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PERSPECTIVE

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Pesticide resistance in arthropods: Ecology matters too

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Abstract

Pesticide resistance development is an example of rapid contemporary evolution that poses immense challenges for agriculture. It typically evolves due to the strong directional selection that pesticide treatments exert on herbivorous arthropods. However, recent research suggests that some species are more prone to evolve pesticide resistance than others due to their evolutionary history and standing genetic variation. Generalist species might develop pesticide resistance especially rapidly due to pre-adaptation to handle a wide array of plant allelochemicals. Moreover, research has shown that adaptation to novel host plants could lead to increased pesticide resistance. Exploring such cross-resistance between host plant range evolution and pesticide resistance development from an ecological perspective is needed to understand its causes and consequences better. Much research has, however, been devoted to the molecular mechanisms underlying pesticide resistance while both the ecological contexts that could facilitate resistance evolution and the ecological consequences of cross-resistance have been understudied. Here, we take an eco-evolutionary approach and discuss circumstances that may facilitate cross-resistance in arthropods and the consequences cross-resistance may have for plant–arthropod interactions in both target and non-target species and species interactions. Furthermore, we suggest future research avenues and practical implications of an increased ecological understanding of pesticide resistance evolution.

KEYWORDS
agroecosystem, co-evolution, diet breadth, insecticide resistance, integrated pest management, plant–insect interaction

INTRODUCTION

Pesticide resistance (see Box 1 for definition of terms in bold) development brings immense challenges for global agriculture and is a prime example of rapid evolution induced by human activities (Chen & Schoville, 2018; Rosenheim et al., 1996). Such resistance has been defined as a 'genetically based decrease in susceptibility of a population to a toxin caused by exposure of this population to the toxin in the field' (Tabashnik et al., 2013). It often follows soon after a new synthetic compound is introduced (Palumbi, 2001) due to the strong directional selection that pesticide application exerts on pests. It was, however, recently highlighted that the evolutionary history of a species might affect the likelihood of developing resistance, making some species more predisposed

BOX 1 Glossary

Agroecosystem: Ecosystem modified and managed by humans through physical and chemical means to produce goods as food.
Allelochemical: A chemical produced by an organism that is toxic to, inhibits the growth or affect the physiology, behaviour or life history of, other organisms; synonymous here with ‘plant defensive chemical’ (adapted from Després et al., 2007).
Biopesticides: Action specific and biodegradable products based on naturally occurring organisms or compounds suppressing the growth and proliferation of pests' population. They are divided into three main categories depending on their mode of action: microbial biopesticides, biochemical biopesticides and plant-incorporated protectants (PIPs).
Cross-resistance: The ability to tolerate and resist chemical toxins from a new source following adaptation to chemical toxins from another source, for example cross-resistance to pesticides following adaptation to a new host plant.
Eco-evolutionary: interactions between ecology and evolution, where evolutionary responses to ecological changes occur in the same time scale, integrating both of them in a single dynamic framework (adapted from Schoener, 2011; Hendry, 2018).
Generalist: Phytophagous species utilising an extensive range of host plant species belonging to different, potentially unrelated Families; synonymous here with ‘polyphagous’ and in contrast to specialist (or monophagous) species.
Gut microbiota: All bacterial, fungal and microbial communities present in the gut of the host.
Host plant range: The entire span of host plant species that a phytophagous species can feed on; synonymous here with ‘diet breadth’.
Pesticide: Synthetic chemical substances used to control a species presenting negative impacts. It includes fungicides, herbicides, insecticides or biopesticides.
Plasticity: The differential phenotypic expression of a given genotype depending on the environment.
Resistance: Mechanisms developed by an organism to overcome a toxin; in this paper, the genetic, metabolic, physiological and behavioural adaptations in arthropods to overcome plant allelochemicals or pesticides.
Specialist: Phytophagous species utilising a single or a few related host plants species.

to evolve resistance than others (Dermauw et al., 2018; Hardy et al., 2018; Walsh et al., 2022). In this context, phytophagous arthropods have been suggested to be pre-adapted to handle chemical insecticides since they have evolved to tolerate and resist their host plant's **allelochemicals** (Rosenheim et al., 1996; Després et al., 2007; Box 2). As a general extension, we can thus define **cross-resistance** as resulting from prior exposure to a different, possibly not chemically related, toxin in a species' evolutionary history. The evolution of cross-resistance is expected to be more prominent in **generalist** arthropod species (Dermauw et al., 2018; Hardy et al., 2018) since they have to detoxify or metabolise a broader range of plant defensive chemicals than **specialist** species (Cheng et al., 2017; Box 3). The influence of plant–arthropod evolutionary interactions on pesticide resistance development has furthermore been shown as insects feeding on herbaceous plants are more likely to evolve pesticide resistance than insects feeding on other plant groups (Hardy et al., 2018). Although this pattern may be confounded by the amount of pesticide use (Dermauw et al., 2018), correction for this factor still implies that certain insect groups are more likely to develop pesticide resistance (Crossley et al., 2021; Hardy et al., 2018). Moreover, experimental evidence suggests that pesticide resistance can evolve when arthropods expand their **host plant range**. For example in the two-spotted spider mite, when a susceptible strain adapted to a novel host, the detoxification gene expressions resembled those of multi-insecticide-resistant populations (Dermauw et al., 2013).

