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Global change calls for novel plant protection: reviewing the potential of omnivorous plant-inhabiting arthropods as predators and plant defence inducers

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Global change poses new challenges for pest management. Omnivorous predatory arthropods play an important role in pest management, yet their potential has not been fully explored. Not only do they consume prey, but their plant-feeding induces plant defences that decrease herbivores' performance, and increases production of volatiles that attract natural enemies. Growing evidence from different plant-arthropod systems indicates the generality of plant defence induction following omnivore plant-feeding. Furthermore, these responses appear to affect other organisms (e.g. plant viruses), altering multi-trophic interactions. Here, we review the dual role of omnivores (as predators and plant inducers), identify knowledge gaps and provide future perspectives to increase our understanding of omnivores' multiple functions, and how this can be applied to advance plant protection strategies.

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Introduction

Global change brings new challenges for pest control. Global change factors, such as carbon-dioxide enrichment, climate warming, land-use change, changed precipitation and atmospheric nitrogen deposition, are expected to bring large shifts in species composition and trophic interactions [1–3]. Plant–insect interactions will likely be altered, making plants more or less susceptible to damage [4,5], and at the same time, novel interactions with insect pests can also be expected [6,7]. Moreover, there is pressing need to reduce the use of pesticides in our agroecosystems [8,9]. Therefore, complementary and new plant protection strategies that better tackle these challenges are needed.

One strategy that could provide plant protection benefits is to enhance the performance of omnivorous predatory arthropods (hereafter: omnivores) (Box 1). Omnivores possess traits that make them potentially efficient pest control agents in a changing world (Box 2). For example, they are more resilient to disturbances caused by biotic and abiotic factors than non-omnivorous predators [10], and can stabilize food webs depending on the type of omnivory they exhibit [11]. Omnivores can build up and maintain their populations before pest invasion, and even when prey density is very low. Furthermore, zoophytophagous omnivores (which require plant-feeding) can efficiently suppress pests not only through direct consumption, but also by inducing plant defences through plant-feeding. Omnivore plant-feeding can induce plant defences that decrease herbivore performance, and trigger production of volatiles that attract other natural enemies (Figure 1). In other words, omnivores can serve a two-in-one function — as predators and plant defence inducers. Moreover, omnivores can directly and indirectly interact with other organisms (e.g. plant viruses) through plant-mediated effects, indicating that omnivores play multiple roles. Clarifying their multifaceted role can aid in moving from a simplified bi-trophic to a tri-trophic or multi-trophic perspective [12,13], which will improve our ability to make predictions within plant protection and result in more sustainable practices.

So far, the plant-inducing or 'vaccinator' role of omnivores has been mainly studied in greenhouse crops, with a focus on omnivores in the mirid (Hemiptera: Miridae) and anthocorid (Hemiptera: Anthocoridae) families [14,15•,16•,17,18]. Evidence from these and other systems (e.g. citrus plants, spider mites and omnivorous mites; willow plants, leaf beetles, and omnivorous mirids/anthocorids) suggests that the two-in-one function has potential to be further exploited [19,20•,21•,22•]. Hence, this calls for a synthesis of knowledge accumulated thus far on omnivores' various roles. Here, we provide a review on plant responses induced by omnivores and its consequences for herbivores, natural enemies, and other plant-associated organisms. We present results from a systematic literature search over the past two years

Box 1 Definition of omnivores, with particular emphasis on zoophytophagous predators and their potential as biocontrol agents

