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Pesticide-Induced Stress in Arthropod Pests for Optimized Integrated Pest Management Programs

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Abstract

More than six decades after the onset of wide-scale commercial use of synthetic pesticides and more than fifty years after Rachel Carson's *Silent Spring*, pesticides, particularly insecticides, arguably remain the most influential pest management tool around the globe. Nevertheless, pesticide use is still a controversial issue and is at the regulatory forefront in most countries. The older generation of insecticide groups has been largely replaced by a plethora of novel molecules that exhibit improved human and environmental safety profiles. However, the use of such compounds is guided by their short-term efficacy; the indirect and subtler effects on their target species, namely arthropod pest species, have been neglected. Curiously, comprehensive risk assessments have increasingly explored effects on nontarget species, contrasting with the majority of efforts focused on the target arthropod pest species. The present review mitigates this shortcoming by hierarchically exploring within an ecotoxicology framework applied to integrated pest management the myriad effects of insecticide use on arthropod pest species.

CONCEPTUAL FRAMEWORK

Pesticides, particularly insecticides and acaricides, are toxicants deliberately released into the environment to reduce target species populations. As such, pesticides are also environmental contaminants, as their presence in the environment occurs at levels higher than their natural background levels. Furthermore, pesticides can be justifiably recognized as pollutants because they are environmental contaminants that adversely affect living species. Although pesticides are pollutants of deliberate use, this characterization does not minimize their importance in agriculture, animal husbandry, and public health (1, 31, 104). However, this perception facilitates recognition of the negative and positive impacts of these compounds. In this review, we hierarchically explore within an ecotoxicology framework the multitude of responses sparked by pesticide use against arthropod pest species.

(Mis)Conceptions About an Influential Tool

Pesticides are arguably the most influential pest management tool since the onset of their wide-scale use in the late 1940s. This range of influence surpasses their realm of practical use, encompassing the general public and adding pressure to regulatory agencies. Despite their recognized importance for food production as well as human and animal health (31, 104, 120), the layperson's perception of pesticides is largely negative, especially when synthetic compounds are considered (11, 15, 18, 29).

The enduring prominence of pesticides has led to divergent conceptualizations of these compounds, which convey the equivocated notion that particular pesticides are safe for humans and the environment. Biopesticides, for instance, refer to the natural origin of the compounds (38, 135, 137), not their toxicity or safety (29, 72). Reduced-risk pesticides refer to compounds exhibiting at least one of six advantageous traits when compared with existing pesticides (134); thus, it is not a particularly stringent definition. In the present review, we make no distinction between the neologisms, pleonasm, and/or misnomers used when referring to pesticides, including pesticidal toxins.

Pesticide Use, Exposure, and Assessment Limitations

Despite the high overall costs of use and the worldwide drive toward sustainable agricultural production, pesticide use is increasing (47, 51, 117). Insecticides and the acaricides of the older generation, encompassing four pesticide groups, were replaced in part by a plethora of 25 main groups of nonpersistent compounds with distinct modes of action and improved safety profiles (25, 52). These new groups, however, are amenable to a higher number of applications per year, resulting in higher amounts of pesticides being applied, particularly under intensive agriculture production and vector control (105, 117, 120).

Efficacy studies usually focus on the short-term mortality of target arthropod pest species. Similarly, regulatory agencies focus mostly on short-term endpoints when deciding to register compounds. Nevertheless, long-term effects may occur, and even short-term mortality in arthropod pest complexes may not be the primary endpoint to consider (4, 40, 115), a point too often neglected by academia and regulators alike. Ecotoxicology studies do not usually focus on arthropod pest species, and the few studies that do are physiologically oriented and use short-term mortality assessments, in contrast to the abundant comprehensive studies focusing on nontarget arthropods, such as the honey bee (*Apis mellifera* L.) and the natural enemies of pest species (39, 41, 78).

Direct and Indirect Hierarchical Effects

The importance of the lethal effects of insecticides cannot be denied; however, underestimating potential sublethal effects of pesticides on target organisms and their potential ecological consequences is a mistake. Although pesticides are usually applied at concentrations that will result in rapid death of pest species, residues degrade over time on plants, animals, water, and soils, resulting in sublethal exposures (10, 42). Furthermore, nontarget species, including secondary arthropod pest species, can be exposed to sublethal concentrations of pesticides for long periods, leading to unforeseeable consequences such as pest outbreaks (34, 62).

An arthropod pest species may be directly and indirectly affected by a pesticide application. Direct effects include mortality and various sublethal effects of pesticide exposure, and indirect effects encompass habitat changes (e.g., food and shelter contamination) and changes to other species within food webs that alter pest population viability (**Figure 1**). Both direct and indirect effects of an applied pesticide could impair the physiology of an organism, reducing its survival and/or reproduction. Other organisms that interact with the pest species in an ecosystem may also be negatively affected, which may result in unpredictable outcomes in the demographic vital rates of the pest species (48, 122). The population-level effect on a given species can translate into a community-level effect, adding another hierarchical level of pesticide-induced stress and emphasizing the complexity of effects that may potentially accrue from pesticide use (**Figure 2**). Such effects may affect the original arthropod pest species targeted by the insecticide application, leading to ecological backlashes that compromise integrated pest management.