Taken together, these findings indicate that both (i) the evolutionary history, that is the evolved host plant range and abilities to handle plant allelochemicals, and (ii) the current ecological context, that is host plant availability, may have a large impact on pesticide resistance development in arthropods. Considering the rapid evolutionary development of pesticide resistance as well as the ecological impact of cross-resistance, an **eco-evolutionary** perspective seems then suitable to understand the ecological consequences of such process (Fussmann et al., 2007). While several studies have been devoted to assessing molecular mechanisms underlying pesticide resistance (see, e.g. the special issue in Insects, Le Goff & Nauen, 2021; Box 2), there is, however, an apparent knowledge gap on the significance of the ecological context of pesticide resistance evolution as well as on its ecological consequences (Chen & Schoville, 2018; Maino et al., 2018; Figure 2). A similar trend is observed

BOX 2 Pesticide resistance evolution and cross-resistance in phytophagous arthropods

Resistance to pesticide treatments was first noted over 100 years ago (Melander, 1914), and since then, an increasing number of insects have evolved resistance to at least one or more of the available insecticides (Feyereisen et al., 2015; Taylor et al., 1983). As in other cases of resistance evolution, pesticide resistance develops following strong directional selection on the pest. Arthropods have developed several different mechanisms, from behavioural to molecular, to withstand pesticides (Figure 1) that are similar to the strategies that arthropods have evolved in response to chemical host plant defences (e.g. behaviour or detoxification) (Després et al., 2007; Heckel, 2014). Recent advancements also pinpoint epigenetic and epitranscriptomics mechanisms (Brevik et al., 2021; Oppold et al., 2015; Oppold & Müller, 2017), transcription factors (Amezian et al., 2021; Hu et al., 2021; Palli, 2020; Xu et al., 2022) and in-house microbial allies (Gomes et al., 2020;

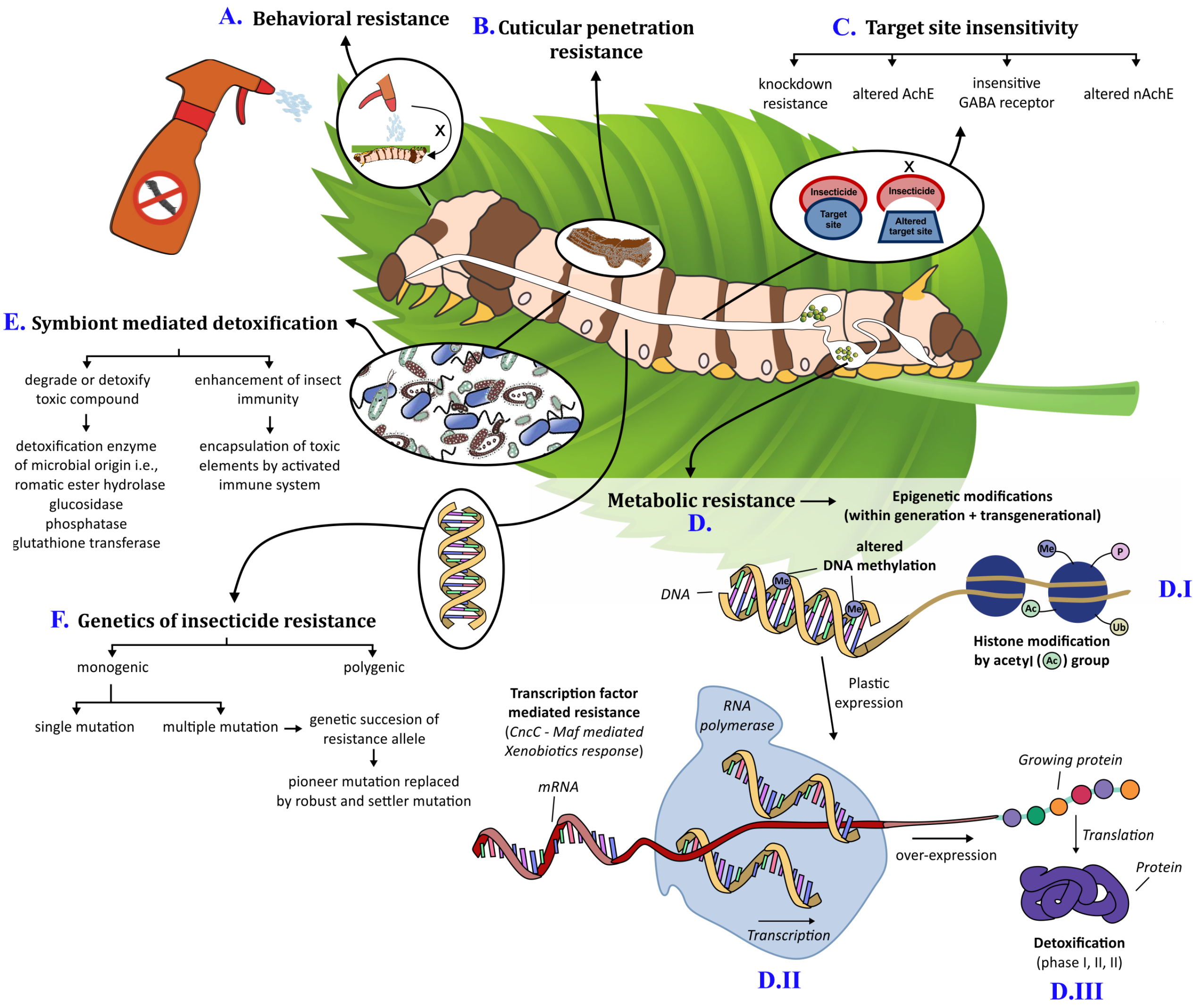


FIGURE 1 Mechanisms for pesticide resistance evolution in the insect. (A) Resistance acquisition via avoidance of the toxin, that is insecticides often fail to reach target insects under the leaf. (B) Reduce toxin penetrability through thickening of the insect cuticle. (C) Mutation in the binding site inside the target pest causes pesticide insensitivity. (D) Pesticide metabolism exploiting internal molecular machinery. I modifications may occur at the epigenetic level via DNA methylation or histone modification, leading to target gene expression alteration upon pesticide exposure. Epimutations are often heritable. II transcription factors (TFs) can modulate the expression of xenobiotic response elements, that is CncC-Maf mediated xenobiotic response. III overexpression of phase I (i.e. Cyt P450s), phase II (i.e. GSTs), phase III (i.e. ABC transporters) enzymes can lead to detoxification or excretion of the entomotoxic pesticide molecules. (E) In-house microbial symbionts can facilitate resistance development via detoxifying the toxic compound or facilitating the encapsulation of toxic molecules by activating the insect's immune system. (F) Single gene or multigene mutations can facilitate genetic resistance against pesticides.