Omnivores are organisms that feed on more than one trophic level and are widely distributed in nature. Many predatory arthropods are omnivores, (e.g. lady beetles, spiders, lacewings, ants, true bugs and phytoseiid mites), and they can feed on plant foods including foliage, pollen and nectar [45]. In general, omnivores can be divided into three groups: opportunistic, obligatory, and facultative based on the relative importance of plant-food and prey-food for their performance [46]. Plant-feeding and prey-feeding vary in time and space, and with the species in question. For example, in the case where omnivory depends on life history, plant-feeding and prey-feeding occurs at different life stages [46]. In the past decades, omnivorous predators (also referred as zoophytophagous predators) have been increasingly used in pest biocontrol in greenhouse cropping systems. Many of these predators are true omnivores meaning that they are obligated to feed on both plants and herbivore prey. We focus on this group of omnivores in this review. Omnivores have evolved specific morphological and physiological traits that allows them to have a mixed diet of plant and prey. For example, they can produce both plant-digesting and protein-digesting enzymes, whereas herbivores and predators produce only one type [47]. Omnivorous hemipterans (e.g. true bugs) have piercing-sucking mouthparts with characteristics of both herbivores and predators [48]. These features allow omnivores to establish and maintain their populations in crops, both early and later in the season since they can feed on plants when prey is scarce, which is a major advantage of omnivores compared to carnivorous predators. Thus, omnivores can provide efficient suppression upon pest arrival and prevent pest populations to rapidly build up. Omnivorous predators also play an important role in pest control in open field systems like willow crops and fruit orchards [22•,29•,49], however their contribution to pest suppression in many systems has been less acknowledged.

Box 2 Global change factors and their known effects on omnivores

Compared to other natural enemies, omnivorous predators are expected to be more resistant to disturbances and stabilize food webs, due to their ability to feed on both herbivorous prey and plants. Nonetheless, they can be affected by global change directly and indirectly through changes in the quality of plants and herbivorous prey. To evaluate their potential in providing and maintaining predation and plant-defence induction services, we need to examine how omnivores, their prey and host plants are simultaneously affected by global change factors. This will allow us to determine if asynchronous or synchronous responses occur across the three trophic levels, and if any of the plant protection services provided by omnivores shift negatively or positively. Few studies have examined all three trophic levels, but there are some studies on how factors such as temperature, precipitation and nitrogen affect omnivores directly with evidence of positive and negative effects. We review a few of these below.

Different omnivores respond differently to changes in temperature [50]. For example, among six omnivore species (*N. tenuis*, *M. pygmaeus*, *Dicyphus bolivari*, *D. eckerleini*, *D. flavoviridis and D. errans*), *N. tenuis* and *D. bolivari* were the only species that reached adulthood at constant high temperatures of 35°C, whereas *D. eckerleini* and *D. errans* were the only ones still able to move (walk) below 0°C (temperatures used in the lab experiment ranged from −8 to 48°C) [50]. For these species, male and female mirid bugs are more vulnerable to cold and heat, respectively. Note, however, that the above mentioned species inhabit different geographical regions and will not necessarily experience the same low and high temperatures.

For willow crops (*Salix* spp.), and its most common herbivore (*Phratora vulgatissima*) and omnivorous predator (*Orthotylus marginalis*), it has been shown that the three trophic levels can respond similarly to elevated temperatures in Sweden (simulated temperature scenarios from 16 to 24°C), and thus this system is less likely to be disrupted under warmer climates [51]. For another global change factor, nitrogen, it has been shown that higher nitrogen levels can enhance the performance and stabilize populations of omnivorous predators (mirids and anthocorids) in willow cropping systems [10]. But, high quality plants may satiate omnivores and free herbivorous prey from predation [52].

Similarly, changes in precipitation could also affect omnivores. Water levels in the soil can affect *M. pygmaeus* performance directly and through bottom-up effects [53]. A decrease in water levels was shown to shorten the longevity of *M. pygmaeus* [54]. More specifically, *M. pygmaeus* fed equally on tomato plants with different nitrogen and water levels when prey was absent, but fed more on prey when plants received higher water inputs [54]. Furthermore, elevated CO_2 can affect omnivores' performance via changes in the nutritional quality of plant and prey. Increased CO_2 levels can negatively affect performance of the omnivorous bug *Oechalia schellenbergii* (Hemiptera: Pentatomidae) at adulthood, but benefit their performance through increasing vulnerability of its prey, a chewing insect *Helicoverpa armigera* (Lepidoptera: Noctuidae), resulting in higher predation risk for the pest [55].