INDIVIDUAL STRESS RESPONSES

Pesticides suppress arthropod populations by interacting with a primary site of action within an individual organism and impairing at least one of its basic physiological processes, leading to its demise (25, 52). This is the basis on which commercial pesticide molecules are developed for managing arthropod pest populations. Nonetheless, any given pesticide is likely to interact with secondary sites of action, which may not lead to the death of the organism but may produce sublethal consequences that compromise its homeostasis and interfere with its survival and/or reproduction. This is the case for the insecticide baits used against leafcutting ants, where forager mortality is actually an undesirable trait because colony suppression is the objective. Colony suppression requires the unaffected foragers to carry the toxic bait to the nest, impairing the colony either by directly compromising the fungus garden (as a fungicide) and its cultivation by the minor workers or by impairing progeny production by the ant queen (3, 4, 40).

Physiological Responses

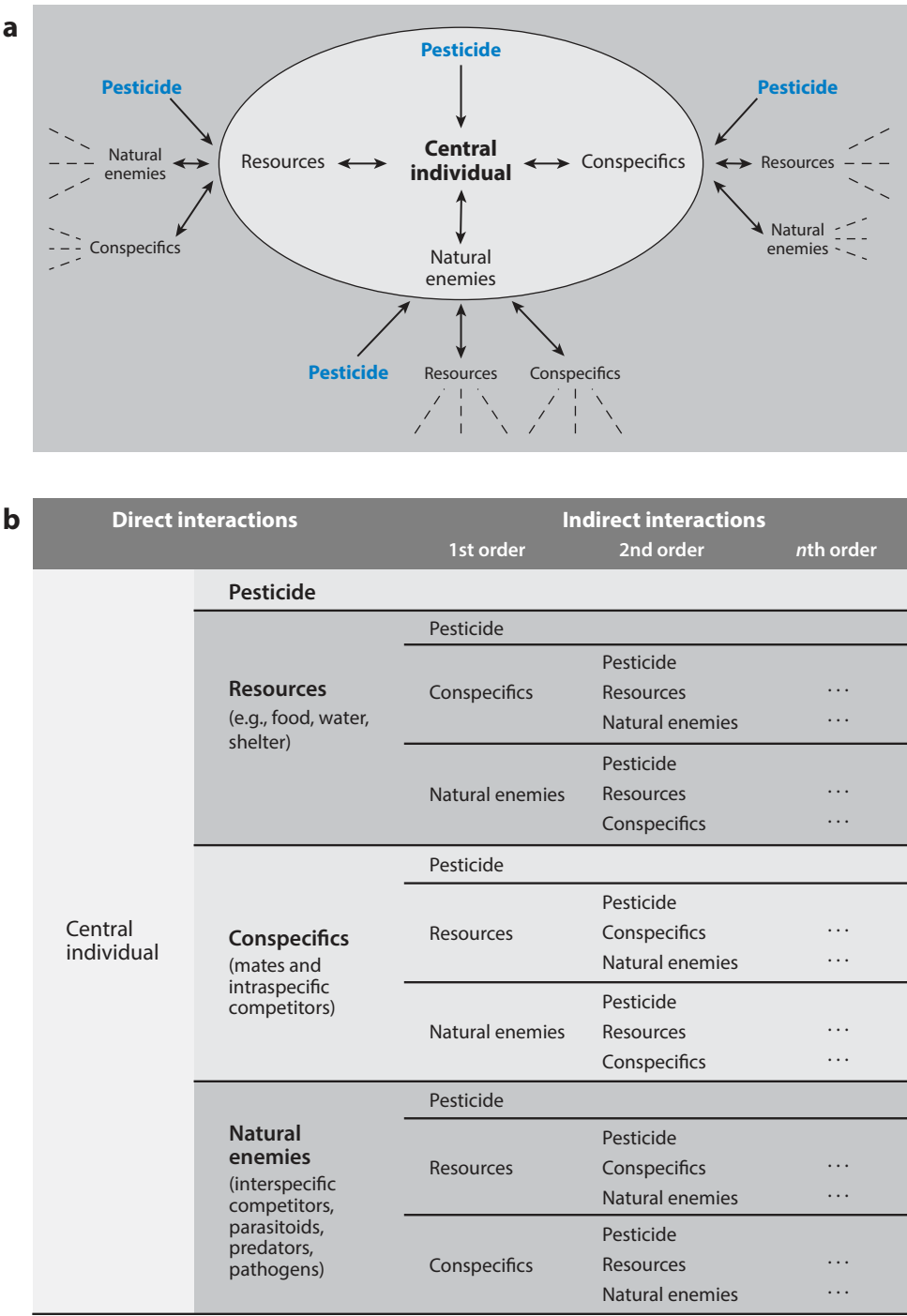
Pesticides affect individual arthropods, the consequences of which may manifest at higher hierarchical levels, i.e., populations and communities. Studies at the individual level elucidate how a pesticide interacts with its target sites in the organism. Therefore, toxicological studies on the mode of action of pesticidal compounds are the first step to understanding how pesticides work on individual insects, as well as how they eventually lead to effects on the structure and function of populations and communities (93).

