Transfer and bioaccumulation of pesticides in terrestrial arthropods and food webs: State of knowledge and perspectives for research

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HIGHLIGHTS

- Arthropods are important mediators of pesticide transfers in food webs.
- We review evidence of trophic transfers mediated by arthropods in terrestrial food webs.
- Sublethal doses are probably critical for biomagnification processes.
- The trophic structure and complexity of communities influence pesticide transfer.

GRAPHICAL ABSTRACT
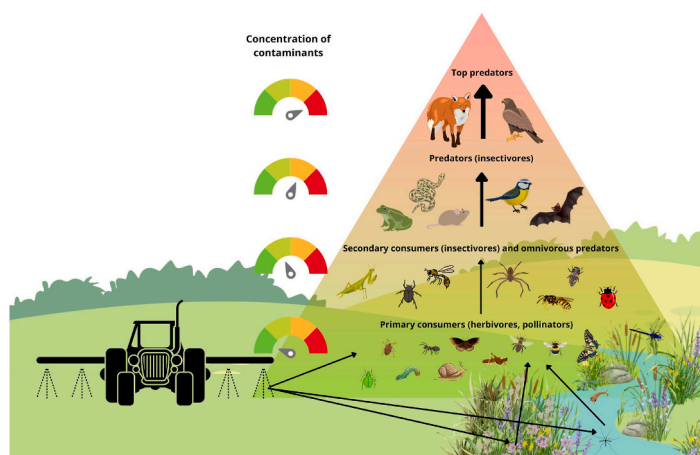
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ABSTRACT

Arthropods represent an entry point for pesticide transfers in terrestrial food webs, and pesticide accumulation in upper chain organisms, such as predators can have cascading consequences on ecosystems. However, the mechanisms driving pesticide transfer and bioaccumulation in food webs remain poorly understood. Here we review the literature on pesticide transfers mediated by terrestrial arthropods in food webs. The transfer of pesticides and their potential for bioaccumulation and biomagnification are related to the chemical properties and toxicokinetic of the substances, the resistance and detoxification abilities of the contaminated organisms, as well as by their effects on organisms' life history traits. We further identify four critical areas in which knowledge gain would improve future predictions of pesticides impacts on terrestrial food webs. First, efforts should be made regarding the effects of co-formulants and pesticides mixtures that are currently understudied. Second, progress in the sensitivity of analytical methods would allow the detection of low concentrations of pesticides in small individual arthropods. Quantifying pesticides in arthropods preys, their predators, and arthropods or

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vertebrates at higher trophic level would bring crucial insights into the bioaccumulation and biomagnification potential of pesticides in real-world terrestrial food webs. Finally, quantifying the influence of the trophic structure and complexity of communities on the transfer of pesticides could address several important sources of variability in bioaccumulation and biomagnification across species and food webs. This narrative review will inspire future studies aiming to quantify pesticide transfers in terrestrial food webs to better capture their ecological consequences in natural and cultivated landscapes.

1. Introduction

The total amount of pesticides used in agriculture worldwide has reached 3.5 million tons of active ingredients in 2021, an amount which has doubled since 1990 (FAO, 2023). In recent years, the risk of pesticides, especially neonicotinoids, for biodiversity and ecosystem functioning has received considerable attention (van der Sluijs et al., 2015; Giorio et al., 2021). So far, the efforts made to reduce the use of insecticides and their direct impacts on human and vertebrate health have been at the expense of an increased invertebrate toxicity (Schulz et al., 2021). The impact of pesticides on invertebrates by direct exposure or indirectly through incoming food via the food chain likely contributes to the current arthropods decline (Ewald et al., 2015; Seibold et al., 2019; Outhwaite et al., 2020; Wagner et al., 2021; Schulz et al., 2021; Sánchez-Bayo and Wyckhuys, 2021). Yet, the functioning of terrestrial ecosystems depends on the occurrence of invertebrates and their predators (Wilson, 1987; Eisenhauer et al., 2023). Arthropoda is the largest animal phylum, accounting for about 80% of the total number of species in the animal kingdom (Zhang, 2011). From pollination services to pest control to the regulation of soil quality and decomposition, arthropods are involved in many ecosystem services. Arthropods contain insects, which is the dominant group of arthropods with an estimate of 5.5 million species, as well as myriapods and spiders (Stork, 2018). Synthetic insecticides were developed and targeted towards vectors or insect crop pest populations and evidence of their accumulation in the environment rapidly appeared. The specificity of insecticides has increased in the last decades to reduce their toxicity to non-target species (Narahashi et al., 2007), but despite all efforts made, so far, no substance that targets insect pests leaves non-target unaffected (Köhler and Rita, 2013), only the temporal frame and mode of application of the substances can influence their bioavailability.

In the environment, non-target arthropods are exposed in various ways to a large range of products used in crop protection (i.e., fungicides, insecticides herbicides), active substances, but also to their co-formulants. Most pesticides used in conventional agricultural systems are applied during the crop-growing season, which corresponds to the breeding periods of arthropods. They can be exposed orally to various pesticides while feeding on treated plants, nectar, and pollen or when drinking contaminated water or spray droplets in or near agricultural fields (primary poisoning). Secondary poisoning occurs through trophic interactions, by consuming contaminated preys (predation) or developing inside a contaminated host (parasitism). The increased selectivity of pesticides coupled with the reduction of doses raised the problem of sub-lethality. Effects on organisms and at the level of communities may primarily arise through indirect and sub-lethal effects of pesticides. Following exposure to low doses, arthropods can uptake pesticides and accumulate pesticide residues in their tissues without dying (bio-accumulation). In 1981, Rudd and collaborators (Rudd et al., 1981) showed that herbivores exposed to DDT rapidly took up the chemical, followed by a precipitous decline and a slight long-term increase in concentrations. Contaminated arthropods stay alive with often-reduced fitness or displacement capacities and are prayed by predators. Carnivorous arthropods such as arachnids and coleopterans as well as birds feeding on these herbivorous arthropods initially showed a similar pattern but on a greater timespan, followed by an unexpected increase though the trophic chain. Multiple evidence points to the potential of several pesticides to show increasing concentrations with trophic levels, leading to high contamination of top predators (biomagnification). Over time, this might induce lethal or sublethal effects on the top predators. As an important food source for a wide range of organisms, arthropods thus represent an entry point of pesticides and other environmental pollutants into food-webs (Lv et al., 2014). Such evidence has been mostly collected in aquatic ecosystems, and our understanding of trophic transfers of pesticides in terrestrial food web remains limited. Yet, since several decades, evidence accumulated that several pesticides (mostly carbamates, neonicotinoids and pyrethroids) can transfer and potentially bioaccumulate in trophic chains, leading to unexpected effects on different traits related to individual fitness (Kumar and Chapman, 1984).

