




Induction of plant defenses: the added value of zoophytophagous predators

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Abstract

Several biological control agents of the hemipteran insect families Miridae, Anthocoridae and Pentatomidae, as well as mites of the family Phytoseiidae are known as zoophytophagous predators, a subset of omnivores, which are primarily predaceous but also feed on plants. It has been recently demonstrated that zoophytophagous predators are capable of inducing defenses in plants through their phytophagy. Despite the vast fundamental knowledge on plant defense mechanisms in response to herbivores, our understanding of defense induction by zoophytophagous predators and applied implications is relatively poor. In this review, we present the physiological basis of the defense mechanisms that these predators activate in plants. Current knowledge on zoophytophagous predator-induced plant defenses is summarized by groups and species for the predators of economic importance. Within each group, feeding habits and the effects of their induced-plant defenses on pests and natural enemies are detailed. Also, the ecological implications of how the induction of defenses mediated by zoophytophagous predators can interact with other plant interactors such as beneficial soil microorganisms and plant viruses are addressed. Based on the above, we propose three approaches to exploit zoophytophagous predator-induced defenses in crop protection and to guide future research. These include using predators as vaccination agents, employing biotechnological approaches, as well as applying elicitors to elicit/mimic predator-induced defenses.

Keywords Phytophagy · Omnivory · Volatiles · Plant resistance · Biological control · Defense elicitors

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Key Message

- Zoophytophagous predators elicit plant defenses similar to those induced against herbivores.
- Predator-induced plant defenses could be exploited in sustainable crop protection.
- Understanding mechanisms underlying these defenses is crucial for novel pest control tools.
- Ecological implications of plant defense induction by predators should be also considered.

Introduction

In recent years, the use of omnivorous natural enemies in horticultural crops, in particular, zoophytophagous predators has given rise to some of the most resounding successes of biological control (van Lenteren et al. 2018). This success has been mainly attributed to their efficient predation on a wide range of important pests and to their phytophagy (Wheeler 2001), which allows them to survive in periods of prey scarcity and to establish before pest appearance (Pérez-Hedo et al. 2021d; van Lenteren et al. 2020). The most well-known cases occur in horticultural greenhouse crops, but zoophytophagous predators are also key players in perennial outdoor crops.

Omnivorous predators are defined as consumers of more than one trophic level. True omnivores feed on both plant and prey (Coll and Guershon 2002). Here, we use the term ‘omnivore’ for predators that actively feed on living plant tissue and prey, which are also defined as ‘zoophytophagous’ predators. ‘Generalist’ predators are defined here as predators that can sustain their development, survival, and reproduction with a suite of arthropod pest species belonging to different families. They usually can also feed on nectar and/or pollen (Symondson et al. 2002).

In horticultural crops, zoophytophagous predators are managed mainly through augmentative biological control, where natural enemies are mass-reared for periodic releases (van Lenteren et al. 2020). The two paradigmatic crops that use zoophytophagous predators as a basis for pest control are sweet pepper and tomato. In sweet pepper, the release and conservation of the predatory mite *Amblyseius swirskii* (Athias-Henriot) (Acari: Phytoseiidae), together with the anthocorid *Orius laevigatus* (Fieber) (Hemiptera: Anthocoridae), successfully suppress the populations of the key pests of this crop: the whitefly *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) and the thrips *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (Calvo et al. 2012b). In recent years, the use of predatory mirids (Hemiptera: Miridae) is being promoted in sweet pepper.

These mirids can, in addition to attacking *B. tabaci* and *F. occidentalis*, regulate aphid populations, that are beyond the control exerted by the use of *A. swirskii* together with *O. laevigatus* (Bouagga et al. 2018a; Brenard et al. 2020). The combination of the zoophytophagous predators *O. laevigatus* and *M. pygmaeus* gives excellent control of both thrips and aphids in sweet pepper crops (Messelink and Janssen 2014). Moreover, in combination with leaf pruning, *M. pygmaeus* proved successful at controlling aphid populations in commercial sweet pepper crops (Brenard et al. 2020). In tomato, the release of the predatory mirid, *Nesidiocoris tenuis* (Reuter) enables the effective control of *B. tabaci* and the South American tomato pinworm *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) in the Mediterranean basin (Biondi et al. 2018; Calvo et al. 2012c; Kocourek et al. 2021), whereas the release of *Macrolophus pygmaeus* Rambur effectively controls populations of *B. tabaci* and *T. absoluta* in greenhouse tomato (Bompard et al. 2013; Jaworski et al. 2015; Zappalà et al. 2013).

In perennial outdoor crops, the use of zoophytophagous predators is mainly managed through conservation biological control. As in horticultural crops, the phytophagy of these natural enemies allows them to remain in the crop in periods of prey scarcity. Historically, the conservation of these predators had been achieved by using selective pesticides (Bostanian et al. 2000; Bouvet et al. 2019; Mansour et al. 2021). At present, alternative sustainable strategies have been also promoted to enhance the conservation of these predators, such as the implementation of ecological infrastructures (i.e., cover crops) (Álvarez et al. 2021; Horton et al. 2003) or the addition of supplementary foods (Beltrà et al. 2017).

Recent works have shown that several species of zoophytophagous predators used in biological pest control are able, due to their phytophagy, to activate the same defense mechanisms triggered by herbivorous arthropods (Halitschke et al. 2011; Kessler and Baldwin 2004; Pappas et al. 2015; Pérez-Hedo et al. 2015a; Zhang et al. 2018). These inducible defenses mediated by zoophytophagous predators are valuable and if properly managed could offer an excellent tool to increase crop resilience. Here, we review the current literature on plant defense induction by these predators and its implications for biological control (Fig. 1) by (1) providing an overview of plant defense to herbivory, (2) discussing the ways zoophytophagous predators such as mirid bugs, anthocorids, pentatomids and phytoseiid mites (here not referring to other omnivores such as thrips that are mainly considered as pests (Trichilo and Leigh 1986)) may protect plants not only directly but also indirectly via the elicitation of plant defenses, (3) briefly exploring current knowledge on the implications of plant defense induction by predators in a multitrophic context with a special focus on beneficial microorganisms and plant viruses, and finally, (4)