BOX 2 (Continued)

Itoh et al., 2018; Liu & Guo, 2019; Muturi et al., 2021) facilitating pesticide and host plant resistance. Arthropods may also frequently develop pesticide resistance from standing genetic variation combined with de novo mutations, rather than only from novel mutations (Hawkins et al., 2019), suggesting that phytophagous arthropods are pre-adapted to resist pesticides. Cross-resistance between host plant allelochemicals and pesticides could thus be a possible mechanism for rapid pesticide resistance development in arthropods (Hardy, Despres and others suggesting this), which may be facilitated if the chemical structure of the pesticides is similar to the plant defence chemicals (e.g. pyrethroids and nicotinoids) (Després et al., 2007). Comparisons of genomic studies of host plant adaptation with pesticide resistance have highlighted that the detoxification mechanisms involved are similar (Dermauw et al., 2013), which suggest that changes in host plant use could favour pesticide resistance and the other way around. Hence, depending on evolutionary history and the standing genetic variation availability, some species may be more prone than others to evolve resistance to pesticides.

BOX 3 Host plant utilisation: generalist versus specialist species

Phytophagous species vary along a continuum in their host plant range and can crudely be categorised into specialists feeding on a single or a few related plants and generalists that utilise many different unrelated plant species. Transitions between specialist and generalist forms driven by phylogenetic processes have been suggested to frequently occur over evolutionary time, where also geographical co-occurrence and ecological processes, such as ecological fitting (process whereby organisms colonise and persist in novel environments without change of their biological traits [Agosta & Klemens, 2008]) and phenotypic plasticity, can be important (Nylin et al., 2018). Changes in the insect environment can trigger such transitions, for example driven by human activities or through natural range expansions that affect host plant occurrence and quality for herbivorous insects (Hamann et al., 2021; Hardy et al., 2020).

A majority of the studied phytophagous arthropods are considered specialists (Ali & Agrawal, 2012). Specialisation could lead to a competitive advantage by developing more fine-tuned morphological and metabolic features for plant utilisation, digestion and detoxification of the host plant (Nishida, 2002), which is also shown in a better correspondence between mothers' host plant preference and offspring host plant performance in specialists (Gripenberg et al., 2010). In contrast to generalists, specialists can have a higher tolerance to their host plant allelochemicals and utilise these defence compounds for host plant selection or protection (Ali & Agrawal, 2012).

Specialists may also have more efficient information handling during host choice than generalists who take longer during decision-making and may choose sub-optimal plants for larval development (Bernays, 2001). This may be due to limitations in generalists' neural capacity to handle sensory information from many potential hosts (Bernays, 2001). Individual generalist insects can mediate this through phenotypic plasticity, where experience can facilitate host selection and increase salience to specific host plants (Anderson & Anton, 2014). From a distance, volatile and visual cues and once landed taste (contact chemicals) and tactile cues are available during host plant choice. For olfactory cues, both specialists and generalists rely on blend composition and ratios of ubiquitously emitted compounds, while specialists also can have peripheral receptors for specific compounds emitted from their host (Bruce & Pickett, 2011).

Differences between generalists and specialists are also observed at the molecular level. For example neofunctionalisation of gene copies and horizontal gene transfer often enhances genomic flexibility in generalists to facilitate diverse host usages (Heidel-Fischer et al., 2019; Kirsch et al., 2014; Prasad et al., 2021; Wybouw et al., 2015). In addition, the genomes of polyphagous species often show dramatic expansion of chemosensory and detoxifying gene repertoire resulting in more remarkable plasticity during herbivory, which often accounts for the observed difference in the diet breadth between generalist and specialist insects (Grbić et al., 2011; Li et al., 2013; Xu et al., 2016).

Whether and how cross-resistance affects the traits involved in host plant location and acceptance is still to be empirically tested. Considering the various mechanisms involved in plant–arthropod interactions, such research could involve comparative studies between specialist and generalist species at the genetical, behavioural and physiological levels. Using cross-resistance and rapid adaptation to pesticides as a model framework may also shed light on processes involved in 'natural' host plant shifts and transitions between specialist and generalist states in phytophagous arthropods.

when taking cross-resistance into consideration, with less than 20 articles assessing either its ecological or evolutionary aspect.