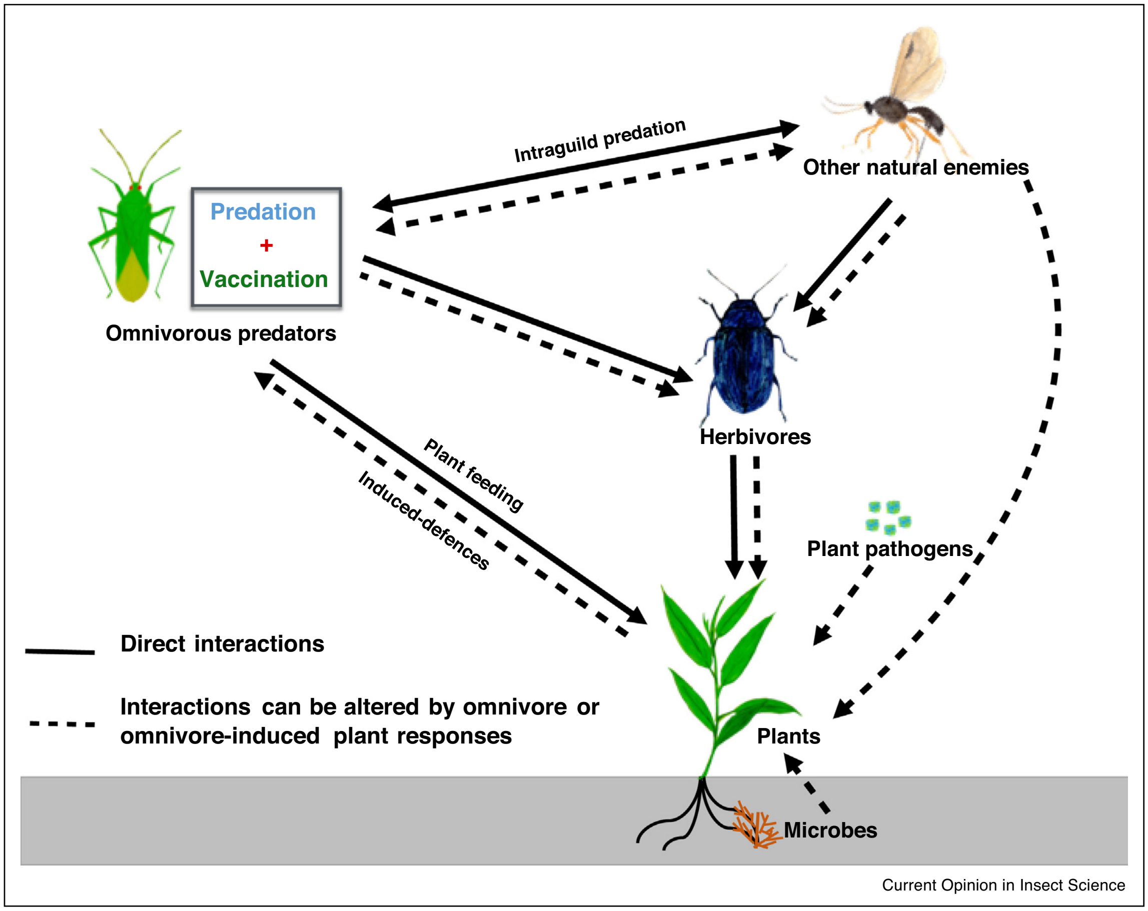
Research on the effects of other global change drivers (e.g. ozone, land-use change) on omnivorous predators, is needed.

(Supplementary material, Table S1), summarize findings on omnivores' two-in-one function and highlight gaps that deserve further attention.