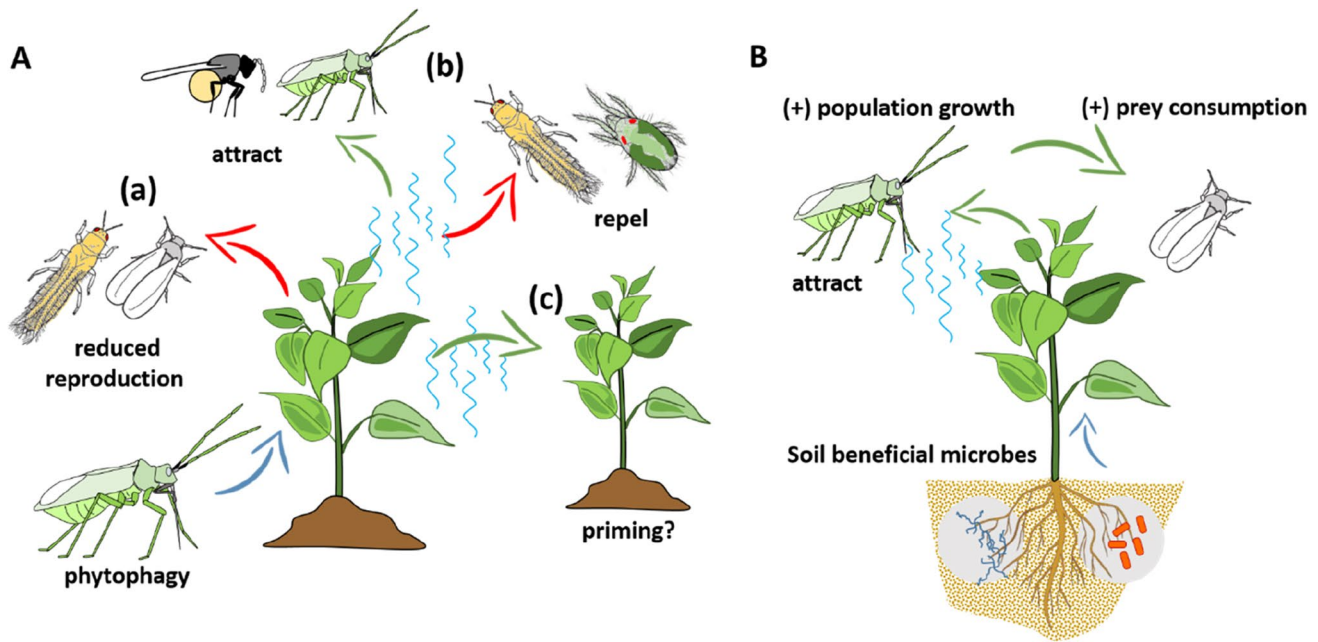


Fig. 1 Implications of plant defense induction by zoophytophagous predators on pest control. Zoophytophagous predators induce plant defenses via their phytophagy resulting in the emission of volatiles or the transcription of defense-related genes. **A** These responses can exert plant protection effects via impacting herbivore performance (a), repelling arthropod pests or attracting their natural enemies (b), or via activating induced-defenses in neighboring plants against

future attackers (c). **B** Beneficial soil microbes can impact zoophytophagous predator performance positively, to increase the attractiveness of inoculated plants to predators or enhance their consumption with prey over phytophagy. Although few such positive interactions (in terms of plant protection) have been studied so far, they should be considered in future studies aiming at the development of innovative tools in sustainable pest control

presenting our views on the future exploitation of predator-induced defenses in crop protection.

Plant defenses in response to herbivory

Upon herbivory, plants activate the production of signaling molecules that upregulate the biosynthesis of specific compounds (Kant et al. 2015; Karban and Baldwin 1997). These compounds can act directly against herbivores by reducing their growth, survival, or reproductive rate (Howe and Jander 2008; Kant et al. 2015), referring to as direct plant defenses. Moreover, they can be expressed locally at the damage site, and signals can be produced and transmitted systemically to undamaged plant parts. Subsequently, plant defenses can be induced or primed in those sites, providing resistance to future herbivore attacks (Conrath et al. 2015; Heil and Ton 2008; Howe and Jander 2008; Karban and Baldwin 1997). Depending on the herbivore species and time since attack, defenses may differ qualitatively and quantitatively (De Vos et al. 2005; Kant et al. 2004; Rodriguez-Saona et al. 2010). Phytohormones play important roles in regulating induced defenses, among which the most important ones are jasmonic acid (JA), salicylic acid (SA), and ethylene (Erb et al. 2012; Pieterse et al. 2012). Moreover, different

defense pathways can be antagonistic and synergistic to each other (Koornneef and Pieterse 2008). Although the number of studies that refer to the induction of direct defenses with zoophytophagous predators is still scarce compared to those carried out with strict herbivores, it seems that plants respond similarly activating the same defensive machinery, but differentially depending on the predator species, as will be described in the next sections.

Plants can also recruit natural enemies to reduce herbivore damage, referring to as indirect plant defenses (Dicke and Sabelis 1989; Karban and Baldwin 1997; Sabelis et al. 2001). Following herbivory, they release a plethora of volatile compounds known as Herbivore-Induced Plant Volatiles (HIPVs). These can activate defense responses in distal parts of the attacked plant, trigger defenses in neighboring plants, and also attract beneficial organisms, such as predators and parasitoids. Among volatiles released, there are three main characterized groups of secondary metabolites: (1) the green leaf volatiles (GLVs) mostly short-chain aliphatic alcohols, esters, and aldehydes (Ameye et al. 2018), (2) aromatic compounds such as benzene and indole derivatives (Dudareva et al. 2004; Erb et al. 2015) and (3) terpenoids (Arimura et al. 2002). These compounds are released and perceived differently by plants, herbivorous arthropods, and their natural enemies. Moreover, growing evidence suggests

that indirect defenses may also happen through microbiota recruitment triggering effective defenses against herbivores (Gruden et al. 2020). As regards the role of zoophytophagous arthropods in the elicitation of indirect plant defenses, there are two different aspects to consider: those responses triggered in the plant by the phytophagy of zoophytophagous predators leading to indirect defenses, as well as responses produced following herbivory from purely phytophagous species that lead to attracting zoophytophagous predators.

Volatiles are not only effective by attracting natural enemies but can be primed for enhanced resistance without fitness costs (van Hulten et al. 2006). Defense priming is an adaptive immune response that prepares plants to respond faster and stronger to a forthcoming stress (Mauch-Mani et al. 2017; Wilkinson et al. 2019). Different stimuli as a consequence of the interaction between a plant and an arthropod can trigger systemic-induced resistance (De Kesel et al. 2021). These stimuli may be responsible for priming, which can be expressed in distal tissues or neighboring plants (Mauch-Mani et al. 2017). Besides, plant genotypes and mutants with specific blocked genes may display constitutive priming at no fitness costs (Agut et al. 2016; Blanc et al. 2018; Camañes et al. 2012; van Hulten et al. 2006). The GLV (Z)-3 hexenyl propionate was shown to display a strong repellent effect against whiteflies when applied in dispensers without any apparent fitness cost (Pérez-Hedo et al. 2021b; Pérez-Hedo et al. 2021d). Whether zoophytophagous predators can induce plant defense priming and if there is any fitness cost involved, is not studied yet. This could relate to plants' sensitization against future attackers via volatiles release or stronger direct responses against forthcoming herbivores.