Physiological responses to pesticide exposure at the individual level encompass not only the pesticide toxic responses (both primary and secondary) mentioned above, but also nontoxic or protective responses (93). For example, pesticide-induced production of detoxification enzymes (46, 95)

Figure 1

(a) Weblike representation of potential direct and indirect effects of pesticides departing from a central organism, and the major environmental components that might influence the central organism's chance of surviving, reproducing, and irradiating to subsequent interrelated components. The dotted lines denote the continued progression of effects as in the central components of the web, the ellipse delimits the direct interactions, and the rectangle in which panel *a* is set delimits the progressive range of potential indirect interactions with the central organism.

(b) Horizontal progression expanded from the weblike representation in panel *a* illustrating potential direct and indirect effects of pesticides affecting a given central organism.



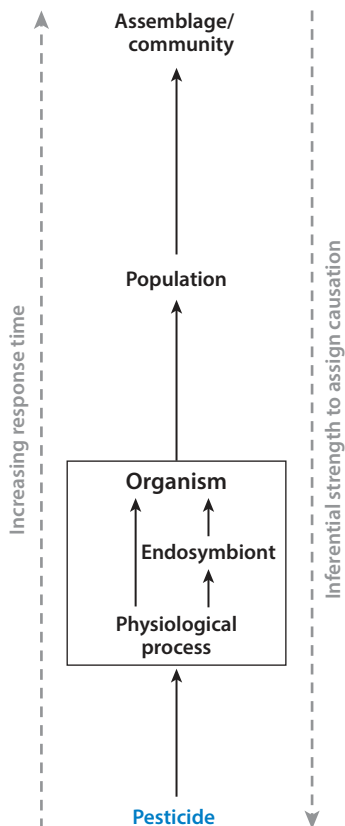


Figure 2

Schematic hierarchical representation of the chain of potential effects of pesticides.

provides the mechanistic basis of pesticide-induced stress tolerance and resistance. Protective responses may also involve shifts in metabolism, particularly digestive and energy metabolism, allowing physiological trade-offs that favor protective mechanisms leading to survival at the expense of body growth and/or reproduction (74, 136), as is apparently the case for the maize weevil (*Sitophilus zeamais*) (6, 60, 89).

Differing pesticide target-site sensitivity, detoxification, sequestration, excretion, and penetration allow for the differential physiological toxicity of pesticides, a subject widely explored in insecticide resistance and selectivity studies (35, 36, 140). In addition to these physiological mechanisms, reduced pesticide exposure based on behavior should also be considered because it may play a fundamental role in pesticide efficacy and its consequences (53, 68). Both physiological and behavioral responses may also be non-self-determined when considering the individual arthropod as a symbiont-inhabited ecocosm in which endosymbionts play relevant roles, allowing their host better adaptation to the external environment (44, 127). Evidence of endosymbiont-mediated arthropod adaptation to chemical plant defenses should not be a surprise (126); therefore, endosymbionts are also likely to play significant roles mediating arthropod responses to insecticidal stress (21, 77, 129). The latter issue has received little attention and is worthy of further study.

Behavioral Responses

Arthropod behavior is an integrated result of changes in the organism's physiology while it interacts with its environment; it is an organism-level response potentially affected by pesticide exposure and is a useful early-warning signal, because behavior is 10–1,000 times more sensitive to environmental quality than conventional LC_{50} estimates (70, 71). Behavioral changes due to pesticide exposure occur either as a result of the mode of action of the compound, or as a result of the organism's innate response to the pesticide itself or to alterations in the environment in which the pesticide is used, which can minimize or even enhance the effects of exposure (53, 68). Therefore, by examining an organism's behavioral response(s), researchers can determine the primary and secondary modes of action of a pesticide and recognize potential insecticide resistance (or selectivity) mechanism when altering the exposure and thus the efficacy of the compound, further contributing to arthropod pest management.

Repellence (i.e., the behavioral response after extensive contact with a pesticide) and irritability (i.e., the behavioral response with little or no pesticide contact) are two components of the arthropod behavioral avoidance response to pesticide exposure that are usually neglected in studies of arthropod pest species, unlike natural enemies (26, 41, 54, 88). In addition, arthropod behavioral responses to pesticide exposure may be either stimulus dependent, when taking place after compound detection (with or without contact) and the response is enhanced by the stimuli, or stimulus independent, when due to an independent and innate behavioral trait, such as the exophily (i.e., tendency to rest outside human-made shelters) in mosquitoes (45). Both behavioral responses may co-occur in an arthropod when exposed to a given pesticide. For example, maize weevils exhibit stimulus-dependent feeding responses and stimulus-independent locomotory responses after exposure to deltamethrin (54, 55).