To bridge the existing knowledge gap and stimulate new research, we take an ecological perspective on pesticide resistance development where we begin to propose ecological and evolutionary contexts where pesticide resistance development through cross-resistance would be at a higher risk to happen (section II). In addition, we suggest that the converse cross-resistance may also occur: arthropods that evolve an increased tolerance to host plant chemical defences following pesticide resistance evolution, may as a consequence, increase their ability to widen their host plant range further (section III). We thus propose that cross-resistance could be seen as a dynamical and reciprocal process between adaptation to natural or synthetic allelochemical and arthropod–host plant interactions. We discuss these ecological causes and consequences of pesticide resistance evolution, intending to emphasise that both evolutionary and ecological research would be needed to understand cross-resistance comprehensively. The gathered knowledge of such research would then help to develop more sustainable pest management strategies. We focus mainly on pest species, the targets of pesticide treatments, among which many have developed resistance (Sparks & Nauen, 2015), for example the fall armyworm, *Spodoptera frugiperda*, an important worldwide crop pest that has evolved resistance to a large array of insecticides challenging its management in South-America, Asia and Africa (Babendreier et al., 2020; Muraro et al., 2019). However, we also consider non-target organisms such as pollinators and natural enemies, as they could be subject to cross-resistance evolution due to unintentional exposition to pesticides (Dubey et al., 2020; Main et al., 2020; Mansoor & Shad, 2020; Rainio et al., 2019). For example among predatory phytoseiid mites, pesticide exposure has been shown to cause non-target effects such as reduction in fecundity and egg hatch for several species, but others were less sensitive to certain insecticides due to resistance development (Schmidt-Jeffris et al., 2021).

ECOLOGICAL CONDITIONS THAT MAY FACILITATE PESTICIDE RESISTANCE EVOLUTION

Ecological research has provided numerous examples of host plant shifts or expansions in arthropods, in some cases due to geographical range changes (Audusseau et al., 2017; Battisti et al., 2005; Diegisser et al., 2009; Sánchez-Guillén et al., 2016; Singer & Parmesan, 2021). In light of this gathered knowledge, we develop below different contexts where arthropods may be exposed to new host plant species, and pesticide resistance may evolve as a consequence through cross-resistance.

During geographical range expansion, a phytophagous species may encounter novel plant species, which could lead to a modification of its diet breadth (i.e. Hill et al., 2011; Jahner et al., 2011; Lancaster, 2020) where the ability to change or increase its host plant range could favour the species establishment by exploiting new resources (Battisti et al., 2005). Under natural or climate-driven expansion, the expanding arthropod population may encounter a gradual shift in the plant community. On the contrary, part of the arthropod population is transported via human activities outside their native range during invasion (Blackburn et al., 2011). In this case, the introduced individuals may have to face entirely novel host plant communities and need to adapt to those communities in order to persist in the new environment (Hill et al., 2016). Therefore, selection for adapting to new host plant species may be more assertive in invading species than in species naturally expanding their range (Renault et al., 2018). Hypothetically, cross-resistance to pesticides would thus be more often found in invading species if they have been repeatedly selected to adapt to new host plant communities.

The host plant community available for a herbivorous arthropod may also change due to plants' geographical expansion, and native arthropods will then encounter novel plant species that enter their geographical range either naturally or introduced by humans. While it may be challenging to incorporate new plants as hosts (e g. Amarillo-Suárez et al., 2017), there is also evidence that arthropods could integrate non-native plant species into their diet breadth (Andersen et al., 2019; Bezemer et al., 2014; Brown et al., 2017; Graves & Shapiro, 2003; Janz et al., 2001; Lakatos et al., 2016). One example is the aphid *Myzus persicae* which probably adapted to tobacco after its introduction to Europe in the 16th Century by overexpressing P450 genes to detoxify nicotine (Simon & Peccoud, 2018), a gene family that has been shown to be involved in pesticide resistance in arthropods (Feyereisen, 2006; Nauen et al., 2022; Box 2).

Arthropod host plant range may also be affected by human activities in their native range under different circumstances. For example the domestication process of wild plant species or selective breeding may alter plant defence, resulting in plant varieties being more susceptible to pest attacks (Bernal & Medina, 2018; Chen et al., 2015; Turcotte et al., 2017). Another scenario is when humans alter land use, for example when urban areas increase, and rural arthropod species come in contact with various non-native species in parks and gardens. Finally, new plant-arthropod associations may occur when neither of the organisms has moved in space but rather in time. For example when climate changes or warmer urban areas alter the synchronisation between arthropod's lifecycle and their host plant's phenology (Backe et al., 2021; Pureswaran et al., 2018), leading to new species interactions.