Plant defense induction by zoophytophagous predators

Predatory mite-induced plant defenses

Predatory mites of the family Phytoseiidae comprise an important group of biological control agents of key insect and mite pest species. More than twenty species of the family are commercially available and used mainly in vegetable and ornamental greenhouse crops to combat spider mites, thrips, and whiteflies (van Lenteren et al. 2018). The feeding habits of phytoseiids are quite diverse, ranging from strict monophagy of specialist spider mite predators (i.e., *Phytoseiulus persimilis*) to polyphagy of generalists [among others, *Amblyseius swirskii*, *Neoseiulus californicus*, *Iphiseius degenerans* (Berlese) and species of the genus *Euseius*] (McMurtry et al. 2013). In a comprehensive review, phytoseiids had been allocated in four trophic groups/types based on their nutritional ecology and feeding habits (McMurtry

and Croft 1997; McMurtry et al. 2013). Two of the latter groups (type III-generalists and type IV-pollen feeding generalists) include species that consume prey and also plant-derived foods, mainly pollen and in some cases even plant cell sap. The latter, being able to pierce plant cells and actively consume plant cell sap are characterized as zoophytophagous predators, supplementing prey consumption with herbivory. With the use of dyes, radioactive isotopes and systemic insecticides, plant sap-feeding has been proven indirectly since the early '60 s; however, the mechanisms underlying this behavior were still not known (Chant 1959; Cruz-Miralles et al. 2021b; Magalhães and Bakker 2002). Only during the last decade, with the use of scanning electron microscopy, generalist phytoseiids such as *Euseius scutalis* (Athias-Henriot) and *I. degenerans* were shown to be able to disrupt the walls of epidermal leaf cells with their chelicera (Adar et al. 2012, 2015). Such plant feeding behavior of phytoseiids has not been directly related to any measurable plant damage or even symptoms with the only possible exception of *Typhlodromus pyri* (Scheuten) plant feeding which was related to visible scars on apple leaves and fruits (Sengonca et al. 2004). Plant cell sap-feeding provides predators access to water and plant-derived nutrients, which supplements their prey diet, and possibly extends their survival and presence on plants during periods of prey scarcity or when pollen is not available (Magalhães and Bakker 2002). In this context, plant feeding by phytoseiids may enhance their efficacy in biological control. Recent studies in citrus revealed that the phytoseiid *Euseius stipulatus* (Athias-Henriot) (Acari: Phytoseiidae) can feed on at least two citrus species: sour orange (*Citrus aurantium*) and Cleopatra mandarin (*Citrus reshni*) (Cruz-Miralles et al. 2021b). *Euseius stipulatus* triggered genotype-dependent responses similar to those elicited by the phytophagous mite *T. urticae* (Agut et al. 2014; Cabedo-López et al. 2019). The JA, SA, and flavonoids defensive pathways were upregulated in sour orange after exposure to the predator, whereas Cleopatra mandarin upregulated the JA pathway only (Cruz-Miralles et al. 2019). Differences were also observed in the volatile blends induced by *E. stipulatus*, which interestingly did not prevent *T. urticae*, a potential prey for *E. stipulatus*, from choosing *E. stipulatus*-infested plants. Although phytophagy prevails as the most likely trigger for these responses, recent studies have shown that *N. californicus*, which co-occurs in citrus with *E. stipulatus* but does not feed on plant cell sap (Cruz-Miralles et al. 2021a) can also induce genotype-specific defense responses in the same citrus species (Cruz-Miralles et al. 2021b). In this case, the JA and flavonoids defensive pathways were downregulated in sour orange whereas the JA was upregulated in Cleopatra mandarin. Changes in the volatile blends produced by plants infested with *N. californicus* were also observed. However, in this case, both sour orange and Cleopatra mandarin HIPVs proved repellent

for the shared prey, *T. urticae*. Cineol was the only common component of the volatile blends induced by these two phytoseiids in the two citrus species, whereas infestation by *E. stipulatus* decreased the emission of this compound (Cruz-Miralles et al. 2019), that of *N. californicus* increased it (Cruz-Miralles et al. 2021b). This terpenoid may play a crucial role in the ambulatory decisions of *T. urticae* and deserves further studies. The fact that *N. californicus* does not feed on plant cell sap opens new questions about the actual trigger of the observed responses in phytoseiids, which could be different from or additional to phytophagy. Other triggers, including oviposition, excretion, and walking have been described for insects (Hilker and Meiners 2010; Hilker and Fatouros 2015; Schuman and Baldwin 2016; Wu and Baldwin 2010). Because phytoseiids lack a specialized ovipositor, mechanical damage to plant tissues during oviposition can be discarded as a trigger. Therefore, touch and touch-associated secretions (i.e., oviposition fluids, frass) should be further investigated. Cruz-Miralles et al. (2021b) included in their studies the phytoseiid, *P. persimilis*, which co-occurs in citrus with *E. stipulatus* and *N. californicus*. This specialist, which does not feed on plants (Cruz-Miralles et al. 2021a; Magalhães and Bakker 2002) did not trigger any defense response in citrus. Because there are conspicuous differences in the (Okassa et al. 2010)morphology, size, and chaetotaxy of *P. persimilis* legs compared to those of the other two predators (Athias-Henriot 1960; Beaulieu and Beard 2018; Croft et al. 1999), that allow this predator to smoothly penetrate *T. urticae* dense webs (Sabelis and Bakker 1992), touch should be further investigated as it could be the trigger for the observed responses. Likewise, oviposition, excretion, and secretions related to these activities deserve attention.

Overall, the results obtained so far demonstrate that plant defense responses triggered by phytoseiids are species-specific, depend on plant genotype, and may not be exclusively related to direct plant feeding (Cruz-Miralles et al. 2019, 2021a, b). Studies aimed at disentangling the mechanisms responsible for these responses and whether they occur in other important crops are needed. These studies could pave the way for more efficient use of direct and indirect plant defenses to protect our crops.

Anthocorid-induced plant defenses

Many species belonging to the Anthocoridae family such as the genera *Orius* and *Anthocoris* (Hemiptera: Anthocoridae) are considered important beneficial insects in various agroecosystems (van Lenteren et al. 2018). In Europe and North America, natural populations of anthocorid species, such as the Palearctic *O. laevigatus* (Fieber), *Orius niger* (Wolff) and *O. majusculus* (Reuter) or the Nearctic *O. insidiosus* (Say), are abundant and often effective in suppressing thrips

infestations in their native ranges (Desneux et al. 2006; Harwood et al. 2007). Another anthocorid predator *Anthocoris nemorum* (Linnaeus) is one of the most efficient and abundant predators that suppress the leaf beetle *Phratora vulgatissima* (Linnaeus) (Coleoptera: Chrysomelidae), in willow cropping systems (*Salix* spp.) (Björkman et al. 2003), where this beetle is a key pest. Various *Orius* spp., such as *O. laevigatus*, are nowadays mass-reared and augmentatively released in horticultural and ornamental greenhouse crops. Anthocorids are considered omnivores. Although many species are primarily prey-feeders, they also feed on plant resources (i.e., pollen, nectar, and plant juices). For instance, *O. insidiosus* adults can feed on xylem and mesophyll contents, consisting of mostly water with small amounts of sugars, starch, and amino acids (Armer et al. 1998), whereas nymphs are also able to feed on the nutritious phloem. The plant-feeding of *O. insidiosus* allows its survival for several days and facilitates the population establishment during prey shortage (Lundgren et al. 2008).