Omnivore-induced plant responses

It has been shown that plant-feeding by various omnivores can induce-specific defence pathways and trigger production of plant volatiles, even when the extent of plant-feeding is very low [16•,23]. The regulation of plant defence following damage or infection occurs through the hormones salicylic acid (SA), jasmonic acid (JA), ethylene (ET) and abscisic acid (ABA), with each hormone regulating its own pathway but also influencing others [24]. The defence responses following omnivore plant-feeding differ with omnivore and plant species [15•,16•,18,22•], however most work involves mirid bugs and greenhouse crops (e.g. tomato, sweetpepper). One of the most examined omnivores is the mirid bug *Nesidiocoris tenuis*, a biocontrol agent for pests like whiteflies, aphids and spider mites. This omnivore induces JA, ABA and SA defence pathways in tomato and sweetpepper plants [15•,18], and this induction can persist up to 14 days in tomato [15•]. Furthermore, omnivore-exposed tomato plants produce volatiles that differ from those of non-exposed plants [23]. Another mirid bug, *Macrolophus pygmaeus*, systemically induces JA and ABA, but not the SA pathway, in tomato and sweetpepper [16•,25]. Different plant volatiles were also produced by

Figure 1



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Schematic overview of interactions between omnivorous predators and plants, herbivores, other omnivores or natural enemies and other plant-associated organisms.

Solid lines indicate direct interactions through predation or plant-feeding. Dashed lines indicate interactions that can be altered by omnivorous predators or omnivore-induced plant responses.

sweetpepper plants exposed to *M. pygmaeus* compared to those from clean plants (XN Zhang, PhD thesis, University of Amsterdam, 2018). Similarly, greater amounts of six green leaf volatiles and methyl salicylate were released from tomato plants exposed to *M. pygmaeus* and *N. tenuis* [23].

Omnivores from other families can also induce plant defences and trigger emission of plant volatiles. *Orius laevigatus* induces JA and SA in sweetpepper, and alters plant volatile production [14]. Similarly, the omnivorous predatory mite, *Euseius stipulatus*, can induce genotype-specific defences in citrus plants with JA, SA, and flavonoid pathways induced in resistant plants, and JA alone in susceptible plants. The predatory mites also trigger production of quantitative and qualitatively different volatiles from different genotypes [22•]. Taken together, there is evidence that omnivores induce defences through plant-feeding, but a broader spectrum of plant-omnivore systems needs to be examined.

Effects of omnivore-induced responses on herbivores and other predators

Omnivore-induced plant defences can affect herbivore performance and their host plant selection, but effects vary with plant-insect system and type of experiment. In tomato, *N. tenuis*-induced defences do not appear to affect the oviposition and host plant selection by the two-spotted spider mite *Tetranychus urticae* in olfactometer experiments [18]. However, *N. tenuis*-induced tomato plants exhibit lower spider mite infestation rates in the greenhouse [18]. Likewise, the reproduction rate of spider mites and the western flower thrips, *Frankliniella occidentalis*, is lower on *M. pygmaeus*-induced sweetpepper plants than non-induced plants, but no such effect is found for the green peach aphid *Myzus persicae* [16•]. Furthermore, spider mites and thrips prefer non-induced sweetpepper plants over *M. pygmaeus*-exposed plants, whereas aphids do not show such preference [17]. Likewise, the sweetpotato whitefly (*Bemisia tabaci*) and thrips prefer non-induced plants over omnivore-induced (*M.*

pygmaeus, *N. tenuis* and *O. laevigatus*) sweetpepper plants; whereas another herbivore, the South America tomato pinworm (*Tuta absoluta*), is attracted to *M. pygmaeus*-induced tomato plants [14,15•,23].