Stimulus-dependent impairment of swimming speed and wriggling movements, which may compromise feeding, refuge seeking, and escape responses in larvae of the yellow fever mosquito (*Aedes aegypti*), have been reported as sublethal effects of three different insecticides, deltamethrin, imidacloprid, and spinosad (132). In fact, locomotory responses are usually very important because they express a synthesis of the arthropod's physiological process, as in the mosquito larvae (16, 132), and its anatomical condition while remaining central to more complex inter- and intraspecific interactions that determine the extent of pesticide exposure (54, 57, 108, 130).

Pesticides may interfere with feeding behavior, and in vectors such as whiteflies (*Bemisia tabaci*), they may affect not only vector control but also their ability to transmit virus to host plants. Fluorescence staining and electrical penetration graphs in particular are promising tools with which researchers can assess such effects (24, 28, 69). Arthropods may also respond to pesticide gases. For example, psocids (*Liposcelis bostrychophila*) move away from products undergoing fumigation and can delay egg-hatching under such conditions, thus compromising their control with phosphine (101). Arthropods can therefore withstand pesticide exposure by behaviorally avoiding or minimizing contact with the pesticides, which is sometimes difficult to assess in laboratory settings. When these traits are inheritable and differ among populations, behavioral resistance occurs, which may or may not be associated with pure physiological (i.e., nonbehavioral) pesticide resistance (20, 55, 88).

Isolated behavioral traits as well as the individual's integrated set of behavioral tendencies should be given more attention because these factors may affect insecticide exposure. The recognition of the existence of personality among animals, insects included, and its eco-evolutionary importance support this notion (79), which has been considered in the context of insecticide control of arthropod pest species (97). Arthropod personality involves within- and between-individual behavioral

consistency translated into suites of behavioral correlations that may mediate pesticide-induced stress response, which is a subject that has yet to be explored.

PESTICIDE-INDUCED STRESS AT THE POPULATION LEVEL

The central tenet of toxicology is illustrated by Paracelsus's 1538 adage "the dose makes the poison." The rationale is that increasing the dose or concentration of a given compound to which an organism is exposed will lead to the increased response of the exposed organism, resulting in a dose (or concentration)-response relationship. A quantal dose-response relationship represents the variation in response due to increased doses of a compound, translating the effect from each individual, in which the response is assessed, to the population (i.e., an interbreeding group of individuals within the same species).

Dose-Mortality and Demographic Responses

Although pesticides target individual arthropod pests, the goal of a pesticide application is to control pest populations. Therefore, the population of the pest species as well as the individual organism is a matter of concern, and the quantal dose (or concentration)-response is a target of attention. Regarding the response to pesticide-induced stress, mortality is the primary endpoint used to estimate prevalent toxicological endpoints, namely the median lethal dose (LD_{50}) (or concentration, LC_{50}), or analogous estimates, and eventually the no observable effect dose (NOED) (or concentration, NOEC).

Mortality assessment and LD_{50} (or LC_{50}) estimates are ubiquitous in studies of arthropod pest species because mortality is the perceived main objective of pest management; mortality assessment is conceptually simple to understand and is quick and inexpensive to perform. Other life-history traits are also sometimes used when a major sublethal effect is of interest, especially reproductive impairment and growth inhibition, allowing the related toxicological endpoint (e.g., median effective dose, ED_{50} , or concentration, EC_{50}) to be estimated. The subtler effects of some modern insecticides may require the assessment of alternative responses (e.g., feeding) and the simultaneous assessment of different responses (e.g., mortality and feeding) (69, 124, 130, 131). However, such approaches and protocols, particularly when emphasizing mortality as the sole universal response of choice regardless of the pesticide and arthropod species involved, are woefully simplistic.

Any given pesticide will generally contribute to the mortality of a given species, and mortality is easily and readily recognized as an important life-history trait that determines population size. However, other life-history traits, such as fertility, life span, and age at which first reproduction occurs, are important for determining population size, and these traits vary among species and are potentially affected by pesticide exposure (123). Therefore, population growth rate is generally recognized as a more suitable ecotoxicological endpoint (48, 49, 122, 123). However, even such a robust estimate may be of limited value when density-dependent regulation, either bottom-up (i.e., restricted food availability) or top-down (i.e., predation), and environmental variability (stochasticity) occur and may demand the use of more complex models for better predictions (64, 65, 81). The potential occurrence of transgenerational effects of pesticides further limits the usefulness of growth rate estimates (61, 111).

The impact of pesticides on the density-dependent regulation of pea aphids (*Acyrtosiphon pisum*), for which population density at the start of the pesticide intervention has been a concern (81), has been investigated. Although pesticide-mediated intraspecific competitive interactions have seldom been investigated, the issue was explored for mosquitoes and grain beetles (2, 32, 76).