The quantification of terrestrial arthropods' exposure to pesticides is complex since contamination with pesticide residues can occur via multiple routes, directly or indirectly, and vary during the season and from year to year. Although the occurrence of pesticide residues is the highest in agricultural fields, field margins are also affected because the wild vegetation near treated crops is also contaminated by mixtures of pesticides (Botías et al., 2016; Long and Krupke, 2016; Mogren and Lundgren, 2016; Main et al., 2020; Zioga et al., 2023). Neonicotinoid insecticides are widely used for protecting crops against a large range of insect pests (Simon-Delso et al., 2015). Their residues can persist for years in soil (Schaafsma et al., 2015; Wood and Dave, 2017; Giorio et al., 2021; Wintermantel et al., 2020), even in organically managed soils (Riedo et al., 2021) or in nectar and pollen from fields yet untreated with neonicotinoids (Henry et al., 2015; Botías et al., 2016; Zioga et al., 2023). Other routes of exposure such as honeydews, attracting parasitic wasps and pollinating hoverflies were identified (Luquet et al., 2021) and possibly cause acute or chronic deleterious effects on non-target organisms (Calvo-Agudo et al., 2019; Quesada et al., 2020). Systemic insecticides can also be found in the phylloplane like fungi present on treated plants, indirectly poisoning non-target organisms, e.g., powdery mildew eaters such as ladybugs (Choudhury et al., 2020), fruit tortricid moth larvae, or even honeybees. Extra-floral nectar containing systemic pesticide residues can also become a death trap for beneficial entomo-fauna such as the common green lacewing (Gontijo et al., 2014) or nectar-feeding parasitoids (Stapel et al., 2000).

The toxicokinetic of pesticides in arthropods as well as their detoxification abilities are still relatively poorly understood. Research on pesticides side effects on arthropod communities have concentrated their efforts on understanding the effects of pesticides on terrestrial species but less on how pesticides are transferred to upper trophic levels. Individual fitness traits (traits relative to reproduction and survival) condition the population dynamics of arthropods involved in the trophic chains. If contaminated arthropods stay alive, they are more likely to be eaten or parasitized, becoming an entry point of pesticides into the food web. The sub-lethal effects of pesticides on arthropods have been largely reviewed (Desneux et al., 2007) and extended research have been done on pollinators, mainly bees, that are seen as a bio-indicator of environmental contamination and pesticides' side effects (Goulson and Nicholls, 2016). Indirect effects of pesticides on arthropods are however much more complex and derive from the ecological structure of communities and ecosystems, depending on complex interactions involving competition for resources and trophic relationships such as predation and parasitism (Sánchez-Bayo and Wyckhuys, 2021). There is a growing number of studies addressing the complex issue of pesticide transfers and their sublethal effects on arthropods, but currently we are lacking a

synthesis and conceptual framework to guide future research on pesticides transfer and bioaccumulation in arthropod food webs. Here, we conduct a narrative review of the literature aiming to fill this gap. We retrieved relevant literature dealing with pesticides transfers in arthropods and terrestrial food webs using Google Scholar without restriction on the time period. Our keywords involved combinations of terms such as "pesticide", "pesticide transfer", "arthropod", "predator", "food web", "bioaccumulation", "biomagnification", and "trophic level". We specifically looked for studies measuring pesticide concentrations and sublethal effects in two or more trophic levels. Most of the retrieved literature concerned agricultural pesticides including legacy pesticides such as organochlorines or more recent ones such as neonicotinoids. Most of the currently used pesticides are underrepresented in the literature and offer future directions of research. Based on the retrieved article, we first address the dynamics of pesticides transfers in insects and other arthropods. We then review the evidence for trophic transfers and bioaccumulation/biomagnification processes in terrestrial food webs involving arthropods and other invertebrates when relevant. Finally, we discuss the transfer of pesticides in terrestrial food webs and complex networks.

2. Toxicokinetics of pesticides in arthropods

2.1. Exposure and sensitivity

Pesticides trophic transfers in food webs are related to the amount of pesticides that come into contact and is retained by organisms as well as the tolerance of the species to a particular compound (Jepson et al., 1990). Pesticides are entering living organisms in different ways, according to their habitat and their behavior. In terrestrial systems, pesticides are mostly absorbed through the skin, cuticle, respiratory, or digestive organs of animals (Hayes' *Handbook of Pesticide Toxicology*, 2010). The bioavailability of pesticides in terrestrial ecosystems, the toxicokinetic, metabolism, and excretion of the substances, will influence the absorption and bioaccumulation of pesticides into food chains. The biomagnification potential of a pesticide depends on the persistence and lipophilic characteristics of the pesticide, as well as on metabolism and elimination processes. Organochlorines such as DDT (persistent compounds), are well known to have higher biomagnification rates compared to organophosphates (non-persistent compounds) (Favari et al., 2002).

Sensitivity to pesticides is extremely different among and also within arthropods species. Variations in sensitivity can be related to toxicokinetics (uptake, distribution, biotransformation, elimination of a substance by an organism) or toxicodynamics (interaction of a substance with biological target sites) (Nyman et al., 2014). Higher tolerance to stress by an organism is usually linked to its lower sensitivity to xenobiotics (Lushchak et al., 2018). The body size, weight, age and lifespan of an organism will also influence its sensitivity to pesticides. For example, in honeybees, the heavier bees are, the less sensitive they are to pesticides. However, the relation with age might be more complicated as switch in behavioral functions during lifespan (i.e., age polyethism) can also influence arthropods' sensitivity. In bees, it is now evident that the glycoprotein vitellogenin has a protective role against oxidative stress and aging (Seehuus et al., 2006), explaining the greater tolerance of queens and winter bees to toxicants compared to summer worker bees. Nutrition also influences their tolerance to pesticides, with the quality of pollen linked to the ability of bees to metabolize pesticides and withstand their detrimental effects (Barascou et al., 2021).

The metamorphosis from larvae to adults is a specific stage in arthropods that plays differential roles is the concentration and bioaccumulation of chemicals in arthropods. Terrestrial insectivores such as riparian spiders are exposed to high concentrations of chemicals when consuming insects that developed into contaminated water as larvae (Kraus et al., 2014; Kraus, 2019; Graf et al., 2020). Differences in susceptibility and persistence between different stages of arthropod

development have also been demonstrated for the lacewing *Chrysoperla externa* exposed to spinetoram and indoxacarb (Armas et al., 2023).

