. In turn, a species with low physiological tolerance, but with low dispersal capacity, may be more vulnerable to stress than a sensitive species with high dispersal capacities, enabling them to escape pollution events [49] and so recolonize after the event. The different types of traits that contribute to vulnerability have been conceptualized as physiological sensitivity and biological avoidance and recovery traits [47]. Recent studies show that they can be interrelated (i.e., only some trait combinations occur) [47]. In the resilience context, the variability in the trait combinations that explain community responses to disturbance has been referred to as *response diversity* [50,51]. Response diversity [50] summarizes the range of responses a *functional group* possesses against environmental change, depending on the multiple traits of a species (e.g., dispersal capacity, reproduction capacity, and growth) and how they are distributed in a functional group.

The response diversity of those functional groups that are subject to substantial risk by an individual or set of stressors may, in the ecotoxicological context, be described using species sensitivity distributions (SSDs) [52], with the reservation that SSDs mainly capture diversity in the physiological sensitivity. Nevertheless, it follows that if response diversity is low, many species will be similarly affected (or not affected) by a perturbation, and this mediates whether systems can recover from, or shift to, a new regime in response to stress [53]. If the response diversity is high, the possibility of recovering to the original functional status quickly after the release from stress should be high [53]. However, this can depend on the duration and timing of the chemical stressor as well as the relationship between the traits determining the response to stressors (response traits) and those traits governing ecosystem processes (effect traits). This idea is partly incorporated in the concept of pollution-induced community tolerance (PICT) [54].

The concept of PICT assumes that chemical stress replaces sensitive species with more tolerant members of the community, ultimately increasing the tolerance at the community level and potentially sustaining the functions these communities

provide [55]. As indicated, redundancy describes the capacity of species to compensate for the loss of any other species within a functional group, thereby maintaining the function (e.g., grazing, pollination, predation). For instance, leaf-associated fungal communities provide 2 functions, which are decomposition of leaf material and the increase in nutritious value of leaves for shredders. These communities can be modified in response to fungicides, but can continue to maintain stable decomposition rates of organic material [56]. Depending on the context [57], this suggests some level of functional redundancy within this functional group regarding the functions they deliver. Nonetheless, the loss of individual species that are key for other processes and functions (keystone species) might still have a disastrous impact on the integrity of ecosystems.

Ecological resilience, and its quantification, uses measurements of response diversity (for instance, SSDs) and redundancy within functional groups to take into account how functional traits of species are distributed within and across an ecological scale. Scale refers here to both space and time, that is, the distinct area and temporal dimension in which processes operate. For example, the activity of zooplankton is diurnal and changes substantially within a range of only a few meters of water depths [58]. By contrast, plate tectonics operate at a global scale, and the associated formation of faunas and floras relates to geological time scales.

Quantifying ecological resilience

A range of methods is available to deduce scale-specific patterns and therefore the distribution of functional traits (including response diversity), their combinations, and redundancy in ecological systems across distinct spatiotemporal scales [59]. These methods differ in their underlying assumptions and have different advantages and limitations, which substantially influences the interpretation of the data, particularly when inferring resilience or comparing results obtained with different methods.

Discontinuity analysis focuses on the identification of scales in ecological systems by identifying ecological transition zones in terms of organisms' capacities to exploit resources (food, shelter, and other resources; Figure 2) in complex systems [60]. In this context, animal body sizes and masses, which are indicative of transitions [61] and integrate many physiological and ecological attributes based on allometric relationships [62], are often used as surrogates. The discontinuity analysis identifies aggregations of organisms that presumably perceive and exploit resources similarly relative to species in other aggregation groups [60]; for instance, communities of ants and large mammals in a Savannah obviously operate at different

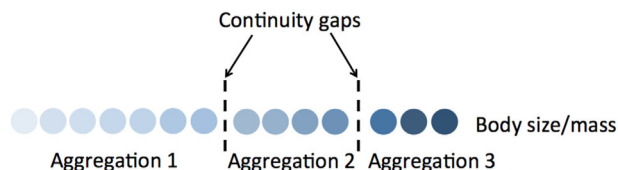


Figure 2. Schematic illustration of the discontinuity approach. Species (each dot represents 1 species) within a community are rank-ordered from the smallest/lightest to the largest/heaviest (indicated by the different shades of blue). Continuity gaps (= discontinuity) are identified using statistical approaches and separate the species into aggregation groups (in Figure 2: 1–3), which are hypothesized to mirror scale-specific structures/properties in ecosystems. Continuity gaps thereby reflect transition zones, with higher variability close to these zones. (Modified from Angeler et al. [58]).

scales, while also in the group of mammals several aggregation groups may be formed that deviate from one another. Statistical tools defining transition zones/scales include classification and regression tree analyses [63] and their Bayesian implementations [64], kernel density estimation [65], and the gap rarity index [66]. The results of such analyses allow for an estimation of disturbances, including those triggered by toxic compounds released by wastewater or repeated exposures to peak concentrations of pesticides in the field or during mesocosm experiments. Such analyses provide opportunities to assess whether the scaling structure and associated within-scale and cross-scale redundancies in the system change as a result of chemical stress. Such scaling patterns can change substantially after a regime shift has taken place [59]. Discontinuity analyses therefore provide opportunities to assess more rigorously whether a system remains in the same regime after disturbances, and where engineering resilience can be used as a measure of recovery from pesticide pulses, or whether it has shifted to a new regime with new structures, and a bounce-back to conditions prior to the regime shift becomes untenable [67].