Competitive release, likely due to the increase in resources available to the surviving individuals, was recorded for insecticide-exposed mosquitoes (*Aedes aegypti* and *Aedes albopictus*) (2, 98)—a phenomenon not observed for the lesser grain borer (*Rhyzopertha dominica*) and the maize weevil (*S. zeamais*), for which crowding enhanced the insecticidal effect on each species (32). Because it is a stress factor, crowding may synergize insecticide activity against grain borers and weevils under such conditions, allowing for the distinct response from the mosquitoes.

Pesticide-Induced Hormesis

Hormesis is the stimulatory effect associated with low (sublethal) doses of compounds that are toxic at higher doses, and is characterized by a reversal in response between low and high doses of a stressor (58, 73). Hormesis was initially observed in the early 1940s and was subsequently generalized after its prevalence was recognized in diverse scenarios (22, 23, 73). This widely recognized and accepted stress response phenomenon is frequently neglected within entomology and acarology in favor of hormoligosis, which is a hormesis-like phenomenon first reported in 1968 (58, 91). However, insecticide-induced hormoligosis, which refers to the expression of hormesis in organisms already under stress (e.g., due to suboptimal conditions or a second stress agent), was defined by Thomas D. Luckey (91) in his influential paper exploring the effects of pesticides on crickets maintained under a high-salt diet and suboptimal temperature. This issue was addressed in a research paper and two reviews about the hormesis phenomenon and its relevance among insects and mites (37, 59, 58).

Two current, alternative hypotheses provide a mechanistic explanation for hormesis: the growth hormesis theory (or overcompensation theory) and the principle of physiological resource allocation (58, 73). The former theory recognizes hormesis as a response to overcompensate for a disruption in homeostasis; the latter theory posits that hormesis results from individual shifts in the balance of potentially energy-conflicting physiological trade-offs, favoring one (e.g., reproduction) at the expense of the other (e.g., longevity) (58). Current evidence with springtails (*Collembola*) and the Mexican bean beetle (*Zabrotes subfasciatus*) seems to favor the principle of physiological resource allocation (74, 136). Improved arthropod performance was observed in both cases, leading to beneficial fitness consequences to the exposed individuals with potential carryover effects on the subsequent generation (7, 58, 111, 136), but these effects likely depend on the underlying mechanisms involved, which are far from resolved. Whatever the cause of hormesis, it has been recognized as a potential link to pest outbreaks (34, 56, 58) and therefore deserves careful attention in arthropod pest management.

Behavior

The effects of sublethal pesticide exposure may exhibit a substantial impact on density-dependent relationships and pest population dynamics when the behavior of the individual organism mirrors that of the population. Behavioral studies that extrapolate the recorded individual responses to the population and the individual's suites of behavior (or insect personality) are usually overlooked, as has also been the case for studies on arthropod-pesticide interactions (97). If the behavioral effect of a pesticide is strong enough, individual variation in behavioral responses can be overlooked, allowing researchers to focus on behavioral avoidance of and behavioral resistance to pesticides in arthropod populations (20, 54, 55, 88). However, if the pesticide sparks subtler and plastic behavioral responses, then between-individual variation may be more important, because such variation is more representative of the existing behavioral variation of a species than between-population variation is (97).

Attention to behavior-mediated responses to pesticides is necessary and growing in importance with modern pesticides. Some of these compounds, such as the feeding blockers pymetrozine, flonicamid, and pyriproxyfen and the (transgenic) plant-produced aphid alarm pheromone, function primarily as behavioral modulators, while others exhibit secondary behavioral effects, particularly noticeable under sublethal exposure, that prevail much longer under field conditions (17, 25, 52, 80). Furthermore, pesticides may interfere not only with conspecific behavioral interactions but also with heterospecific behavioral interactions with potentially unrealized consequences to pest management and to biological invasion by key exotic pests (14, 102).

BEYOND POPULATIONS

Pesticide bioassays with arthropods, regardless of laboratory or field studies, focus on a single species, particularly a single arthropod pest species. Although this approach allows researchers to better control experimental conditions and is simpler and cheaper to perform, the effort is grievously unrealistic because single-species environment do not exist in nature, not even when only agroecosystems are considered. Multiple-species bioassays are receiving increased attention in environmental studies (82, 103, 109) but not in arthropod pest management and related fields, despite their potential importance.

Co-Occurring Pest Species

Competition is the likely result of mutually negative interactions between two species sharing the same niche. Competition between species may reduce their abundance or compromise their fitness components and thus may potentially regulate communities. Environmental disturbances, whether natural or artificial, can interfere with ecological interactions, leading to changes in the (realized) niche shared by competing species (112). Therefore, as agents of environmental disturbance, pesticides may alter ecological relationships and shift the prevalence or dominance of competing species and may even lead to competitive displacement (32, 112).

The few available studies exploring the effect of pesticides as the disruptive agent in interspecies competition have focused on marked differences in the occurrence of competing species in areas where insecticides are and are not used. These studies, which focused on whiteflies and leafminers, provide indirect evidence of a shift in the prevailing species in areas under intensive insecticide use, leading to competitive exclusion (50, 84, 128). A study on mosquitoes explored the effect of density dependence on the competition outcome (2) but did not consider the dose-dependent effect of the insecticide. However, dose-dependent and density-dependent effects on grain beetles have been investigated (32).