2.2. Resistance and detoxification

Pesticide trophic transfer are also influenced by resistance and detoxication mechanisms. To deal with an exposure to contaminants such as insecticides, arthropods are using behavioral, physiological, and genetic mechanisms that can be metabolically costly, affecting biological and fitness traits (Gul et al., 2023). Arthropods can exhibit diverse mechanisms of resistance such as target-site mutations, avoidance (Easton and Dave, 2013), resistance mechanisms leading to transgenerational positive fitness effects in the offspring of exposed pests (Margus et al., 2019), and an upregulation of detoxification genes. Detoxification abilities depend on other factors such as the health status of the organism, its immunity, age, and co-exposure to other hazards. Arthropods also possess specific gut microorganisms involved in the resistance against pesticides by degrading chemical compounds (Itoh et al., 2018).

There are generally three phases of detoxification in arthropods. The first involves predominantly oxidation, usually catalyzed by mixed function oxidases, e.g. cytochrome P450 enzymes, reduction, and hydrolysis, catalyzed by various esterases (Sharma et al., 2020). In the second phase, the toxin can be metabolized, for example by glutathione transferases (Koirala et al., 2022). Finally the third phase of detoxification is the excretion of the toxins from the organism by specific ATP-binding transporters (Wu et al., 2019). Chemical substances are eliminated by contaminated organisms either in their original form, either as a product of biotransformation, more or less toxic to the organism than the initial compound.

The family of P450 enzymes is involved in many biosynthetic pathways related to arthropods growth and reproduction but also plays important roles in detoxication processes (Feyereisen, 1999; Johnson et al., 2012). Increased catabolism of insecticides can thus decrease growth, shorten longevity or decrease investment in reproduction.

2.3. The basics of bioaccumulation in arthropods

Pesticides can be fixed and persist in the tissues of terrestrial arthropods through bioaccumulation, "a process by which chemicals are taken up by an organism either directly from exposure to a contaminated medium or by consumption of food containing the chemical" (Ecological Risk Assessment Glossary of Terms, 2012). For example, insects like aphids can bioaccumulate toxins if the plants they feed on are contaminated with pesticides or if the fields they live in are routinely sprayed. If the toxin builds up at a faster rate than the aphids can metabolize it, the aphids will bioaccumulate the toxin in its tissues, potentially to dangerous levels that can affect its health. Then, if the aphids are consumed by larger insects such as ladybugs, they would pass on their toxins on to the next trophic level. If birds consume the contaminated ladybugs, they might concentrate higher amounts of the toxin due to biomagnification.

The bioaccumulation behavior of chemicals can usually be assessed by the chemical's Bio-concentration Factor (BCF), Bioaccumulation Factor (BAF), and the octanol-water partition coefficient (KOW). If there is evidence that a chemical can bioaccumulate in certain species or if bioaccumulation is revealed through the monitoring of contaminated organisms, the bioaccumulative behavior of a chemical can be highlighted (Gobas et al., 2016). Bioaccumulation models for fish and aquatic food-webs have been widely used to assess the risk of pesticides to aquatic organisms because the BCF, BAF, and KOW are descriptors of chemical distribution between aquatic organisms and water (Gobas et al., 2009). These indicators cannot represent accurately the bioaccumulation behavior in air-breathing organisms. Limitations and gaps in terrestrial bioaccumulation modeling include the lack of QSARs (Quantitative structure-activity relationships) for biotransformation and

dietary assimilation efficiencies for terrestrial species. Models of bio-accumulation exist for earthworms but not for other important terrestrial taxa groups such as arthropods, amphibians and reptiles that lack specific adapted models and QSARs values more than any other terrestrial species (Gobas et al., 2016).

Former theories explained bioaccumulation processes by focusing on a single aspect such as the trophic level of the organism or the lipophilicity of the substance. Biomagnification factors (BMF) and trophic magnification factors (TMF) are usually calculated in aquatic systems and for aquatic species, which make these values not relevant for terrestrial species.

In the last two decades, research has concentrated its effort on understanding the bioaccumulative behavior of heavy metals and lipophilic organic contaminants such as PCBs, mainly focusing on aquatic systems (Maul et al., 2006). Models for ionic and ionogenic organic chemicals including pesticides, that may be distributed differently in organisms as a result of non-lipid partitioning, are urgently needed.

Regulatory standards continue to rely on acute paradigm testing (e. g., 48-h LC50s or NOECs) that fails to capture bioaccumulation and biomagnification despite the serious consequences these processes can have on non-target species and terrestrial ecosystems. Laboratory tests, field studies, and modeling techniques need to be developed to evaluate the bioaccumulation potential of chemical substances in terrestrial arthropods and food chains (Gobas et al., 2016). Better incorporating toxicokinetic processes will be key. Furthermore, it remains very difficult to assess how chemical changes in arthropods during metamorphosis can alter or increase the concentration of contaminants and no model exists for predicting these effects and estimate biomagnification. Food web studies and contaminants regulation strategies now need to consider how metamorphosis, detoxification, and trophic relationships influence the transfer of contaminants between aquatic and terrestrial ecosystems (Kraus et al., 2014).

3. Evidence and effects of trophic transfer of pesticides in natural enemies

Evidence is raising on the latent, chronic contamination of arthropods via the consumption of contaminated preys. Here, we review studies focusing on pesticides trophic transfers to arthropod natural enemies because they play important roles in agricultural systems but are exposed to trophic transfers by feeding on invertebrate pests, i.e., through secondary poisoning. Predatory and parasitoid arthropods such parasitic hymenopterans, ladybirds, dragonflies, crab spiders regulate pest populations through larvae parasitism or predation. If these pests are not susceptible to a pesticide, resistant to it, or if they receive doses too low to kill them, they will stay alive while contaminated, exposing their consumers to pesticides, and potentially persisting in food webs (Frank and Tooker, 2020). Contamination of natural enemies or non-target insects by sublethal doses of pesticides can occur when two or more pests experience differential toxicity to a given pesticide or when predators are more sensitive to a pesticide than the pest itself. Contamination of natural enemies by pesticides will likely influence the regulation of pest population levels by their natural enemies and could even lead to secondary pest outbreaks. Table 1 summarizes the main effects of pesticides through trophic interactions between preys and predators described in sub-sections 2.1 - 2.3.

3.1. Predator survival impairment and secondary pest outbreaks

In some cases, the trophic transfer of pesticides between preys and their predators can lead to significant impairment of the predator's survival. Lacewings (Chrysopidae) are major predators in agricultural systems and several studies found evidence on pesticide-induced mortality through the consumption of contaminated preys. The use of imidacloprid and pirimicarb to control lettuce aphids induced respectively 96 % and 30–40 % of mortality of larvae of the lacewing *Micromus*

Table 1

Examples of trophic transfer of pesticides in natural enemies and their lethal or sub-lethal effects.