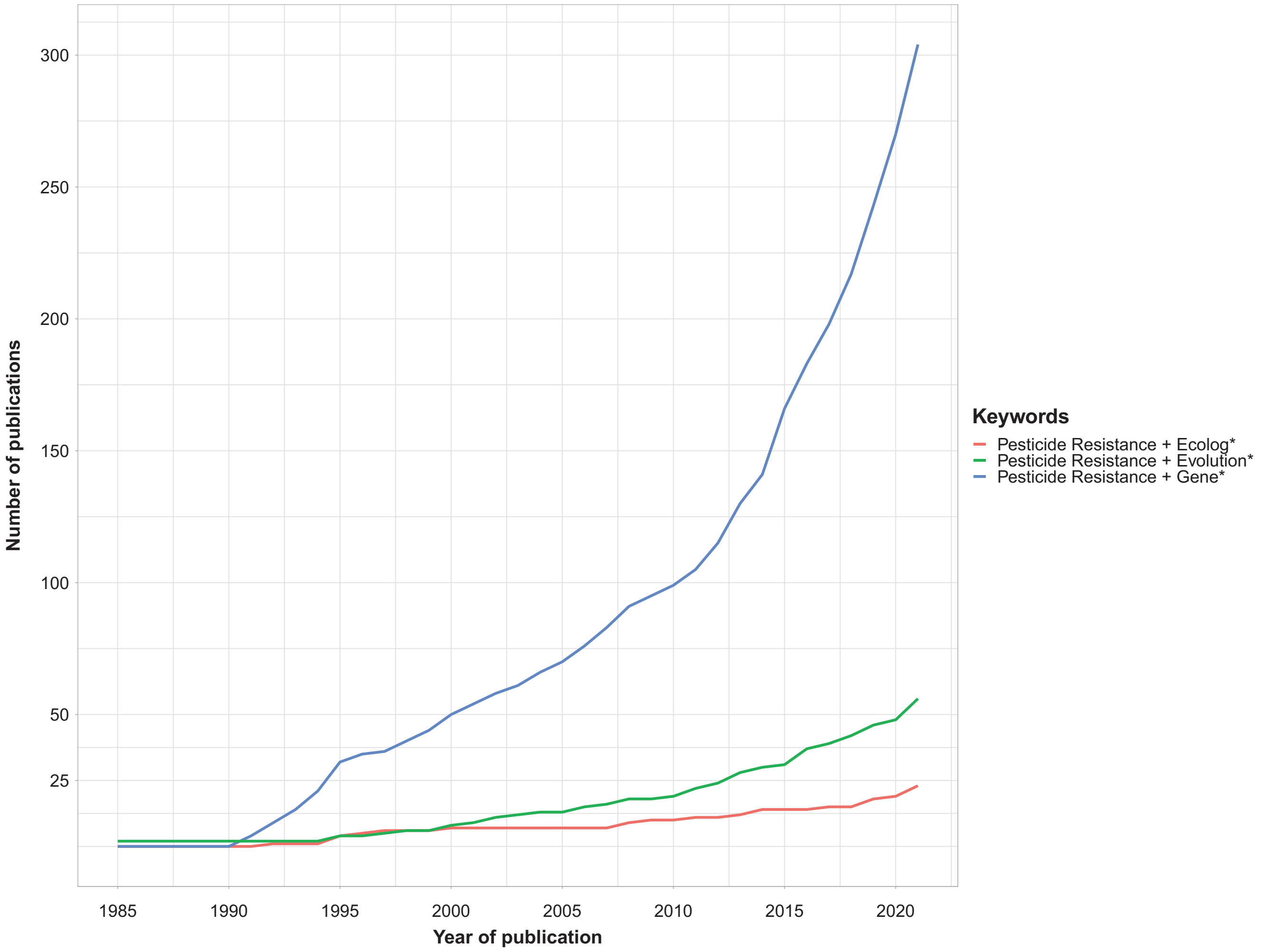
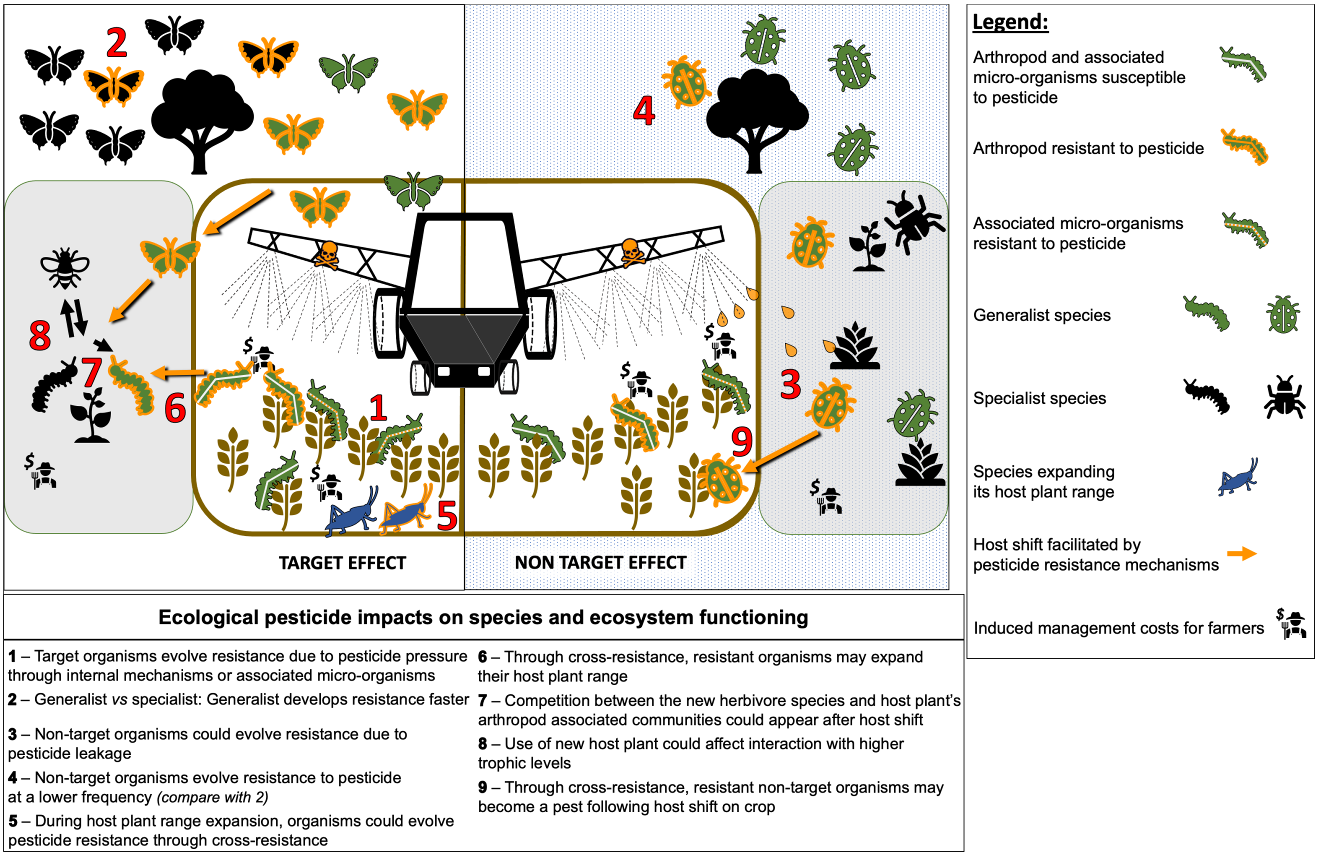


FIGURE 2 Number of publications found on primary research on web of science investigating the proportion of studies on pesticide resistance with an ecology, evolution or genetic approach from 1985 to 2021. The searches were done by using the keywords “pesticide resistance” with one of the following keywords “Ecolog*”, “gene*” or “evolution*” (done in November 2021).