The co-occurring cereal grain beetles, the maize weevil (*S. zeamais*) and the lesser grain borer (*R. dominica*), share a common realized niche and directly compete for the same resources. The maize weevil is the dominant species in maize grains, prevailing under natural conditions in the Neotropical region without insecticide exposure. However, dominance and species prevalence shifted from the maize weevil to the lesser grain borer under insecticide exposure, indicating that insecticide compounds are relevant mediators of species interaction (32). These findings lend credence to the intermediate disturbance hypothesis, which predicts that under intermediate levels of environmental disturbance species diversity is increased in proportion to the reduction of the competitively dominant species (30, 118). This hypothesis is reasonable because high insecticide doses and rates of application are likely to suppress one, if not both, competing species, which is illustrated by the grain beetle study. Very low doses of insecticide will not interfere significantly with competitive interactions, but intermediate doses compromise the population growth of the

maize weevil and comparatively favor the lesser grain borer, which is inherently more tolerant of fenitrothion, the insecticide used in the experiments (32).

Pest–Natural Enemy Systems

Systematic testing of arthropod pest species and their natural enemies that considers their potential (multifactorial) interaction is not common. Furthermore, the relevance of pesticide-induced stress on pest–natural enemy dynamics is an overlooked issue that has only recently drawn attention owing to its potential consequences for integrated pest management; this attention seems particularly important in consideration of the pesticides currently in use and their usually mild short-term effects (18, 19, 116, 125).

An issue of increasing concern is the generalization of the potential long-term impacts of pesticides on biocontrol agents. This long-term impact is not a characteristic of pesticide persistence but rather of persistent or continuous pesticide use, which has been a prevailing trait of the use pattern of such compounds, mainly in warmer climates (43, 105, 117). Furthermore, the diversity of the biocontrol agents and their distinct life histories require not only the incorporation of more ecologically relevant measures of pesticide-induced stress, such as delays in population growth of both pest and natural enemy species and their temporal dynamics (107, 139, 140), but also the integration of their life histories and their associated landscape (114, 116). The simplified agricultural landscape, for instance, which was initially thought to drive insecticide use despite little available evidence to support this position, seems to be a misleading notion, but the landscape itself is bound to affect both pesticide use and biological control (83, 90, 114, 116).

The periodic use of pesticides aided by biological control in integrated pest management programs is recognized as pulses or impulsive interventions that add complexity to the dynamics of pest–natural enemy models (75, 86, 110). This attitude starkly contrasts with the prevailing view of pesticide activity against pest species and recognizes that the integration of pesticide use and biological control will influence each of these components as well as the pest management efficacy provided (86, 141).

Assemblages and Communities

A species assembly (i.e., a random collection of species populations occupying the same given habitat) is a potential target for pesticides, because both direct and indirect effects, as well as lethal and sublethal effects of pesticide exposure, can be generated at the individual and population levels (**Figure 1**). Pesticides can also prevent communities (i.e., groups of interacting populations of different species in a given time and place) from forming.

Community ecotoxicology of environmental contaminants is the focus of intensive debate aiming to describe the mechanisms shaping the patterns of community structure under anthropogenic stressors, isolating such effects from natural variability (103). This effort, however, does not extend to the impact of pesticides on terrestrial arthropod assemblages and communities, for which the advance has been modest. Pesticides themselves may not only affect a community but may also play a relevant role in creating the initial community context, such as influencing the pattern of species colonization of a contaminated area, a possibility that has also been largely neglected (138).

Natural enemy assemblages are the main targets of attention. Pesticide-induced stress in natural enemies tends to vary with the species, but indigenous natural enemies, such as parasitoids, predatory mites, hunting spiders, and small carabids, are usually negatively affected by pesticides (96, 99, 100, 106, 119); however, large carabids and invasive millipedes have been reported to benefit from such chemical interventions (100, 119). Nonetheless, pesticide exposure is not limited to

target arthropod pest species and natural enemies; pesticide exposure also affects different herbivorous species, including potential competitors, detritivorous species, and pollinators—organisms that potentially affect not only pest density but also crop yield (9, 10, 119).

By assessing the impact of pesticides on comprehensive arthropod assemblages and communities using before-after control-impact designs (i.e., with unsprayed plots and starting assessment before pesticide spraying), researchers can better regulate such effects (9, 10, 103, 121). The findings obtained from limited pesticide applications with short-term impacts (i.e., one cultivation cycle) indicate a lack of significant impact on the overall arthropod community, with stronger effects from the cultivation system rather than the pesticide application itself, particularly in warmer climates (8, 9, 10, 27). However, nontillage cultivation seems to buffer against the impact of pesticides, whereas conventional systems enhance such impact (5, 8–10). Continuous pesticide use and long-term assessments are likely to provide evidence of the significant impact of pesticides on arthropod assemblages and communities (92), and the results obtained with transgenic *Bacillus thuringiensis* crops provide support for this contention (90, 133, 142).