Unlike certain predatory mirids, the plant feeding by *Orius* spp. is considered safe for the plant. Given the apparent lack of damage on plants exposed to *Orius* spp. and growers not having reported effects on plant growth, less attention was paid to the direct interaction between *Orius* spp. and plants and the consequences for plant performance. The feeding behavior of *O. laevigatus* on sweet pepper plants has been recently assessed in comparison to other relevant behaviors (Bouagga et al. 2018c). The predator was observed to spend almost 40% of its lifetime on plant feeding, mainly on apical meristems and apical fresh leaves, which are also its favorite residence locations. The same authors highlighted for the first time that plant feeding by *O. laevigatus* induces plant defenses in sweet pepper. Responding to this phytophagy, plants upregulated the JA and SA pathways and increased the emission of HIPVs. These volatile blends differed quantitatively between activated and non-activated plants, therefore, orchestrating the insect's host plant choice. *Frankliniella occidentalis* and *B. tabaci* preferred less the activated plants over *O. laevigatus*-induced plants. Furthermore, oviposition by *O. laevigatus* can upregulate the JA-mediated wound response that increases tomato plant resistance to *F. occidentalis* (de Puyssseleir et al. 2011). Thereby, in accordance with the dual role that many omnivorous predators play, *Orius* bugs may also impose positive effects on host plants by consuming detrimental herbivores and, inducing plant defenses. Altogether, these results reinforce and explain the potential use of *Orius* spp. and should be further explored to develop new approaches for pest management.

Evidence from systems other than greenhouse crops suggests that other species of zoophytophagous predators can suppress pests through plant-mediated effects (e.g., induced-defenses). For example, the omnivorous predator *A.*

nemorum cannot only prey on eggs of the willow leaf beetle *P. vulgatissima*, but also decrease the prey's egg clutch size through non-consumptive effects (i.e., predator effects that are not related to prey consumption) (Stephan et al. 2017). On willow plants that are less suitable for the predator bug, non-consumptive effects are between one-third and twice as strong as the consumptive effects (Stephan et al. 2017). In the same plant system (willow), another omnivorous predator (*Orthotylus marginalis* Reuter) can reduce leaf damage caused by leaf beetles through predation, but its plant feeding had detrimental effects on plant growth (Puentes et al. 2018). The simultaneous damage effects by this predator and prey were additive and more detrimental than individual effects. Further research is needed to investigate whether plant feeding by omnivorous predators in other systems (e.g., perennial plant systems) can induce plant defenses that contribute to the reduced performance of their herbivore prey.

Pentatomid-induced plant defenses

Another group of natural enemies that can feed on plants is predatory stinkbugs (Hemiptera: Pentatomidae) of the subfamily Asopinae. These are mainly recognized as generalist predators, attacking a wide array of prey in diverse habitats (Conti et al. 2021; De Clercq 2005). Predatory stinkbugs attack mainly slow-moving, soft-bodied insects, primarily larval forms of the Lepidoptera, Coleoptera, and Hymenoptera. They feed by inserting their stylets into the body of the prey and injecting toxins, enzymes, or both before sucking prey tissues (De Clercq 2005; Fialho et al. 2012). Furthermore, these insects can feed on plant sap during times of prey shortage (Coll and Guershon 2002; Zeng and Cohen 2000), obtaining nutrients mainly from plant xylem (Torres et al. 2010). This zoophytophagous behavior can reduce the duration of the nymphal stage, increase nymphal survival and longevity, and fecundity of the adults (Holtz et al. 2009; Lambert 2007). Such flexibility in their feeding habits probably helps predator maintenance when prey are scarce, allowing their existence in areas subjected to prey fluctuation, such as in annual agricultural crops thus favoring their use as biocontrol agents in these conditions (Pires et al. 2015). In contrast to other zoophytophagous predators, plant-feeding asopines have not been reported to injure plants (De Clercq 2005).

Investigation on this predatory group was intensively conducted with main focus on the biology, physiology, biological control, ecology, systematics and morphology, toxicology, and mass rearing methods (Pires et al. 2015), while less attention was given to the impact of their phytophagy on triggering induced defense. Only recently Martorana et al. (2019) observed that feeding and oviposition by *Podisus maculiventris* (Say) induced the emission of VOCs in *Vicia faba* L. (Fabaceae), attracting the egg parasitoid,

Telenomus podisi (Ashmead) (Hymenoptera: Scelionidae). Interestingly, both *T. podisi* and *Trissolcus basalis* (Wollaston) showed specificity in their response to VOCs emitted by infested plants, as neither species were attracted by plants on which the exotic *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae) had fed and oviposited (Martorana et al. 2017; Rondoni et al. 2017). This lack of response, probably due to the absence of a history of coevolution between the interacting species, might allow egg parasitoids to optimize their time and energy by exploiting cues only from suitable hosts (Martorana et al. 2017, 2019). Apart from inducing plant defenses, *P. maculiventris* may adapt its behavior and physiological traits to the host plant. Lifetime development, growth, fecundity, and preference were negatively affected on tomato plants with overexpression of MeSA (Thaler et al. 2015). Also, its predation rate on *Manduca sexta* (L.) (Lepidoptera: Sphingidae) caterpillars was lower than expected, indicating that *P. maculiventris* are adversely affected by JA-induced defenses (Kaplan and Thaler 2010).

To the best of our knowledge, no other study emphasized induced plant defenses by zoophytophagous stinkbugs. In fact, *P. maculiventris* studied by Martorana et al. (2019) is the only asopine that has been commercially available for augmentative biological control of tomato and cotton pests in North America (De Clercq 2005). Another possible reason is probably the absence of visible damage by predatory stinkbugs that prompt studying plant defense induction. For instance, the feeding site of *P. nigrispinus* Dallas and *Brontocoris tabidus* Signoret (Hemiptera: Pentatomidae) on cotton plants, revealed that both stinkbugs do not cause damage to plant cells, neither reach the plant cell cytoplasm nor trigger mechanical plant damage (Torres et al. 2010). Hence, they do seem not to harm the host plants, and are not able to use the content of the cell cytoplasm as a dietary supply. Further studies are needed to emphasize plant defense induction by pentatomid predatory bugs, support or claim this approach.

Mirid-induced defenses

The interest in mirid bugs has increased considerably and many researchers emphasize their importance in agroecosystems (reviewed by Pérez-Hedo et al. 2021d; Puentes et al. 2018; van Lenteren et al. 2020). Insects belonging to this family are polyphagous following a feeding habit that ranges from phytozoophagy (prey-feeding herbivores) to zoophytophagy (plant-feeding carnivores). Thus both, plants (aerial part, vascular tissues, pollen, and nectar) and arthropod prey may comprise mirid diets (Wheeler 2001). Zoophytophagous species feed on both prey and plant during the same developmental stage. Within zoophytophagous species, many generalist predators such as *N. tenuis* and *M. pygmaeus*

are biological control agents in tomato (Pérez-Hedo et al. 2021d). Their ability to switch between zoophagy and phytophagy can boost their establishment and sustain population densities.