Thus, ample evidence shows that arthropods can expand or shift their host plant range when encountering novel plant species. In these novel plant–arthropod interactions, both generalist and specialist arthropods have to develop strategies to survive on the new host plant (Simon et al., 2015; Näsvall et al., 2021; Snell-Rood & Ehlman, 2021; Zalucki et al., 2021; Box 3), setting the stage for cross-resistance to evolve as a consequence. We hypothesise that cross-resistance to pesticides may develop incredibly quickly during the evolution of arthropod host plant range if arthropods adapt to novel host plants that present new classes of allelochemicals, that is if the arthropods during host plant range expansion develop new abilities to detoxify or metabolise toxins. Following Pearse et al. (2013), we suggest that the risk for pesticide resistance may be highest when the arthropod develops a preference for a novel host plant, and there is a selection for improved performance on this host plant. Extensive surveys on the change of host plant range over time and space coupled with experimental manipulation under control conditions would be useful to test such a hypothesis and assess the potential of eco-evolutionary dynamics for such process.

ECOLOGICAL CONSEQUENCES OF PESTICIDE RESISTANCE DEVELOPMENT

The insight that pesticide resistance may evolve as cross-resistance through new or improved abilities to tolerate and resist plant allelochemicals, opens up the possibility that pesticide resistance development, in turn, may facilitate an expansion of arthropods' host plant range, that is a converse cross-resistance scenario. Since also non-target species may be exposed to enough insecticides to evolve resistance mechanisms (e.g. *Rdl* dieldrin resistance in *Drosophila melanogaster*, ffrench-Constant et al. 2000), converse cross-resistance may thus have significant ecological consequences for the **agroecosystems** through altered host plant ranges in both pests and non-target species (Figure 3). Adaptation to a novel host plant



Ecological pesticide impacts on species and ecosystem functioning

1 – Target organisms evolve resistance due to pesticide pressure through internal mechanisms or associated micro-organisms

2 – Generalist *vs* specialist: Generalist develops resistance faster

3 – Non-target organisms could evolve resistance due to pesticide leakage

4 – Non-target organisms evolve resistance to pesticide at a lower frequency *(compare with 2)*

5 – During host plant range expansion, organisms could evolve pesticide resistance through cross-resistance

6 – Through cross-resistance, resistant organisms may expand their host plant range

7 – Competition between the new herbivore species and host plant's arthropod associated communities could appear after host shift

8 – Use of new host plant could affect interaction with higher trophic levels

9 – Through cross-resistance, resistant non-target organisms may become a pest following host shift on crop

FIGURE 3 Scheme over pesticides' direct and indirect impacts on ecosystem functioning following cross-resistance, from target species to non-target species. Pesticides, the development of resistance due to their use and their potential side effects are represented in yellow. The impacts listed in the figure are not exhaustive.

may affect various biological traits (Box 3), making the evolutionary outcome unpredictable (Fox et al., 2017). Such trait evolution may further lead to both direct and indirect eco-evolutionary effects up to the species community scale (Utsumi, 2011).

Besides the notion that arthropods' adaptation to novel host plants may lead to pest problems on their new hosts, an increased host plant range in pest arthropods could enhance the ability to persist in unexplored areas and thus facilitate geographical range expansion. For pest arthropods, utilising additional hosts may further disrupt control strategies as pests could persist using alternative host plants as refuges (Montezano et al., 2018; Figure 3). However, adopting a novel host plant comprises arthropods' ability to feed, but also locate and accept the host plant through oviposition (Harvey et al., 2010). Cross-resistance may thus likely increase arthropod performance on new host plants through the ability to withstand and detoxify the allelochemicals, but whether preference for the new host plant species also could be affected or not needs to be assessed. Perhaps cross-resistance enhances performance on novel hosts in the first step, while preference evolves later. However, in cases where females prefer a plant species on which larvae perform poorly, cross-resistance that allows her offspring to have a better feeding performance on this plant may allow both the preference and performance of this host plant to spread rapidly in the population. This may be a more likely scenario in generalist species, where mothers' preference and offspring performance are not always correlated (Gripenberg et al., 2010).

If pesticide resistance development could lead to host plant range changes through cross-resistance, this may have consequences for general food-web and community dynamics involving non-target species. For example host shifts may affect herbivore competition on the novel host plant (Carrasco et al., 2018), and the evolution of new feeding traits may impact the arthropod community through indirect eco-evolutionary effects mediated between the shared host plant (Utsumi, 2015). Furthermore, we predict that adopting novel host plants through cross-resistance could involve acquired mechanisms to tolerate new classes of allelochemicals which could affect higher trophic levels' preference and performance. If a phytophagous species uses those new allelochemicals to defend against parasitoids and predators (compare Harvey et al., 2010; Bezemer et al., 2014), through sequestration (Beran & Petschenka, 2022), the efficiency of its natural enemies may be affected. This could have suppressed or released effects on the herbivore, depending on whether the higher trophic levels have advantages or disadvantages from the novel host traits (compare Harvey et al., 2010; Grosman et al., 2017), and may lead to further evolutionary responses between the host and the natural enemy. Moreover, an altered host plant range in herbivorous pollinators such as within Lepidoptera may affect plant–insect mutualisms and their ecosystem service capacity. It has previously been argued that a multitrophic perspective should be taken on novel host plant–insect associations to fully understand their consequences (Harvey et al., 2010), and this may therefore be relevant also for cross-resistance following pesticide resistance development.