Other natural enemies (including conspecifics) that share the same herbivorous prey with omnivores, can also be affected by omnivore-induced plant volatiles. For example, conspecifics showed gender-specific responses to *N. tenuis*-induced volatiles, with females being attracted to female-induced plants and males being attracted to plants induced by both genders [26]. In another case, a parasitoid (*Encarsia formosa*) of whiteflies was attracted to omnivore-induced sweetpepper plants [14,15•]. Similarly, the natural enemy of spider mites, the predatory mite *Phytoseiulus persimilis*, preferred *M. pygmaeus*-exposed plants to unexposed clean plants (XN Zhang, PhD thesis, University of Amsterdam, 2018).

Although most work has been conducted in greenhouse crops, there are a few comparable studies in other systems. Herbivorous spider mites were shown to be attracted to citrus plants exposed to the omnivorous predatory phytoseiid mite *E. stipulatus* regardless of plant genotype [22•]. On the other hand, conspecifics were attracted to the *E. stipulatus*-exposed susceptible genotypes, and preferred clean citrus plants over omnivore-exposed resistant genotypes [22•]. In another system, the egg parasitoid, *Telenomus podisi*, was also attracted to broad bean plants exposed to the omnivorous spined soldier bug, *Podisus maculiventris* (Hemiptera: Pentatomidae), and the herbivorous host eggs were laid on these plants [21•].

Taken together, there is support from several systems that omnivores can provide more than predation services and enhance plant protection in several ways. Our systematic search findings (Table S1) are in line with the conclusions made by a recent review focused on predatory mirid bugs, which called for optimizing the use of mirids in pest control and expanding their use beyond horticultural crops [27•]. To fully explore the multiple roles that omnivores can serve, several knowledge gaps need to be addressed. Below, we highlight some of the most important ones.

Omnivores' two-in-one function: knowledge gaps

The first gap to address is to determine how widespread omnivore-induced responses are, and describe their effects on herbivores and other natural enemies. Research in other cropping systems and non-herbaceous plants, and examining a wider range of omnivores is needed. Moreover, studies from lab settings should complement field or semi-field experiments. There is already some evidence that omnivores play an important role in pest suppression in open field systems, for example in willow (*Salix* spp.) cropping systems and apple orchards [28,29•,30]. In these settings, both herbivores and omnivores coincide in time and feed on the same plants. Thus, a second gap to address is if (and how) responses differ when both omnivores and herbivores simultaneously feed on plants, and the consequences for pest control. For instance, when omnivores function as plant 'vaccinators' they might lower plant quality for herbivores, which may result in herbivores feeding more or less on their host plants [31,32]. Moreover, herbivores feeding on these plants may, in turn, become of lower nutritional value for their natural enemies. This may drive omnivores to feed more on their prey and less on plants, which could also affect strictly carnivorous enemies that may predate more on these prey [33,34]. Interestingly, a recent experimental greenhouse study found that exposure of tomato plants to mirid-induced volatiles (through a dispenser) can increase plant defence and lower damage by the pests *T. absoluta* and *T. urticae* without reducing yield [27•]. A natural question that follows is what are the consequences on other predators. Thus, a third gap to address is how omnivores (and the associated plant responses) influence the performance, in particular feeding behaviour, of their conspecifics and other natural enemies through induced responses.

In addition to plant-mediated interactions, omnivores can also interact with natural enemies that share the same herbivore prey through intraguild predation (IGP) [35]. These interactions may or may not interrupt pest management when omnivores co-occur with other enemies. Intraguild predation can be bi-directional or uni-directional, meaning that both members of the same guild feed on each other or only one is being fed upon by the other. For example, *N. tenuis* and the predatory mite *Amblyseius swirskii* exhibited bi-directional IGP (i.e. they both feed on each other), whereas *M. pygmaeus* and *O. laevigatus* and *A. swirskii* exhibited uni-directional IGP (i.e. they both feed on the mite but not the other way around) [36,37]. However, these interactions may not necessarily negatively affect biological pest control [38,39]. A more complex habitat structure in greenhouse or field settings can reduce the likelihood of IGP [39,40]. Hence, both lab and field studies are needed to understand the consequences of direct interactions between omnivores and other natural enemies for pest control. To fill this fourth knowledge gap, we need more in-depth studies of plant-insect-predator systems, identifying which predators share the same herbivorous prey and examining whether or not predators can complement each other and thereby strengthen plant protection.