Mirids are cell rupture feeders which consist of lacerating the plant tissue by stylet movement, then injecting watery saliva around cells. A pocket of diluted cells is eventually formed and ingestion starts (Chinchilla-Ramírez et al. 2021). Plant feeding has well-documented positive effects on the development, longevity, and fecundity of zoophytophagous predators, resulting in larger populations and stronger herbivore suppression (Castañé et al. 2011; Sánchez and Lacasa 2008). Plant feeding by zoophytophagous predators is also assumed to provide them with some crucial resources that facilitate prey consumption. When consuming prey, some mirid predators require a source of water to dilute the digestive enzymes they inject into their prey. Also, plant feeding may allow mirid predators to balance nutrients, proteins, carbohydrates, vitamins, and minerals that would otherwise be restricted in a carnivorous diet (Coll and Guershon 2002). These and results from other studies suggest that phytophagy is essential rather than being occasional in mirids (Gillespie and McGregor 2000; Portillo et al. 2012).

These feeding habits can also result in plant damage which is often the result of complex interactions between the morphological, physiological, and behavioral traits of the mirid species, prey availability, cultivar, and certain environmental factors (Arnó et al. 2010; Castañé et al. 2011; Sanchez 2008; Siscaro et al. 2019). The mechanisms that underlie phytophagy by zoophytophagous predators are not completely understood and all previous works focus

on studying the relation between factors that prompt damage (Chinchilla-Ramírez et al. 2020; Moerkens et al. 2020; Pérez-Hedo and Urbaneja 2016). The consequences of the feeding habits of mirid predators are more profound than inducing visible injuries. Indeed, zoophytophagous predators that cause limited or no visible damage when feeding on plants do nevertheless induce plant defenses (Pappas et al. 2015; Pérez-Hedo et al. 2015b; Zhang et al. 2018). As described below in the following sections, this newly highlighted finding on induction of plant defenses may have been underestimated in their contribution to pest management.

Nesidiocoris tenuis. Plant feeding by *N. tenuis* has been shown to activate different defensive hormonal pathways such as the abscisic acid (ABA), SA, and JA signaling pathways in tomato and sweet pepper plants (Bouagga et al. 2018b; Pérez-Hedo et al. 2015b). Their activation has been proven to influence the performance of various herbivorous pests and natural enemies.

Specifically, the phytophagy of *N. tenuis* in tomato activates the ABA and JA pathways, making them less attractive to the whitefly *B. tabaci* and more attractive to the whitefly parasitoid *Encarsia formosa* (Gahan) (Hymenoptera: Aphelinidae) (Pérez-Hedo et al. 2015b). In addition, the volatiles emitted by the plants punctured by *N. tenuis* induce defenses in intact neighboring plants by activating the JA pathway. This induction also results in the attraction of parasitoids by those intact plants not exposed to *N. tenuis* direct contact. All developmental stages of *N. tenuis* (from young nymphs to adults) can trigger these defensive responses (Naselli et al. 2016). The volatiles (HIPVs) involved in these defensive responses in *N. tenuis* induced-tomato plants have

Table 1 Main plant volatiles triggered by the phytophagy of the mirid predator *Nesidiocoris tenuis* on sweet pepper and tomato plants. Sources: Bouagga et al. (2018b) and Pérez-Hedo et al. (2018b)

Type	Compound	Tomato	Sweet pepper
Monoterpenoids	Linalool		x
	Monoterpene		x
Sesquiterpenoids	Sesquiterpene		x
	(E)-nerolidol		x
	Sesquiterpenoid		x
Norisoprenoids	Unknown ²		x
Green leaf volatile esters	Hexyl butanoate	X	
	1-hexanol	X	
	(Z)-3-hexenol	X	x
	(Z)-3-hexenyl acetate	X	x
	(Z)-3-hexenyl propanoate	X	x
	(Z)-3-hexenyl butanoate	X	x
	(Z)-3-hexenyl 3-methylbutanoate		x
	(Z)-3-hexenyl benzoate		x
Systemic acquired resistance (SAR)	Methyl salicylate	X	x

Volatile compounds were collected using solid-phase microextraction (SPME) and separated and detected using gas chromatography coupled to mass spectrometry (GC/MS). Volatiles were adsorbed in a PDMS/DVB SPME fiber (polydimethylsiloxane/divinylbenzene)

been identified (Pérez-Hedo et al. 2018b): six GLVs and methyl salicylate (MeSA) (Table 1). These HIPVs tested individually demonstrated not only the induction of indirect defenses by being attractive to the parasitoid *E. formosa*, but also a direct effect by repelling the whitefly *B. tabaci* (Pérez-Hedo et al. 2018b).

Apart from the direct and indirect induction of defenses mediated by the emission of HIPVs, the phytophagy of *N. tenuis* also triggers direct defenses in tomato. The transcription of the plant protein inhibitor II (*PI-II*) is higher on *N. tenuis*-induced plants compared to control plants (Pérez-Hedo et al. 2018a). This higher concentration of PI results in reduced performance of *T. urticae* by 35% on plants previously activated by *N. tenuis* compared to the performance on control plants. Recent studies suggest that the induction of direct defenses could also reduce the survival of other tomato key pests, such as *B. tabaci* and *T. absoluta* (Pérez-Hedo, M.; unpublished results). Therefore, taking together all these observations, the ability of *N. tenuis* to induce direct and indirect defenses in tomato may contribute to the great success achieved by *N. tenuis* as a key biocontrol agent in this crop in the South-western Mediterranean basin (Pérez-Hedo et al. 2021d; van Lenteren et al. 2020).

In sweet pepper, the feeding punctures by *N. tenuis* increase the ABA, SA, and JA signaling pathways (Bouagga et al. 2018a), and also trigger the release of a blend of HIPVs (Table 1). These HIPVs repel the herbivorous pests *F. occidentalis* and attract the whitefly parasitoid *E. formosa*. Bouagga et al. (2018a) also demonstrated that *B. tabaci* and *F. occidentalis* were both less likely to thrive on *N. tenuis*-punctured plants than on intact plants. These authors hypothesized that this lower density might be a consequence of direct defense induction mediated by *N. tenuis* activity that increased the content on JA, hence acting as a feeding deterrent for arthropod pests. Interestingly, the phytophagous behavior of *N. tenuis* on sweet pepper plants limits the accumulation of one of the most important widespread plant viruses, the *Tomato Spotted Wilt Virus* (TSWV) (Bouagga et al. 2020). RT-qPCR revealed that 3 weeks after the mechanical inoculation of TSWV, the number of RNA copies in mirid-punctured plants was significantly lower in comparison to intact plants. These authors showed that the upregulation of the JA pathway triggered by *N. tenuis* phytophagy could explain the observed effects on TSWV. Therefore, it seems that the phytophagy of *N. tenuis* also activates direct defenses in sweet pepper. However, further research is needed to elucidate the exact nature of *N. tenuis*-induced direct defenses in sweet pepper.