Trophic levels concerned Species	Substances	Effects	References
Herbivore (H) - Predator (P)			
H: Lettuce aphids *Nasonovia ribisnigri* P: Lacewings *Micromus tasmaniae*	Imidacloprid, pirimicarb	P: Survival impairment	Walker et al. (2007)
H: Aphids *Sitobion avenae* P: Carabids *Pterostichus madidus*, *P. melanarius* Illiger, *Nebria brevicollis*	Dimethoate	P: Survival impairment	Mauchline et al. (2004)
H: Pest slugs *Deroceras reticulatum* P: Ground beetles *Chlaenius tricolor*	Thiamethoxam	H: Increased activity P: Paralysis/ death, reduced activity & predation	Douglas et al. (2015)
H: Lepidoptera *Ephestia kuehniella* eggs P: Mirids *Nesidiocoris tenuis*	Sulfoxaflor	P: Survival impairment, reduced fecundity	Wanumen et al. (2016)
H: Spider mites *Tetranychus* spp. P: Mites *Galendromus occidentalis*, *Amblydromella caudiglans*	Glufosinate, paraquat, oxyfluorfen	P: Survival impairment, reduced reproduction	Bergeron and Schmidt-Jeffris (2023)
H: Aphids *Rhophalosiphum padi* P: Second instars of ladybugs *Coleomegilla maculata*	Thiamethoxam, clothianidin	P: Reduced activity	Bredeson et al. (2015)
H: Diamondback moths *Plutella xylostella* P: Spined soldier bugs *Podisus maculiventris*	Imidacloprid	P: Impaired predatory behavior	Resende-Silva et al. (2019)
H: Ground crickets *Nemobius sylvestris* P: Web spiders *Pisaura mirabilis*	Imidacloprid	H: Reduced herbivory P: Increased predation	Uhl et al. (2015)
Herbivore (H) - Primary predator (P1) - Secondary predator (P2)			
H: Spider mites *Tetranychus schoenei* P1: Predatory beetles *Stethorus punctillum* P2: Lacewings *Chrysoperla rufilabris*	Imidacloprid	H: E enhanced fecundity P1/P2: Survival impairment Other: change in community structure	Szczepaniec et al. (2011)
Omnivore (O) - Predator (P)			
O: Fruit flies *Drosophila melanogaster* P: Wolf spiders *Pardosa agrestis*	Glyphosate	P: Impaired predation rates	Niedobová et al. (2016)
Primary predator (P1) - Parasitoid (Pa)			
P1: Stink bugs *Halyomorpha halys* Pa: Egg parasitoid wasps *Trissolcus japonicus*	Pyriproxyfen	Pa: Emergence failure of the parasitoid	Penca and Hodges (2017)

tasmaniae (Walker et al., 2007). The survival of carabid predators feeding on aphids treated with the insecticide dimethoate was significantly affected as well, in both laboratory and field assays, indicating the possibility of indirect poisoning of natural predators in treated fields or field margins through the consumption of contaminated pests (Mauchline et al., 2004). The same kind of effect, together with an enhanced fecundity of spider mites and thus a change in the community structure was also reported after imidacloprid treatments on elm trees (Szczepaniec et al., 2011). A neonicotinoid of the 4th generation, sulfoxaflor, supposedly less toxic that the well-known neonicotinoids of the third generation, was used at the highest recommended rates on the eggs of the Lepidoptera *Ephestia kuehniella* and lead to a significant increase in mortality but also a reduced fecundity and longevity of the omnivorous mirid predator *Nesidiocoris tenuis* (Wanumen et al., 2016).

Contamination of natural enemies by pesticides is a real concern since it may affect the regulation of pest population and thus increase the probability of secondary pest outbreaks. Predatory mites for example, are more sensitive to several herbicides than phytophagous mites, favoring pest species over their predators (Isenhour et al., 1985; Norris and Marcos, 2000). As an example, slugs do not die from consuming neonicotinoid treated plants, but their predators such as the ground beetles are physiologically susceptible to them and experience increased mortality or sublethal effects after feeding on contaminated prey, that can make them avoid subsequent contaminated preys (Mullin et al., 2005). Another study showed that slug predation by beetles was reduced by 33% the first month after neonicotinoid-treated seedling due to reduced motor function, paralysis or even death of the predatory beetles (Douglas et al., 2015). Slug activity on the contrary, increased by nearly 70 % and soybean yields were 19% reduced by the time of harvest, refuting any beneficial effect of a neonicotinoid seed treatment in this case. Transmission of pesticides through food chains can thus result in some cases in fewer predators and more herbivores than without pesticides. Pest control failure can occur when direct lethal effects of pesticides on natural enemies are observed or in the case of secondary poisoning through predation or parasitism that can have lethal or sublethal effects on the natural enemy (e.g., predatory skills, reproductive abilities, fitness, etc.) which loses its ability to control the pests (Kurwadkar and Evans, 2016).

3.2. Altered predatory behavior in predators

Secondary poisoning can lead to a significant impairment of predatory skills. For instance, slower walking in second instars of the ladybug *Coleomegilla maculata* feeding on aphids *Rhophalosiphum padi* contaminated in wheats treated with thiamethoxam. The neonicotinoid present as seed-coating was however rapidly degraded and only its metabolite clothianidin, was found in the aphids (Bredeson et al., 2015). Also, the predation of the spined soldier bug, *Podisus maculiventris* was impaired as the bugs fed on diamond moths, *Plutella xylostella* exposed to imidacloprid. The neonicotinoid treatment applied at recommended rates failed to reduce the number of moth pests (Resende-Silva et al., 2019), another example of pest control failure. When used at sublethal doses on strawberry plants, imidacloprid reduced herbivory of the ground crickets *Nemobius sylvestris* but increased predation of the crickets by a web spider *Pisaura mirabilis,* suggesting possible impacts and bioaccumulation of the neonicotinoid through trophic interactions (Uhl et al., 2015).

Most insecticide molecules target neural functions (Casida, 2009) leading to direct lethal effects but also sublethal effects (Desneux et al., 2007; Müller, 2018). Neonicotinoids act on the central nervous system of insects and induce cumulative and irreversible blockage of nicotinic acetylcholine receptors, which are involved in many important cognitive processes (Sánchez-Bayo and Tennekes, 2020). Neonicotinoids supposedly targeting only herbivorous pests have deleterious effects on pollinators, predatory arthropods, and soil communities, highlighting the need to consider the risk associated to the trophic transfer pesticides

and especially insecticides in risk assessment. Those exposed to sublethal doses of pesticides may harbor a reduction in their activity and mobility (Stürmer et al., 2014; Rosa et al., 2023), and thus increase susceptibility to their natural enemies (Rackliffe and Hoverman, 2022) or even a decrease in fear of the predator (Tan et al., 2014), making them overall more prone to predation than non-exposed individuals.