TOWARD OPTIMIZED INTEGRATED PEST MANAGEMENT PROGRAMS

Pesticides are a pivotal pest management tool aimed to reduce crop losses, as well as vector control. However, their nontarget impacts and their potential to negatively affect arthropod communities associated with agroecosystems, for instance, may compromise pollinators and detritivorous arthropods important for enhancing crop yield (10, 41, 67, 119). Therefore, the judicious use of selective pesticides, timed to have maximum impact on target species and minimum impact on nontarget species, will increase the likelihood of controlling the arthropod pest without substantially compromising nontarget, yield-favoring agents and at lower costs (Figure 3).

Pesticides may also either reduce or synergize the action of biocontrol agents, and recent modeling efforts have focused on minimizing the impacts of pesticides on natural enemies and maximizing their efficacy for pest management programs (75, 86, 116, 141). Such integrated and optimized approaches will require the review of current action thresholds for decision-making regarding pest management, as reported for the soybean aphid (*Aphis glycines*) (63).

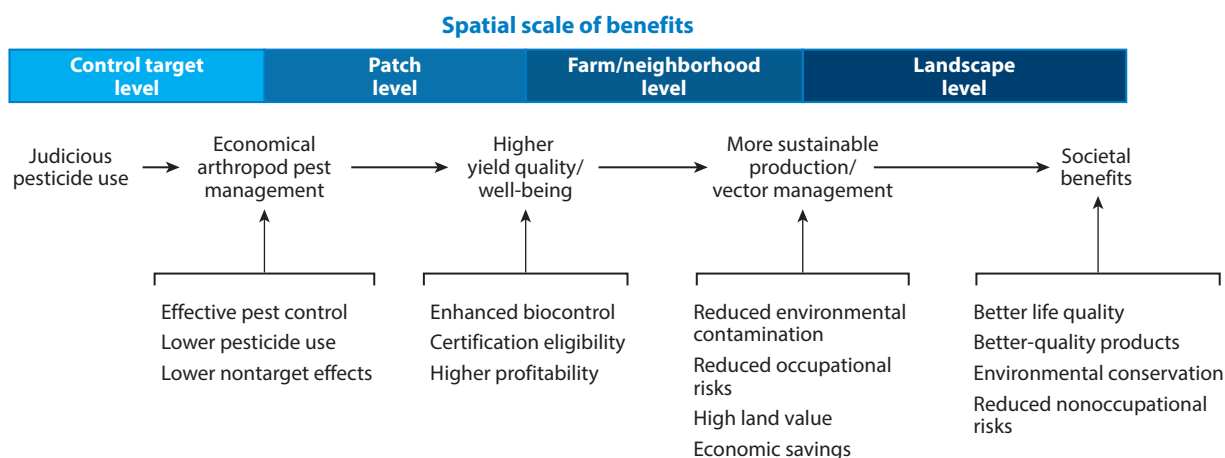


Figure 3

Hierarchy of potential benefits of judicious pesticide use for arthropod pest management.

An intriguing and counterintuitive consequence of pesticide use (or overuse) for pest management programs is increased pest abundance, leading to pest outbreaks. Reports of pesticide use misfiring and fostering pests instead of controlling them date back to the late 1940s (66, 94, 107, 113). Insecticide resistance is a long-term (evolutionary) consequence of insecticide overuse and is the best-known and most widely studied ecological backlash of the pesticide paradox (e.g., 87, 140). However, the possibility of inadvertent selection for insecticide resistance in secondary pest species is usually overlooked (62). In contrast, resurgence and secondary pest outbreaks (pest replacement or type II resurgence) are more frequently short-term (ecological) consequences of pesticide use that are commonly reported for but rarely studied in arthropod pest species (66).

Resurgence refers to an increase in the abundance of a target pest species above that of uncontrolled populations following a pesticide application. Secondary pest outbreak refers to an increase in the abundance of a nontarget pest species after a pesticide application (66, 94). Both phenomena have common causes and mechanisms, which are poorly known and little studied in favor of the assumption of selectivity differences between the arthropod pest and its natural enemies (66). This assumption may, however, be more frequently mistaken than imagined, as exemplified with the southern red mite, *Oligonychus ilicis*, in coffee plantations (34).

Resurgence and secondary pest outbreaks are caused by a reduction in natural enemy populations and/or an increase in pest populations. Pest outbreaks may occur because pesticides are sometimes more toxic to natural enemies than to pest species (36). However, other possibilities may take place, including an avoidance response in which natural enemy populations disperse from sprayed fields (33, 85). Furthermore, pesticide-induced hormesis in an arthropod pest species can lead to increases in pest populations and consequent outbreaks, particularly if the pest population is already resistant to the applied pesticide (34, 55). Because pesticide exposure may shift the dominance of competing species sharing the same niche (32, 50, 128), pesticide-mediated competition is another potential mechanism of secondary pest outbreaks that deserves attention.