An altered host plant range following pesticide resistance development may thus have consequences, for example on trait evolution, competition, niche occupation, trophic interactions and range expansion, which may impact community dynamics in the entire agroecosystem. To understand these dynamics, it may also be relevant to take into account that resistance development itself may come at a cost (Carrière et al., 1994; Gutiérrez et al., 2019), affecting reproduction (Abbas et al., 2012), population dynamics (Boivin et al., 2003) or species interactions (Bendis & Relyea 2016). However, very little is known about the community-scale consequences of pesticide resistance development, and we may thus only have understood a minor part of the effects of pesticide application on species inhabiting the agroecosystem. In this context, it would be useful to take an eco-evolutionary perspective to address plausible feedback loops between trait evolution and community ecology following cross-resistance. Further empirical studies in the lab and the field combined with theoretical modelling are thus warranted to better understand the ecological and evolutionary consequences of pesticide resistance development in arthropods. Such studies will be beneficial from a pesticide resistance management perspective and gather knowledge on eco-evolutionary dynamics *in natura* (Hendry, 2019).

CROSS-RESISTANCE: TAKING ECOLOGY INTO ACCOUNT

Understanding the relation between arthropod host plant range and pesticide resistance evolution is still in its infancy. More research is still needed to (i) empirically investigate the pre-adaptation hypothesis from an ecological perspective, for example to elucidate the differences between specialists and generalists on their predisposition for cross-resistance, and (ii) explore the potential consequences on a host plant range expansion following pesticide resistance development. Results from such research would deliver critical insights into the ecological and evolutionary processes of plant–arthropod interactions and arthropod diet breadth (e.g. the host plant specialisation process, Box 3), and more generally, on the role of ecological interactions for rapid evolution.

More profound knowledge about the emerging field of arthropod **gut microbiota** could provide novel insights on its role in mimicking cross-resistance between pesticides and defensive plant chemicals (Box 2). Herbivorous arthropods harbour gut microbiota that has been suggested to aid in plant allelochemical detoxification (Ceja-Navarro et al., 2015; Després et al., 2007; Francoeur et al., 2020) even if its importance may vary between insect orders (Hammer et al., 2017). Endosymbionts have recently been shown to aid their arthropod host in detoxifying pesticides, but this area is still largely unexplored (Almeida et al. 2017; Itoh et al., 2018; Le Goff & Giraudo, 2019; Wang et al., 2022). Gut microbiota may thus provide a phenocopy of cross-resistance and the possibility for both horizontal and lateral transfer of microbe-mediated resistance between individual arthropods (Acuna et al., 2012; Cheng et al., 2018; Rassati et al., 2019; Taerum et al., 2013). Gut microbiota could be either beneficial or pathogenic, and the host–microbe interactions under the exposure of pesticides may thus be complex (Heithausen, 2021). For example pathogenic gut bacteria could be negatively impacted by pesticides, leading to higher arthropod survival during pesticide exposure (Hilbeck et al., 2018). To better understand the potential of the gut microbiota as a mediator for cross-resistance, integrative approaches combining ecological research with microbiology and molecular studies would be useful. For example studies manipulating gut microbiota with antibiotics in pesticide-resistant and susceptible arthropods may be the first step to investigate whether gut microbiota could detoxify pesticides or otherwise affect host plant preference and performance. Such studies could be carried out in parallel between generalist and specialist arthropods to determine whether microbial communities respond differently to novel toxins depending on the diet breadth of their host.

Understanding how and when arthropod species respond with **plasticity** to pesticide exposure, both within and between generations, and the extent of plastic responses involved in cross-resistance are other aspects to consider. Several studies show that sub-lethal doses of pesticides have diverse effects on insects' behaviour and physiology (Desneux et al., 2007), for example affecting feeding and locomotion (Jung et al., 2018), olfactory systems (Rabhi et al., 2016), mating behaviour (Lalouette et al., 2016) or learning (Sgolastra et al., 2020). Furthermore, pesticide-induced changes may elicit trans-generational effects and influence offspring behaviour and physiology (Brevik et al., 2018). However, little is known about whether adaptive plasticity evolves following pesticide exposure or its role in pesticide resistance development, even though examples exist where pesticide resistance has evolved following genetic assimilation of plastic traits (Hua et al., 2015). Plasticity is an essential part of eco-evolutionary dynamics as it, for example often evolves on ecological timescales and could mediate selection pressures (Hendry, 2016) or could mimic eco-evolutionary dynamics (Hanski, 2012). It would thus be interesting to explore the role of plasticity in cross-resistance through an ecological angle and not only from the genetic perspective (Brevik et al., 2021; Hu et al., 2021). For example plasticity is often crucial during host plant choice in arthropods, where both juvenile and adult insects may base their host plant choice on previous experience (Anderson & Anton, 2014), which could be considered as learning. Could experience of pesticide presence on certain host plants lead to induced shifts in host plant preference in mothers, and what consequences does that have for their offspring?