Neonicotinoids are often studied in terrestrial ecotoxicology but other pesticides such as herbicides can be transferred to natural enemies as well. Niedobova and collaborators (Niedobová et al., 2016) found that glyphosate affected the predation rates of the spider *Pardosa agrestis* on drosophila flies exposed to lethal doses glyphosate. Interestingly, they found that the effects of different formulations were not comparable; pointing out that adjuvants should also be considered in their synergistic toxicity. Another recent study found that three herbicides (glufosinate, paraquat, and oxyfluorfen) either killed adult predatory mites or reduced their reproduction, which could explain pest mite outbreaks in orchards as a result from their increased use (Bergeron and Schmidt-Jeffris, 2023). Such modified responses by predators should be more studied, as it will present unsuspected cascade effects in predator-prey systems.

3.3. Disruption of reproduction in parasitoids

Parasitoids need to feed on the inside of their host to develop and if they lay their progeny in contaminated hosts, it can lead to emergence failure of the parasitoid or a reduction of its fitness (Sánchez-Bayo, 2011). Disruption of sex communication was observed in several parasitoids such as in the parasitoid wasp *Nasonia vitripennis* after exposure to sublethal doses of imidacloprid. Several works report cases of sex pheromonal communication hindered in arthropods with consequences on mating success, but this remains understudied so far (Desneux et al., 2007; Tappert et al., 2017).

The insect growth regulator pyriproxyfen was shown to affect the stink bug *Halyomorpha halys*' eggs and larvae leading to emergence failure of the beneficial egg parasitoid wasp *Trissolcus japonicus* (Penca and Hodges, 2017). The survival of parasitoid wasps could also be altered. Because of their specific mode of action and low toxicity to non-target species, insect growth regulators can also interfere with the natural control of pests by their natural enemies similarly as other insecticides (Lira et al., 2020). Insecticides and insect growth regulators may thus not be compatible with biological control programs. If natural enemies are absent to control pests' populations or if their behavior and fitness is affected by pesticides, additional sprays of chemicals are usually applied and will maintain pesticide contamination and bioaccumulation in pests and predators.

3.4. Quantifying multiples substances in arthropod predators

A key challenge in quantifying pesticide transfers in terrestrial food webs is the fact that arthropods are often contaminated by multiple substances simultaneously. The analysis of ethanol solutions used to preserve insects caught in malaise traps from nature conservation areas allowed the detection of 47 current-use pesticides (13 herbicides, 28 fungicides and 6 insecticides) and revealed significant exposure even in protected areas (Brühl et al., 2021). Without being directly targeted by herbicides and fungicides, arthropods are often exposed to these substances. In honeybee colonies, often used in ecotoxicology for the monitoring of environmental pollution, up to 161 different substances were detected (Chauzat et al., 2006; Sanchez-Bayo and Goka, 2014), including insecticides and fungicides. Evidence suggest that these compounds can interact together synergistically and increase the toxicity to bees (Schuhmann et al., 2022; Favaro et al., 2023). The knowledge on possible interactions of other types of fungicides and insecticides is poor and needs further attention. Future studies need to investigate the interactive effects of multiple class of pesticides on different arthropod communities. We especially lack information on the

interactions between the simultaneous transfer of multiple substances in arthropods and in terrestrial arthropod food webs.

It should be noted that the detected insecticides residues in these screening studies cannot possibly reflect the reality of insects' exposure to insecticides. The high toxicity of insecticides to arthropods induces higher mortality rates, which leads to fewer contaminated individuals that can be sampled alive. Pesticide residues screening in living arthropods allows to evaluate their sub-lethal contamination in natural conditions but does not allow the evaluation of bioaccumulation potential in arthropods and the distinction between different arthropod communities and their trophic links.

To quantify bioaccumulation and biomagnification processes in terrestrial ecosystems, studies analyzing pesticides residues in prey and their predators are urgently needed. Unfortunately, analytical methods that can analyze multi-pesticide residues in predatory arthropods such as spiders or parasitoids are lacking. Analyzing residues dissolved in the ethanol used to preserve insects such as in Brühl et al., (2021) allowed the detection of many different substances but could not distinguish between individuals nor account for trophic relations. Quantifying pesticides with very diverse chemical profiles in complex and low-weight matrices of arthropods is extremely difficult. Techniques exist to quantify pesticide residues in honeybees and other bees (Kiljanek et al., 2016; Suzuki et al., 2023), even in single bumble bee individuals (David et al., 2015) and single Asian hornet individuals (Tison et al., 2023). However, analytical methods need to be further improved to quantify multiple pesticide residues in very small amounts of samples such as single individual arthropods, predators or parasitoids, and other natural enemies sampled in natural conditions.

Our recent study on the Asian hornet *Vespa velutina*, a major predator of honeybees, has identified at least one compound in 75 % of the 24 explored nests (Tison et al., 2023). This analytical method allowed the detections of 42 compounds in a 250 mg sample corresponding to the weight of a single individual. This study revealed the presence of 14 different substances in hornets sampled in their nests, including 8 fungicides, 3 insecticides, 2 miticides and one synergist, piperonyl butoxide (PBO). The latter was found in more than a third of the sampled nests and is well known for inhibiting the activity of P450 enzymes in insects which is involved in detoxication mechanisms. It is often associated to insecticides such as carbamates, pyrethrins and pyrethroids to reduce the number of active substances in a formulation and increase the efficacy of the products. The risk of biomagnification is higher with lipophilic substances such as PBO, which is likely to concentrate in high lipid content tissues, present in most arthropods including the hornets used in this study (Tison et al., 2023).

The systematic analysis of so-called 'inert' ingredients in terrestrial arthropods would provide a better understanding of the complex exposure they are facing. The decrease or loss of detoxication abilities associated with the mode of action of certain substances such as PBO will likely penalize the immune defense system of natural enemies and make them more sensitive to the many chemicals they encounter during their life. Its presence in arthropods and its affinity with lipids make it a good candidate for bioaccumulation and biomagnification in trophic chains. Risk assessment needs to consider the bioaccumulation and biomagnification potential of active substances and co-formulants before considering using them for agricultural purposes (Maurya, 2016).