Macrolophus pygmaeus. Plant defense induction has also been shown for *M. pygmaeus*. As with *N. tenuis*, plant feeding by *M. pygmaeus* on tomato and pepper plants induces plant defense responses that can affect the performance of herbivorous pests and eventually the efficiency of biological

control (Bouagga et al. 2018b; Pappas et al. 2015; Zhang et al. 2018). In tomato, prior exposure of plants to *M. pygmaeus* individuals (either nymphs or female adults) for 4 days resulted in a significant decrease in the number of eggs laid by spider mite females (Pappas et al. 2015), as well as feeding damage on these plants compared to control plants (Pappas et al. 2016). Importantly, these negative effects were still displayed 14 days after exposure to the predators suggesting the existence of long-term effects of predator phytophagy on the tomato immune system. In addition, the decreased performance of spider mites on tomato plants pre-exposed to *M. pygmaeus* was shown parallel to an increased induction of the JA-marker genes *PI-I* and *PI-II* and the activity of proteinase inhibitors in response to the predator phytophagy compared to the control plants, which were recorded both locally and systemically on the same plant. Remarkably, both female predators and juveniles (nymphs) displayed similar abilities to induce defense responses in tomato plants in a density-dependent manner (Pappas et al. 2015). Despite the negative effects on spider mite performance, no such effect was found on the greenhouse whitefly *T. vaporariorum* performance on predator-exposed tomato plants (Pappas et al. 2015).

Similarly, exposing pepper plants to *M. pygmaeus* negatively affected the performance of the subsequently arriving pests, *T. urticae*, *B. tabaci*, and *F. occidentalis* but not the green peach aphid *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) (Bouagga et al. 2018b; Zhang et al. 2018). As with the tomato system, the negative plant-mediated effects of *M. pygmaeus* on spider mites, whitefly, and thrips on pepper, were shown parallel to the activation of the ABA and JA signaling pathways, which triggered the release of HIPVs (Bouagga et al. 2018b; Zhang et al. 2018). Furthermore, the exposure of pepper plants to *M. pygmaeus* reduced the attractiveness of the treated plants to these herbivores, suggesting that *M. pygmaeus* can decrease herbivore densities on plants by indirectly affecting their host plant selection (Zhang et al. 2019b). The natural enemy of spider mites, the predatory mite *P. persimilis* (Acari: Phytoseiidae), was attracted by plants previously exposed to *M. pygmaeus*. Remarkably, pepper plants exposed to *M. pygmaeus* produced more seeds than unexposed plants with recorded changes in plant phenology not affecting the predator performance on these plants (Zhang et al. 2019a).

Overall, the above studies highlight the ability of *M. pygmaeus* to induce plant defense responses in two crop plants and indirectly affect forthcoming herbivorous pests. Therefore, it is suggested that *M. pygmaeus* could serve as a plant vaccination agent at the early stages of the establishment of a crop directly affecting herbivores through predation and indirectly via induced defenses or priming plants against future attackers, eventually enhancing its overall impact as a biological control agent (Pappas et al. 2016).

Other mirids. Most of the work on the ability to induce plant defenses by zoophytophagous mirids has been carried out with *N. tenuis* and *M. pygmaeus*, the two mirid species mostly used in biological pest control programs in horticultural crops (Pérez-Hedo et al. 2021d). As previously mentioned, the induction of defenses could be one of the reasons for the success achieved by these two species. However, it is known that the ability to induce defense responses in plants is species-dependent (Pérez-Hedo et al. 2015a). While *N. tenuis*-induced tomato plants are repellent for *B. tabaci* and *T. absoluta*, *M. pygmaeus*- and *Dicyphus bolivari* (Wagner) (previously *D. maroccanus*)-induced tomato plant defenses do not affect the repellence of *B. tabaci* and even attract *T. absoluta*. Conversely, the phytophagy of the three mirid bugs results in the attraction of *E. formosa*. The ability of *N. tenuis* to make tomato plants less attractive to *B. tabaci* was attributed to the activation of the ABA signaling pathway, which was only upregulated by *N. tenuis*. All three mirid predators activated the JA signaling pathway which explained the attraction to *E. formosa*. However, the identification of the main phytohormones involved in the behavioral responses of *T. absoluta* toward predator-induced plants has not been addressed so far. Therefore, the study of the capacity to induce defenses in other species of mirids is of particular interest and should be considered as a new trait when the potential of a particular mirid species as biocontrol agent is addressed. This could be the case of *Macrolophus praeclarus* (Distant), a polyphagous mirid predator recently reported as highly effective in the control of *B. tabaci* (Roda et al. 2020). The phytophagy of *M. praeclarus* also induces defensive responses in tomato plants through the upregulation of the JA pathway (Pérez-Hedo et al. 2021c). Further studies should elucidate the biological effect of *M. praeclarus*-induced defenses on key tomato pests.

Predator-induced plant defenses: interactions with biotic stressors

In nature and agroecosystems, plants are constantly exposed to a wide range of biotic stressors, many of which are harmful organisms, like herbivorous arthropods and pathogenic microorganisms. To minimize the performance of harmful stressors, plants have evolved sophisticated defense mechanisms that can be induced upon attack (Kant et al. 2015; Karban and Baldwin 1997; Pappas et al. 2017; Walling 2000). Moreover, herbivores and pathogens such as fungi, bacteria, and viruses may interact with the plant's immune system via the activation of different signaling pathways (Gruden et al. 2020). Antagonistic or synergistic cross-talk induced in response to herbivores or pathogens sharing the same host plant may determine the outcome of such interactions (Moultet et al. 2011, 2013). Similar defense

mechanisms can be induced by beneficial organisms, like mutualistic microbes and zoophytophagous predators. The role of the latter in driving interactions in complex food webs via plant defense induction is yet to be determined. This should be attributed to the difficulty of including multiple attackers arriving at different times (i.e., simultaneously or sequentially) (Silva et al. 2021a), and the different species of natural enemies.

Interactions with beneficial soil microorganisms

The fact that not only herbivores but also non-detrimental organisms can alter plant resistance to herbivores arriving later, has attracted recent attention regarding their potential use for biological control. Besides zoophytophagous predators that can activate plant defenses due to their phytophagy, other well-known examples of beneficial organisms inducing plant defenses are soil microbes, such as mycorrhizal- or plant-growth-promoting fungi and rhizobacteria. Their root-colonization cannot only facilitate nutrient uptake but also plant defense capability through activation of JA-regulated induced systemic resistance (Pineda et al. 2010; Rasmann et al. 2017; Shikano et al. 2017). As phytophagy by zoophytophagous predators can exert similar effects, their use as biological control agents may extend beyond the direct top-down suppression of pest populations.

Induced plant defenses trade-off with defense against additional attackers and with plant growth (Herms and Mattson 1992). Nevertheless, we currently have little evidence on the plant-mediated effects of beneficial soil microbes on zoophytophagous predators aboveground. Furthermore, research traditionally focuses on how a beneficial individual influences plant immunity against a single harmful attacker, whereby the potent synergistic effects of different beneficials (such as zoophytophagous predators and beneficial microorganisms) via their ability to induce plant defenses against harmful attackers are largely unknown.