Interestingly, other pesticides, such as herbicides and fungicides, may also select for adaptation in arthropods (Dubey et al., 2020; Rainio et al., 2019). Exposure to multiple pesticides may, at worst, select for pests that become multi-resistant to a wide array of toxins. If there is cross-resistance in both directions, from host plant adaptation to pesticide resistance and vice versa, would such multi-resistant arthropods also be able to shift or increase their host plant range to a larger degree? Perhaps, the additive effects of an increased amount of toxins, both concerning doses and variety of compounds, in the environment may select a higher ability to increase host plant range in both pest and non-pest species with ecological consequences. Pesticide resistance and ecological consequences such as host plant range may thus vary between environments with high or low toxins levels in time and space. Studies at a landscape-scale perspective, taking into account gene flow and dispersal (Hanski, 2012), would be needed to understand the evolutionary ecology of resistance development better. For example if we can predict in what environments we can expect strong eco-evolutionary feedbacks. It may also be interesting to understand whether entire species communities, from the gut microbiota to predators, have increased resistance traits in ‘highly toxic’ environments and how that affects their interactions or if ecological changes are mainly driven by resistance development in one or a few species. Eco-evolutionary community dynamics are, however, often more difficult to interpret since the ecological effects from adaptation in one species may be weaker when studied at the community level (Pelletier et al., 2009). Considering the strong selection that pesticide application exerts and the rapid development of resistance mechanisms, pesticide resistance and cross-resistance may, however, be suitable for addressing questions on such eco-evolutionary dynamics.

Another question that calls for further research is if cross-resistance between pesticide resistance and diet breadth also exists in other crop pests, such as pathogens. For example if generalist pathogens are more prone to evolve pesticide resistance than specialists. However, arthropods may represent a special case since they more often have metabolic resistance compared to pathogens, which often have a gene for gene resistance to plant immune defence, potentially reducing the likeliness to generate cross-resistance (Hawkins et al., 2019; Karlsson Green et al., 2020).

Finally, to fully understand the eco-evolutionary consequences of pesticide resistance development, it may be needed to incorporate societal responses in the future and adopt a socio-eco-evolutionary framework. Feedback loops between society, ecology and evolution have recently been discussed to occur in urban areas, for example with respect to pesticides (Des Roches et al., 2021), and we suggest this to be applicable also for agricultural environments since how farmers manage their fields and what pest control they choose in response to pesticide resistance development may impact both ecological interactions and further evolutionary processes.

TAKING CROSS-RESISTANCE INTO ACCOUNT IN PEST MANAGEMENT STRATEGIES

Increased knowledge about the evolutionary links between pesticide resistance and host plant adaptation, together with the ecological context and consequences, is of great interest both from a fundamental research aspect and a pest management perspective. Indeed, a better understanding of which species and in which circumstances pesticide resistance evolves would improve resistance monitoring and resistance management. Pesticide resistance is a common problem across species groups (Sparks & Nauen, 2015), and preferably resistance monitoring and management should be included in pest control strategies to avoid further resistance development (Karlsson Green et al., 2020). For example reducing pesticide use and developing new control strategies for species that are more likely to develop resistance will be necessary. This perspective may also be of interest for breeding programs to avoid consequences on pesticide resistance development and host plant range from interacting effects between pesticides and plant chemical defences.

In sustainable pest management, **biopesticides** based on naturally occurring organisms or allelochemicals could be used (Fenibo et al., 2021). Due to the potential for pre-adaptation and cross-resistance, these substances should be selected by care to minimise the potential for resistance development and host range expansion. However, overuse of biopesticides can still lead to resistance, for example granulovirus in the codling moth (Asser-Kaiser et al., 2007) or *Bacillus thuringiensis* (Bt) in the diamondback moth (Tabashnik et al., 1991). Perhaps, it may be better to use biopesticides from plants or organisms that do not have relatives in the application area to minimise the potential for rapid resistance development or host plant range expansion (Crossley et al., 2021). Investigating which pesticides are more often involved in cross-resistance and addressing the eco-evolutionary consequences of biopesticides with empirical studies will thus be important to develop long-term sustainable management.

As hypothesised earlier, pesticide resistance may lead to host plant shifts with consequences for higher trophic levels. If this hypothesis holds, the evolution of pesticide resistance also has severe consequences for sustainable management strategies with biological control agents if pests acquire better resistance to natural enemies due to increased host plant range or if pests move to host plants that present an enemy-free space. Gathering deeper knowledge on the potential for cross-resistance will also be essential for other pest management strategies, such as pests increasing their host plant range and escaping to plant species outside the agricultural fields or infesting new crops, potentially leading to economic loss (Figure 3). In this context, assessing the decisions taken by farmers when facing novel pests or pesticide resistance among the local pest populations appears of high importance (Turcotte et al., 2017) as their actions might affect both biodiversity and resistance development. Clear identification of farmers' responses coupled with a better understanding of the links between pesticide resistance and host plant range among arthropods may thus help to develop sustainable strategies and predict management consequences for both natural ecosystems and agroecosystems.

CONCLUSIONS

The widespread use of pesticides in agricultural production has initiated a massive experiment in micro-evolution at a global scale (Rosenheim et al., 1996) and has created ecosystems that can be excellent subjects for evolutionary (Karlsson Green et al., 2020) and eco-evolutionary studies (Hendry et al., 2017). However, it also created, at the same time, environments (more) challenging to manage due to resistance evolution. More research on links between host plant range and pesticide resistance evolution is needed to confirm this pattern. Understanding the ecological and evolutionary consequences of pesticide resistance in target and non-target arthropods will unravel the potential impact of pesticides on multitrophic interactions and ecosystem functioning, which could aid in developing more sustainable pest management strategies.

AUTHORSHIP

AR, DH, PA and KKG conceived the idea. AB performed the literature analysis. KKG, AB, AR, PA and DA, all contributed to the writing of the paper.

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