In this section, we have reported accumulating evidence of trophic transfer of pesticides between arthropods preys and their predators and parasitoids that are associated with significant lethal and sublethal effects. Such processes could have cascading effects on natural pest regulation in agricultural systems, but further research is needed to evaluate the extent to which predators and parasitoids are contaminated with pesticide residues in natural conditions. Furthermore, open questions remain to link these trophic transfer processes with the bioaccumulation and biomagnification potential of pesticides at upper trophic levels in terrestrial food webs that involve arthropods.

4. Bioaccumulation and biomagnification in upper trophic levels

Arthropods are keystone species in terrestrial food web as they represent valuable and abundant food sources for upper vertebrate predators. Vertebrates might be exposed to pesticides orally, through dermal contact or inhalation for instance (primary poisoning) or by contaminated food or water (secondary poisoning). Ingestion is considered the major route especially in birds and mammals while in reptiles and amphibians, there are greater possibilities for dermal exposure (Smith et al., 2007). Then, biomagnification along the trophic chain depends on the chemical properties of the molecules, and the ecology of the prey and their predators (Schiesari et al., 2018).

4.1. Historical contaminations with organochlorines

Biomagnification has been largely described with DDT, DDE and cyclodiene insecticides such as aldrin or dieldrin, largely used in the past but which remains bioavailable in trophic chains (Kesic et al., 2021). These substances accumulated into granivorous birds and rodents, but also in caterpillars through primary poisoning. Pesticide residues climbed up the food chain from these animals and accumulated in the fat bodies of their predators. Top predators such as falcons and eagles ended up with internal concentrations a thousand times higher than those found in treated plants (Sánchez-Bayo, 2011). Residues of DDT and DDE but also of the organophosphate parathion-methyl have been found in the gut of passerine birds in Australia at different levels along the food-chain (Sánchez-Bayo et al., 1999), suggesting a trophic cascade through the ingestion of contaminated food, 20 years after DDT was banned in this country. In the US, about 36 species of birds were collected from three lakes and were found to contain residues of 13 organochlorine insecticides with top chain predators such as the green-backed heron (*Butorides striatus*) and snakes containing much higher residues than secondary consumers such as the bluegill (*Lepomis macrochirus*) or the Blacktail shiner (*Notopis venustus*) (Niethammer et al., 1984). Today, DDT is still used in different developed countries as a cost-effective weapon against malaria and malaria and leishmaniasis (van den Berg et al., 2017). In India, where DDT is still massively used, it poses a serious threat to avian biodiversity (Malik et al., 2018; Moreau et al., 2022).

4.2. Currently-used pesticides

Lethal effects of insectivorous predators through secondary poisoning were reported with highly toxic insecticides such as organophosphates and carbamates at recommended application rates (Mineau et al., 1999). The misuse of certain pesticides has also had severe consequences on vertebrates. For instance, the organophosphate insecticide monocrotophos (dimethyl (E)-1-methyl-2-(methylcarbamoyl)vinyl phosphate) used to control voles for its side effects resulted in the death of hundreds of kites, eagles, buzzards, and owls a few days after they had fed on contaminated preys (Mendelssohn and Paz, 1977).

Although currently used pesticides are overall less persistent and bioaccumulative than restricted substances such as organochlorines, around 50 compounds in Europe meet two criteria of the "persistent, bioaccumulative and toxic" class of substances (Hvězdová et al., 2018). Field surveys are usually performed without any monitoring of bioaccumulation (Fritsch et al., 2022). The rare studies dealing with currently-used pesticides in natural conditions have shown the potential for non-target fauna such as frogs and bats to be exposed and bioaccumulate pesticide residues, highlighting the need for further research on this matter (Kuzukiran et al., 2021; Brodeur et al., 2022). Only a few studies addressed bird poisoning by currently-used pesticides via food webs as they usually only focused on specific compound classes such as neonicotinoids. This new generation of systemic insecticides are the most studied group of currently-used pesticides because of their

persistence in our environment and the deleterious effects they have on bees and on the entomofauna in general (Sánchez-Bayo and Wyckhuys, 2021). They were shown to accumulate in arthropods during their development (Roodt et al., 2023) or in bees foraging repeatedly on a contaminated food source (Tison et al., 2016). Now evidence has raised regarding their transfer and accumulation in diverse systems and food webs (Yamamuro et al., 2019; Roodt et al., 2023; Tison et al., 2023). Because of their affinity with lipids and low depuration rate, they have a high potential to bioaccumulate through terrestrial food webs as well (Qin et al., 2015).

The few studies published so far that investigated biomagnification in upper chain predators mostly focused on mammal and bird species. Indeed, recent advances in chemical analytics with multi-residue approaches in blood or skin appendages (hairs or feathers) have allowed monitoring alive wildlife fauna instead of sacrificing to sample internal tissues (Chata et al., 2016; Taliansky-Chamudis et al., 2017; Rodrigues et al., 2023). Thus, recent studies show the ubiquity of pesticide molecules in mammals and birds, including neonicotinoids that are neither supposed to accumulate nor biomagnify in terrestrial organisms (mammals: Fritsch et al., (2022) and birds: (Taliansky-Chamudis et al., 2017; Byholm et al., 2018; Hao et al., 2018; Lennon et al., 2020; Humann-Guilleminot et al., 2021; Humann-Guilleminot et al., 2023; Anderson et al., 2023; Fuentes et al., 2023). Neonicotinoids are often used for seed coating, potential threatening granivorous species (Hladik et al., 2018) but they also have been detected in several non-granivorous species including insectivorous such as the Alpine swift (*Tachymarptis melba*), the honey buzzard (*Pernis apivorus*) and other higher predators such as the Montagu's harrier (*Circus pygargus*), the red kite (*Milvus milvus),* the barn owl (*Tyto alba*) and the Eurasian eagle-owl (*Bubo bubo*) (Taliansky-Chamudis et al., 2017; Byholm et al., 2018; Badry et al., 2021; Humann-Guilleminot et al., 2021; Fuentes et al., 2023).