A comprehensive understanding of outbreak mechanisms is fundamental to optimize pest management and the consequent prevention of ecological backlashes due to pesticide use. Furthermore, recognition of the underlying mechanisms of community-wide impacts of pesticide use will minimize the possibility of such backlashes, particularly when invasive species are present; this scenario is more common owing to increased international trade and global warming.

REGULATORY AND PRACTICAL CHALLENGES

Pesticide use poses concerns for human health and environmental safety, which are broadly recognized, but also poses risks to agriculture, disease prevention, and pest management, which are not frequently recognized. A likely reason for this oversight is the rather simplistic view of the importance and consequences of pesticide use for pest management. The prevailing focus of pesticide-induced stress in arthropod pest species is usually circumscribed to short-term mortality effects on the pest species and some natural enemies, which are either perceived as important for control or used as surrogate species in these assessments, although the latter use is often dubious, if not questionable (12, 13).

The emphasis on acute mortality as a toxicological endpoint in pesticide assessments is deeply ingrained in public perception and even within academia, which biases pesticide regulation toward this approach. Even the term pesticide (from the Latin *pestis cida*, “pest killer”) favors this perception. The end result is a gross oversimplification of the potential consequences of pesticide-induced stress, particularly on arthropod pests and associated species. The failure to recognize the sublethal and indirect effects of pesticides and their consequences on target species has

resulted in important knowledge gaps. Current regulatory processes of pesticide risk assessment and pesticide registration in both the United States and the European Union encourage the use of acute mortality as the toxicity endpoint of interest for both target and nontarget species. These regulatory approaches discourage the development of data other than acute LD₅₀/LC₅₀ (67, 103).

More comprehensive assessments of pesticide-induced stress and its consequences on arthropod pest species are necessary for proper risk analysis and decision-making regarding pesticide use. More robust toxicological endpoints, such as population growth rates, are necessary in laboratory studies, and the incorporation of density-dependent mediation should improve risk assessments that extrapolate findings from laboratory settings to realistic field conditions. Modeling pest–natural enemy systems with pesticide applications will optimize pest management efforts. However, we are still far from understanding the underlying mechanisms of pest resurgence and outbreaks and the potential effects of pesticides on community structure in agroecosystems. This lack of information may impair current and future agriculture yield, as well as the economic and environmental sustainability of current agriculture practices. Vector management exhibits similar shortcomings, with consequences for animal husbandry and human health.

The role of endosymbionts in arthropod pesticide-induced stress, the increased use of pesticide mixtures for plant and animal protection, and landscape diversity pose new challenges for pesticide use in arthropod pest management when most of the existing challenges remain broadly unrecognized. The largely ignored call to incorporate more ecology into pesticide ecotoxicology, and to integrate ecotoxicology and classical (organismal) studies of pesticide toxicology in arthropods, seems a fitting warning and guide for what lies ahead.

SUMMARY POINTS

1. Pesticide use is guided by short-term efficacy; the indirect and subtler effects of pesticides on their target arthropod pest species have been neglected.
2. Both direct and indirect effects of a pesticide can alter the physiology or behavior of an organism, irradiating such effects to the population, which may translate into community-level effects that further the hierarchical system of pesticide-induced stress.
3. Individual stress response, either physiological or behavioral, may result either from the arthropod itself or from an endosymbiont and may reflect a toxic or nontoxic (protective) response.
4. Quantal dose-response relationships translate an individual stress response into a population stress response, but demographic responses, rather than mortality, provide more robust estimates of stress that should also consider density-dependent regulation.
5. Pesticide-induced hormesis and behavior-mediated responses are current topics of interest and might explain pesticide-induced outbreaks of arthropod pest species.
6. The co-occurrence of multiple species in natural systems indicates that pesticide-induced stress may compromise not only arthropod pests but also nontarget yield-favoring agents, such as pollinators and detritivorous species.
7. The gross oversimplification of the potential consequences of pesticide-induced stress on arthropod pests and associated species leads to knowledge gaps that compromise pesticide risk assessment, pesticide registration, and decision-making regarding their use.

FUTURE ISSUES

1. The prevailing circumscribed focus of pesticide-induced stress in arthropod pest species and some natural enemies, which are perceived as important or are used as surrogate species in such assessments, is questionable and needs revision.
2. Demographic assessments and density-dependent regulation over time must be accounted for in pesticide-arthropod interactions, which likely require revisions to current action thresholds for decision-making regarding pest management.
3. Because single-species environments do not exist in nature, the co-occurrence of multiple species and their potentially simultaneous interdependent responses to pesticide use should be considered, as these factors can affect pest control as well as crop yield. This reasoning is also valid for arthropod vectors of animal and human diseases.
4. New challenges in need of attention by pest management programs include endosymbiont-mediated functions in arthropod pesticide stress, increased use of pesticide mixtures, and landscape diversity.
5. Ecosystem-level studies and pesticide toxicology should be integrated to guide initiatives for economic and environmentally sustainable food production and vector control.

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