Discontinuity analyses are relatively easy to perform in organisms with discrete body sizes or masses (animals). However, their application is limited for taxa with modular growth (e.g., fungi, plants without discrete body sizes or masses) and for assessing species abundances, (e.g., the importance of rare vs dominant species). Angeler et al. [18] suggest using body mass-independent data, such as population size, as input variables to complement discontinuity analyses. Multiscale time series analyses and spatial modeling are useful alternatives for the identification of the scales of temporal frequencies in complex systems, allowing one to track the imprints of environmental change [18]. The application of these tools is particularly useful in a biomonitoring context or in mesocosm studies, to assess the impact of pulse or press (i.e., continuous) releases of chemical stressors in ecosystems in a temporally explicit way. Angeler et al. [68] identified groups of macro-invertebrate species in subarctic lakes that are responding slowly and others swiftly to shifting environmental variables. In a landscape context, spatial modeling provides the opportunity to test the vulnerability of entire networks of ecosystems or regional landscapes to environmental change [69], ultimately informing resilience in a regional context of spatial resilience [70]. Prerequisite for the application of such modeling tools are data sets comprised of longitudinal data of broad spatial extent. Unfortunately, such data are scarce and would require substantial monitoring efforts, which are costly and therefore limited.

ECOTOXICOLOGY AND RESILIENCE: THE BROADER PICTURE

A consideration of the preceding concepts for future research and management applications (biological and chemical monitoring, risk assessment, policy development) seems beneficial considering the fast-changing ecological baselines on a swiftly changing planet. More precisely, consideration of ecological resilience allows for the identification of patterns indicative of disturbances or even regime shifts [21] that might have gone undetected using standard biomonitoring analysis. Analyses of ecological resilience have the potential to inform about the loss of ecosystem integrity [51] and could be used to inform retrospective ERAs about the status of stressed ecosystems. Increases in agricultural production, intensification, and expansion are likely to occur at the cost of increased natural habitat loss [71]. The transformation of relatively pristine ecosystems into anthropogenically impacted agricultural landscapes

may entail synergistic effects on the loss of ecosystem services, via interaction of biodiversity loss and land use change [sensu 3], forcing ecosystems to organize into new regimes with new structures.

The reduction in abundances or even regional extinction of species (e.g., bats and birds) able to control agricultural pests [72] can cause substantial economic losses; for example, pest control services provided by birds in coffee fields in Costa Rica or bats in cornfields in the United States contribute an economic gain of more than US \$300/hectare and year [73] and US \$1 billion/yr [74], respectively, if we assume (likely wrongly) homogenous foraging across agricultural fields. Such a loss of natural services will likely need to be compensated for by a further increase in the application of pesticides and nutrients. Both are inevitably released into nontarget areas during or following their application [75]. In addition, new technologies such as genetically modified crops [76], nanopesticides, and nanofertilizers [77] may further increase the pressure on the integrity of nontarget ecosystems with unpredictable consequences for ecological communities, the ecosystem services they provide [78], and ultimately the resilience of these systems.

Although relatively unreported in the past [79], such unpredictable results from complex interactions of pesticides with other stressors [80] can lead to unexpected system responses. If and how such surprises manifest is highly uncertain, but these manifestations could entail fundamental reorganization of ecosystems, and significant impacts on human health and welfare [81,82]. We suggest that a better understanding and anticipation of potential changes in ecosystems is required to safeguard environmental sustainability and human welfare that critically depend on these ecosystems.

In conclusion, there are 2 mechanistically distinct scenarios of pesticide application in the environment. First, pesticides may help maximize production provided by a limited range of ecosystem services (i.e., crop production) that are desirable for humans. However, the ecosystem regimes associated with provisioning these and other services partially provided by off-crop areas, which can be quantified using ecological production functions [83], may tolerate stressors only to a certain extent. Eventually ecosystem attributes may no longer be able to recover from disturbances and may shift to an alternative regime (e.g., the example of the regime shift from a clear-water to a turbid lake). Second, in such alternative regimes, which may be undesired by humans given the potential loss of organisms providing natural pest control or the potential increase in susceptibility to pests, pesticide application combined with technological interventions may become mandatory for agricultural fields to maintain their services. This may promote a change of system structure and function, further destabilizing the ecosystem. Risk managers and researchers from different scientific disciplines therefore could engage in scenario planning to envision potential alternative futures, and to adapt to and prepare for transformative change [84]. Our perspective may provide a first step in this direction.

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Data Availability—All data can be obtained from the corresponding author on request (mirco.bundschuh@slu.se).

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