4.3. Transfer between freshwater and terrestrial systems

Neonicotinoids insecticides were recently presented has a threat to riparian food webs as well. Several arthropod species display an aquatic larval stage (e.g., hemimetabolous species such as dragonflies and some holometabolous species like mosquitoes), and they leave during imaginal moult. Due to run-off from crops, contaminations are often detected in freshwaters worldwide (Morrissey et al., 2015; Stehle and Schulz, 2015; Stehle et al., 2018). In a recent study, higher concentrations of neonicotinoids were found in emerging arthropods and biomagnified in riparian spiders although their concentrations in water were low (Roodt et al., 2023). Although pesticides might reduce larval survival and thus the probability of becoming adults (Desneux et al., 2007), they may also favor relocating compounds from the aquatic larva to the terrestrial adult through metamorphosis (Kraus et al., 2014, 2021; Bundschuh et al., 2022), even for neonicotinoids (Roodt et al., 2023). Aquatic arthropods will thus emerge as adults with similar or higher concentrations of pesticides within their body, altering the quantity and the quality of these prey for terrestrial insectivores and becoming vectors of pesticides transfer to terrestrial food web (Kraus et al., 2014; Kraus, 2019; Roodt et al., 2023). The transfer of contaminants is thus possible between aquatic preys and their terrestrial predators or between terrestrial arthropods that developed in water as larvae and consumed as adults by terrestrial predators. Tree swallow nestlings and insectivorous bats are possibly exposed to a low to moderate daily exposure to neonicotinoids through the consumption of contaminated preys (Roodt et al., 2023). A non-negligible part of contaminants thus oscillates between freshwater and terrestrial ecosystems mediated by arthropods, but the study of this process seems to be quite neglected to date.

Vertebrates are susceptible to pesticides causing lethal or more silent sublethal effects (amphibians: Mann et al., 2009; reptiles: Fremlin et al., 2020; bats: Torquetti et al., 2021; birds: Moreau et al., 2022 for few examples of synthesis). The study of pesticides biomagnification in vertebrate predators under field conditions remains extremely complex

as several sources of contamination other than trophic interactions can be identified for arthropods and their predators in natural conditions. However, studies comparing granivorous to insectivorous mammal species indicate that the latter suffer higher pesticide loads which is in line with biomagnification processes (mice vs. shrew compared in the same habitat, Fritsch et al., 2022). A better understanding of the trophic links between vertebrate predators and their arthropod preys, for example using metabarcoding approaches to reveal the diet of arthropods, birds and other vertebrate predators in agricultural environments, will be crucial. Such a characterization of food webs in agricultural areas will help us gain visibility into the risk associated with the contamination of arthropods preys by pesticides and their bioaccumulation and biomagnification potential in vertebrate predators.

5. Impact factors of the transfer of pesticides in food webs

So far, research has mostly covered pesticide transfers in simplified bi-trophic food chains such as between preys-consumers (Tison et al., 2023), or tri-trophic food chains between primary producers, herbivores, and their predators (Fremlin et al., 2020). In real-world terrestrial ecosystems, food webs are highly complex, constituting networks of interactions between a high number of species or nodes. Food webs also operate across different compartments (above and below the ground), and across different ecosystems (e.g., linking aquatic and terrestrial ecosystems such as riparian food webs). Food web approaches are increasingly being developed in chemical risk assessment (Preziosi and Pastorok, 2008; Rohr et al., 2006). While studies have primarily focused on the impact of pesticides on food web structure, the latter can also strongly influence trophic transfers and biomagnification levels. Food web approaches could thus help to unravel context-dependent bioaccumulation and biomagnification patterns between different species, as well as between different ecosystems.

5.1. Species diet and trophic level

As mentioned above, species diet determines pesticide trophic transfers (Gall et al., 2015). Incorporating species trophic levels derived from food web approaches has provided important insights necessary to predict bioaccumulation and contaminant transfers (Borgå et al., 2012). For instance, in a stream food web, PCB concentrations measured in different species could be predicted by their trophic position (Walters et al., 2008). Trophic magnification factors (TMF) based on the slope of the regression between contaminant bioconcentration, and the trophic level of the organisms determined from stable N isotope ratios are now widely used to estimate biomagnification potential in food webs and to quantify food chain transport (Borgå et al., 2012). Currently, the application of TMFs in terrestrial food webs exposed to pesticides has been limited by the narrow range of trophic levels considered, as well as methodological limitations to quantify low levels of pesticides in terrestrial organisms, especially at low trophic levels (Fremlin et al., 2020). Nevertheless, such approaches could explain discrepancies between bioaccumulation patterns in different species within the same food web.

5.2. Food web structure

Different food webs can have distinct potentials to biomagnify pesticides. Comparing aquatic and terrestrial food webs exposed to different organic pollutants (Kelly et al., 2007) revealed that pollutants that did not biomagnify in aquatic food webs accumulated along a tri-trophic terrestrial food chain (lichen - caribou – wolf). These differences were due to differences in the partition coefficients of those substances in water vs. in the air. Similar results were observed in a recent study addressing a more complex terrestrial urban food web linking fruits, invertebrates and bird species exposed to organochlorine pesticides (Fremlin et al., 2020). While the compounds considered had no

bioaccumulative potential in aquatic food webs, concentrations increased with terrestrial species trophic position revealing significant biomagnification. Such differences in biomagnification between aquatic and terrestrial systems could also arise from their different trophic structure.

Few studies addressed how food web structure affects biomagnification (Windsor et al., 2020; Borgå et al., 2012). However, variations in pesticides levels in upper trophic levels between different ecosystems could be due to natural variation in their communities' trophic structure (Clements and Rohr, 2009; Clements and Newman, 2006). Studies have been restricted to small food webs, mainly aquatic, and to small range of organisms which limits our understanding of the variable relationships between bioaccumulation and biotic factors across different food webs (Windsor et al., 2018). This is now documented that relationship between food chain length and biomagnification has consequence for biodiversity restoration (Clements and Newman, 2006). The ecological characteristics and complexity of communities could thus influence pesticide transfers in terrestrial food webs (Rohr et al., 2006; Schiesari et al., 2018). Besides food chain length, other food web properties could play important roles, such as the number of nodes in a food web (e.g. species richness), network connectance (the proportion of realized trophic links relative to the total number of links between all nodes included in the food web), or modularity (groups of species having more interactions with each other than with other species in the food web). The distribution of trophic links could affect the ability of pesticides to propagate through different species in a food web. In a simulation study, modularity and species richness enhanced species persistence in communities exposed to bioaccumulative compounds (Garay-Narváez et al., 2014). Although based on simplistic assumptions (i.e., similar sensitivity across food web nodes), the model incorporated pollutant bioaccumulation and biomagnification processes as drivers of species extinctions. Empirical support for this was recently highlighted in riverine food webs linking basal resources to fish and birds, where connectance was positively related with the trophic magnification of persistent organic pollutants (Windsor et al., 2020). To our knowledge, no study demonstrated such relationships in the case of terrestrial food webs exposed to pesticides, but this could be an exciting avenue for future research.