The plant-mediated effects of beneficial soil microorganisms on zoophytophagous predators have been studied mainly in the tomato-*M. pygmaeus* system. The establishment in tomato plants of a root restricted endophyte, the non-pathogenic strain *Fusarium solani* K resulted in the alteration of the headspace volatiles emitted by the plants enhancing their attractiveness to the *M. pygmaeus* (Pappas et al. 2018). Hence, inoculated plants may attract individuals of natural enemies and enhance their indirect defense against herbivorous pests. The inoculation of tomato plants by the FsK resulted in the upregulation of plant defense-related against herbivory and also had a direct negative effect on *T. urticae* performance and inflicted feeding damage (Pappas et al. 2018). Similarly, the inoculation of tomato plants with *Trichoderma longibrachiatum* impacted the population

growth of *M. pygmaeus* positively, while enhancing the attractiveness of plants to conspecifics (Battaglia et al. 2013) as with inoculation by the AMF *Rhizophagus irregularis* (Prieto et al. 2017).

In the case of the root-restricted non-pathogenic endophyte *Fusarium oxysporum* (Fo162), inoculation of tomato plants enhanced the efficiency of *M. pygmaeus* to control the greenhouse whitefly *T. vaporariorum*. This endophyte has been shown to have no effect on the pest's performance but negatively affects the predator. However, an overall positive effect in enhanced suppression of the pest was recorded possibly due to a shift in the feeding preference of the predator from plant consumption toward more frequent prey consumption (Eschweiler et al. 2019). Notably, the inoculation of tomato plants by the FsK has also been shown to reduce the damage (necrotic rings on leaves and stems) inflicted by the plant-feeding predator *N. tenuis* via the upregulation of the ethylene and JA pathways (Garantonakis et al. 2018). Taken together, the outcomes of interactions between soil microorganisms and zoophytophagous predators are shown to be positive in terms of plant protection. Further studies are required to understand the mechanisms involved and estimate their efficiency in agricultural settings.

Interactions with plant viruses

Induced plant responses to multiple attackers may be mediated by interacting plant signaling pathways. Hence, zoophytophagous predators that induce plant defense responses via their phytophagy may variably affect or be affected by other defense-inducing stresses. In this regard, few studies have only focused on the interactions of mirids with viruses, whereas diseases related to pathogens such as bacteria and fungi have not been addressed so far.

Although *M. pygmaeus* does not usually cause damage compared to other mirids such as *N. tenuis* (Pérez-Hedo et al. 2021d), several studies have shown that *M. pygmaeus* can cause severe economic damage on tomato fruits at high population densities (Lucas and Alomar 2002; Moerkens et al. 2016; Moerkens et al. 2017; Puentes et al. 2018; Sanchez et al. 2018). Their zoophytophagous behavior causes yellowish feeding punctures, flower abortion, fruit distortion, and open fruits (seeds visible). The severity of these symptoms is significantly increased when plants are infected with *Pepino mosaic virus* (PepMV) (Moerkens et al. 2016, 2020). Nowadays, most plants are vaccinated by cross-protection using a mild variant of PepMV (Hanssen et al. 2010; Hanssen et al. 2011). Therefore, *M. pygmaeus* fruit damage is common in most tomato greenhouses where this biocontrol agent is released. Interactions between plant defense responses are most likely the explanation for this occurrence (Moerkens et al. 2016). As mentioned above, zoophytophagous mirids are known to induce the JA pathway while PepMV

infection in tomato induces the defense pathway mediated by SA signaling (Hanssen et al. 2011). Antagonistic effects of SA-mediated responses on JA-mediated responses and vice versa have been proven by several studies (Cipollini et al. 2004; Stotz et al. 2002; Wei et al. 2014). Further studies are required to look into the interaction between PepMV and *M. pygmaeus* on a plant physiological level.

The phytophagous behavior of *N. tenuis* results in necrotic rings on stems and leaf petioles, flower dropping, and punctures on fruit (Arnó et al. 2010; Calvo et al. 2009; Pérez-Hedo and Urbaneja 2016; Sanchez 2009; Sánchez and Lacasa 2008). Although *N. tenuis* also triggers the JA pathway signaling (Pérez-Hedo et al. 2015b), no interaction with PepMV was found (Moerkens et al. 2020). Specific differences with *M. pygmaeus* might explain the variation, like the activation of the ABA signaling pathway (Pérez-Hedo et al. 2015b). More research is required to fully understand the underlying molecular processes.

The study of Bouagga et al. (2020) illustrated an interaction between the tomato spotted wilt virus (TSWV) in pepper and two mirids, *M. pygmaeus* and *N. tenuis*. TSWV is transmitted by several thrips species and is considered one of the most harmful plant diseases. Punctured plants by both *M. pygmaeus* and *N. tenuis* activated the gene expression of the JA pathway, which limited the accumulation of TSWV in pepper plants. Noticeably, induced plants by mirid phytophagy appeared less attractive to the thrips *F. occidentalis*, the TSWV vector (Bouagga et al. 2018b). Moreover, TSWV-infected plants became more attractive to thrips compared to healthy plants (Belluire et al. 2005).

Escobar-Bravo et al. (2016) showed that tomato plants with high expression of MeJA were less likely to be infected with the Tomato yellow leaf curl virus (TYLC). Because mirids activate the JA pathway, other mirid-disease interactions may be plausible.

Exploiting zoophytophagous predator-induced defenses in plant protection

Throughout this review, we have shown how the induction of defenses mediated by zoophytophagous predators can be an added value to the main role of this group of arthropods as biological control agents. In most biological control programs, the use of zoophytophagous predators as key components for pest control (i.e., mirids in tomato or the anthocorid *Orius* spp. in sweet pepper), success depends on achieving a permanent establishment in the crop early enough before pest(s) arrival. Once zoophytophagous predators are established, these crops could have their induced defenses activated or primed. Hence, it could be hypothesized that the incidence of pests and diseases could be lower in these

crops. However, most studies carried out on this topic to date have used young plants, whereas more precise studies are needed in crops in production. In addition, in commercial crops, both in greenhouses and outdoor production, many other exogenous factors come into play which could interact with the induction of defenses, such as the presence of more than one pest or disease at the same time or the use of different cultural practices (e.g., pruning or harvesting) that could elicit the induction of defenses themselves. What is clear so far is that predator-induced plant defense is a positive trait that could be used to improve crop protection. Here, three lines of research that could bear fruit soon are presented:

1. *Use of zoophytophagous predators as ‘vaccination’ agents.* The vaccination of plants with zoophytophagous predators is based on the assumption that exposing young plants to mirid individuals before transplanting would result in primed plants against future attackers that could be afterward transplanted to the field (Pappas et al. 2016). Previous studies on the induction of plant defenses by mirid bugs are promising in this regard (Bouagga et al. 2018b; Pappas et al. 2015, 2016; Zhang et al. 2018). This strategy has been extensively conducted for more than ten years in tomato crops with the release of *N. tenuis* in nurseries in Southeastern Spain (Calvo et al. 2012a, 2012c). *Nesidiocoris tenuis* is released in seedling nurseries at a rate of 0.5 adults per plant together with alternative prey [the Mediterranean flour moth *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae)] (Calvo et al. 2012b). Plants bearing the mirid eggs are transported to the greenhouse/field, achieving an even distribution throughout the crop. Soon after transplanting, the mirid nymphs hatch and rapidly start to actively search for and predate on the prey. Although the main reason why these releases are carried out in the nursery is to facilitate the establishment of *N. tenuis* and anticipate its predatory effect, plants that arrive at the greenhouse/field are defensively primed against herbivores (Pérez-Hedo et al. 2015b; Pérez-Hedo et al. 2021a). This approach has already been tested successfully in small-scale experiments with *M. pygmaeus* on young tomato plants for enhancing their establishment in tomato greenhouses (Lenfant et al. 2000). Hence, there is evidence that the concept of ‘vaccinating’ young seedlings by exposing them to mirid individuals has been applied successfully not just as a predator establishment tool but also to prime plants against pests and diseases (Pappas et al. 2015; Pappas et al. 2016; Pappas et al. 2020; Pérez-Hedo et al. 2015b, 2018a; Zhang et al. 2021).
2. *Mimic mirid-induced defenses through biotechnological approaches.* The inclusion or exclusion of selected genes involved in plant defensive mechanisms in plant breed-

ing programs may result in the release in the market of cultivars with high resilience to pests and diseases. The incredible development of the so-called omics techniques in recent years, together with the current knowledge of the complete genomes of most agricultural crops of world importance, makes the identification and characterization of the genes responsible for the increase in defenses in plants due to mirid phytophagy possible. This is a multidisciplinary approach that requires the collaboration of entomologists, phytopathologists, plant breeders, bioinformaticians, and geneticists that can undoubtedly bear fruits in the coming years. However, special attention should be taken so that breeding targets those resistance traits that are also compatible with natural enemies (Pappas et al. 2017). This is specifically true for zoophytophagous mirids whose populations are largely impacted by the host plant (Lins et al. 2014; Silva et al. 2021b), and generalist phytoseiid mites that exert intimate relationships with plants (Paspati et al. 2021).

3. *Imitating defenses induced by zoophytophagous predators with elicitors of synthetic origin.* In tomato and pepper, zoophytophagous predators trigger the release of volatiles via their phytophagy (Bouagga et al. 2018b). Some of these volatiles are responsible for inducing defenses in adjacent intact plants with no previous exposure to mirids (Pérez-Hedo et al. 2015a). A new control approach would be to take advantage of these volatiles as a tool to increase plant resilience against pests. Pérez-Hedo et al. (2021b) determined which volatiles were responsible for this induction and for this, exposed intact tomato plants to each of the mirid-induced volatiles for 24 h. Many zoophytophagous-induced volatiles [1-hexanol, (Z)-3-hexenol, (Z)-3-hexenyl acetate, (Z)-3-hexenyl propanoate, (Z)-3-hexenyl butanoate, hexyl butanoate, methyl jasmonate, and methyl salicylate] were used. All tested volatiles overexpressed defensive genes in exposed tomato plants when compared to unexposed plants. The volatile (Z)-3-hexenyl propanoate [hereinafter (Z)-3-HP] was able to induce the expression of the basic pathogenesis-related protein precursor (PR1), a marker gene for the salicylic acid (SA) signaling pathway, and two plant proteinase inhibitors PI (SI-PI-I and PIN2) (being PIN2 a JA marker too), and hence was selected for further use. Through transcriptomic and metabolomic analyses, genes involved in specialized defenses that are upregulated by exposure to (Z)-3-HP have been identified (Pérez-Hedo et al. 2021a). The (Z)-3-HP exposition resulted in increased production of fatty acid-derived compounds, activation of the lipoxygenase pathway, and accumulation of specific defense compounds (Pérez-Hedo et al. 2021a). Plants previously exposed to (Z)-3-HP were repellent to key tomato pests such as the whitefly *B. tabaci*, the

tomato borer *T. absoluta* and the thrips *F. occidentalis*, but were attractive to their natural enemies such as the parasitoid *E. formosa* (Pérez-Hedo et al. 2021b). Tomato plants exposed to (Z)-3-HP reduced the survival of the two-spotted spider mite *T. urticae* and *T. absoluta* when compared to unexposed plants (Pérez-Hedo et al. 2021a, b). In light of these results, this volatile has been formulated into controlled-release dispensers that emit (Z)-3-HP at constant rates for extended periods. Polymer vial dispensers [4-ml low-density polyethylene (LDPE)] have been selected and the use of these permeable dispensers has already been tested under field conditions (Pérez-Hedo et al. 2021a, b). In commercial tomato greenhouses, (Z)-3 HP-dispensers maintained plant defenses activated for more than two months, reducing herbivore pest damage (60% reduction in *T. absoluta* plant incidence) without reducing plant productivity (Pérez-Hedo et al. 2021a, b). These results are the first to demonstrate how mirid-induced HIPVs released via polymeric dispensers in commercial greenhouses elicit plant defenses and could be successfully implemented as a novel biorational and sustainable tool for pest control.

Concluding remarks

Here, we reviewed current literature and identified several opportunities related to the exploitation of phytophagy-related impacts of zoophytophagous predators on plant protection, via the induction of plant defenses. We argue that studying these approaches can increase the efficacy of zoophytophagous predators and thereby further reduce the dependence of farmers on chemical pesticides. In addition, it is very likely that other groups of natural enemies than those described in this review, are also capable of inducing defenses, as could be the case of the lady beetles which have been recently described as plant feeders (Ugine et al. 2022). On the other hand, artificial selection on behavioral traits such as predator strain selection for zoophagy over phytophagy is an increasingly discussed approach relative to the damage caused by zoophytophagous predators on plants (Dumont et al. 2018). Considering the benefits related to the phytophagy of zoophytophagous predators, caution is needed when planning for this, because selecting for zoophagy could attenuate phytophagy-related assets such as the emission of HIPVs and indirect effects on prey (Dumont et al. 2018). Consequences of predator phytophagy on plant damage and crop performance are only seldom addressed and most studies are performed in tomato and its biocontrol agents (Pappas et al. 2020; Paspati et al. 2021; Puentes et al. 2018). To better understand the mechanisms underlying the modulation of plant–herbivore interactions via zoophytophagous predators, future studies should consider plant costs

along with their biological control efficacy estimates and impact on crop production, also should include more crops and zoophytophagous predator species that induce plant defenses, as well as other beneficial organisms such as soil microbes (Garantonakis et al. 2018; Pappas et al. 2018; Pappas et al. 2020; Zhang et al. 2021). In addition, the contribution of zoophytophagous predators in plant defense induction/priming should be studied in the field where predator densities vary and other arthropods such as herbivores are also present. Finally, the ecological effects of plant defense induction on the predators themselves should be addressed. Plant defenses may interfere directly by affecting their performance and indirectly by affecting prey quality. Overall, taking a community perspective in future research is important in our attempts to identify, develop and exploit eventually the added value of plant defense induction by zoophytophagous predators in agricultural settings.

Author contributions

PML and P-HM conceived and designed the review. All authors contributed to the writing and revision of the manuscript. PML and P-HM revised and edited the final manuscript. All authors read and approved the manuscript.

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Declarations

Conflict of interest Authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants or animals performed by any of the authors.

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