5.3. Community structure and key species

The presence of key species in the food web can also affect trophic magnification. Several studies have documented the large impacts of top predators in aquatic systems. For instance, by feeding on invertebrates and regulating their populations, the presence of a top fish predator strongly reduced mercury exports from ponds to terrestrial systems mediated by dragonflies and damselflies contaminated with mercury through dietary exposure (Schiesari et al., 2018; Tweedy et al., 2013). Similarly, the presence of a piscivorous fish reduced trophic transfers of mercury from invertebrates to fish, by reducing the abundance of other fish species, leading to a greater biomass of macroinvertebrates (Wong et al., 1997). The extent to which the results from such case studies can be transferred to terrestrial food webs exposed to pesticides remain to be investigated, but they illustrate the importance of accounting for community structure to better understand the trophic transfers of contaminants.

Finally, the strength of trophic interactions within food webs can have important implications. Species diet may change over time and space, affecting the strength of trophic links between consumers and their preys. Temporal variation in pesticides bioaccumulation from plants to fungi to large herbivores (white-tailed deer) were linked to seasonal shifts in the diet of those herbivores (Li, 2020). Using uptake models and toxicokinetic models, the study found that higher intake rate in the summer explained the observed higher pesticide bioaccumulation factors in white-tailed deer compared to other seasons. Those results imply that opportunistic species could bioaccumulate differently depending on prey availability. The presence of such omnivores in food webs could then generate important variability on trophic magnification to upper trophic levels over time, or across different sites.

Community and food web structure could thus have important implications for pesticide trophic transfers in terrestrial food webs, but our literature review highlights that this is currently understudied. Methodological and conceptual limitations may explain this knowledge gap. Indeed, quantifying pesticides in complex terrestrial food web is challenging due to detection limits, as well as cost limitations (Fremlin et al., 2020). The fact that ecotoxicology rarely incorporates community ecology and food web theories, and often focus on individual and population levels could further explain the lack of studies (Rohr et al., 2006; Schiesari et al., 2018; Beaumelle et al., 2021). However, quantifying the influence of trophic structure of pesticide trophic transfers could help to achieve more accurate predictions by addressing several important sources of variability in bioaccumulation and biomagnification factors across species and food webs. Furthermore, such studies would bring crucial insights into the potential synergistic effects between biodiversity loss and pesticide effects in terrestrial ecosystems.

6. Conclusion

Our review of the growing corpus of literature on pesticides transfer, bioaccumulation, and biomagnification in terrestrial food webs with arthropods being the primary consumers and entry point of pesticides into food webs reveals important insights into the complexity of those processes, as well as the technical limitations for analyzing residues in arthropods. Fig. 1 represents the transfer of pesticides in terrestrial food webs and summarizes identified directions for future scientific research. Future developments in analytical methods able to quantifiy pesticides in small arthropods, single individuals and different body parts will be crucial to improve our knowledge on the transfer and bioaccumulation potential of pesticides between preys and their predators.

Our findings highlight that sublethal doses probably represent a critical point in biomagnification processes that should receive future attention. The reviewed literature also shows that pesticides can strongly affect a variety of life history traits (immune system, mobility and migration, metamorphosis, predation) that can profoundly alter the transfer and bioaccumulation in upper trophic levels. This has important implication, as most biocontrol methods used in agriculture to reduce the use of pesticides are based on the consumption of pests by predatory arthropods, which are themselves consumed by small mammals and birds. The contamination of the first trophic levels in a food web will be an important first step potentially leading to biomagnification in upper trophic levels. Biocontrol methods based on pest control by predators or parasitoids should thus consider bioaccumulation and pesticide transfers patterns. Research studies involving pesticides that are currently-used is limited. The range of molecules used for crop protection is also in perpetual evolution, from active substances to co-formulants that make active substances more active and arthropods more susceptible, but little is known about their influence on the bioaccumulation and biomagnification patterns and their effects through the food webs.

Incorporating community and food web structures in ecotoxicological studies could also provide important insights. The food chain length, number of nodes, network connectance or modularity of a food web, may play an important role in the transfer and biomagnification of pesticides in foods web and need further attention from the research community.
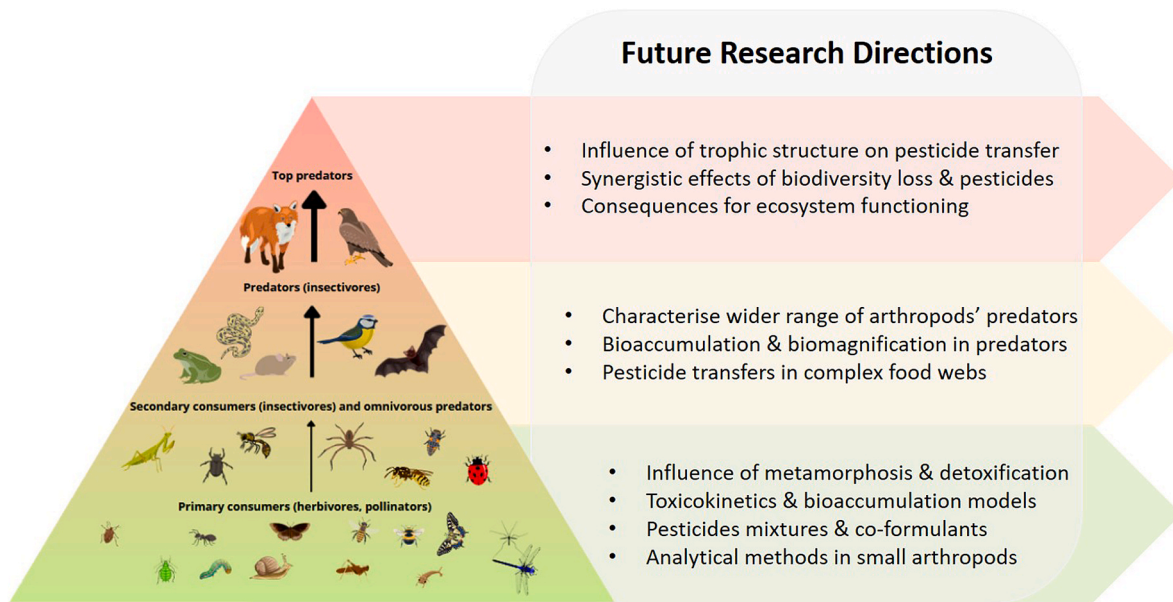
Fig. 1. Trophic transfer of pesticides in terrestrial food webs and identified future directions for scientific research.

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CRediT authorship contribution statement

Léa Tison: Writing – review & editing, Writing – original draft, Supervision, Investigation, Funding acquisition, Conceptualization. **Léa Beaumelle:** Writing – review & editing, Writing – original draft, Conceptualization. **Karine Monceau:** Writing – review & editing, Writing – original draft, Conceptualization. **Denis Thiéry:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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