It is also important to consider that omnivores may indirectly interact with other plant-inhabiting organisms through induced plant responses. For example, *N. tenuis* and *M. pygmaeus*-induced defences limited the accumulation of the tomato spotted wilt virus in sweetpepper

Box 3 Optimizing plant protection services provided by omnivores.

Different approaches can be used to enhance omnivores' performance in plant protection. These approaches entail maximizing their predation, and maintaining plant damage at levels that induce defences, but do not entail large negative effects on the target plant. We provide some suggestions for open field settings based on ecological knowledge and previous studies in greenhouse settings:

1. Enhancing population build-upsDiversification measures implemented in cropping systems will most likely benefit omnivores. For example, flower strips that benefit pollinators can also enhance omnivores' performance by providing food and shelter [56,57]. It has been shown that flowering banker plants (*Calendula officinalis* L.) can increase the abundance of omnivorous predators [Dicyphini (Hemiptera: Miridae)] and other natural enemies in tomato fields, and thus reduce pest damage [58]. Ecological field experiments also indicate that increasing plant species richness can shift the omnivore community to more predatory and less mobile species [59]. This suggests that diversifying cropping systems should greatly benefit omnivores in various ways. Moreover, when introducing or enhancing omnivorous predators in the system of interest, screening and use of native omnivores is increasingly encouraged [43,60].
2. Enhancing prey-feedingSelecting omnivores with behavioral traits that benefit pest control and limit plant damage can improve plant protection services provided. Identifying native species of omnivorous predators, and quantifying their feeding behaviour and predatory efficiency, can provide a reservoir of omnivores suitable for various conditions and pests. Other organisms can also be involved in shaping their feeding preferences. For example, it has been shown that soil-borne beneficial microbes (e.g. root-associated endophyte: *Fusarium solani* K) can shift the feeding preference of omnivores from plant-feeding to more prey consumption, resulting in enhancement of pest suppression and reduction of plant damage [61,62•].
3. Enhancing trophic interactions that increase plant protectionOur understanding of trophic interactions has already been integrated into some systems (e.g. agroforestry) and approaches (e.g. push-pull, integrated pest management) to enhance the trophic interactions of interest [63]. These interactions include direct prey consumption by omnivores, but also indirectly reducing herbivory through non-consumptive effects (e.g. fear). Such effects are known for other predators. For example, the decrease in oviposition of *F. occidentalis* due to the presence of predatory mite eggs [64]. Non-consumptive effects of omnivores can hinder or interrupt herbivores' feeding, and this in turn can be altered by bottom-up effects (e.g. plant quality) and interactions with other organisms [19]. The importance of omnivores for biological control has been acknowledged in several systems, however, the new insights gained from understanding their 'vaccinator' role and the consequences for multitrophic interactions, will provide added value to the plant protection services they can provide.

plants [41•]. This is a nascent field of research and little is known; nevertheless, it suggests that omnivores may serve multiple functions in plant protection. Thus, a fifth knowledge gap to address is if (and how) omnivores interact with other plant-associated organisms through induced plant responses and if there are extended consequences at the community-level.

Lastly, from an applied perspective, it is important to determine if omnivores' plant protection services can be achieved at plant damage levels that are economically acceptable. One concern is that plant damage by omnivores can negatively affect plant performance and reduce yield, and this effect may be greater than the benefits omnivores provide. Several mirid omnivores have been shown to cause damage to leaves, flowers, fruits, and stems of plants, especially when herbivore density is low [20•,42,43]. Short-term greenhouse experiments showed that *M. pygmaeus* increased sweetpepper seed production by five-fold and altered phenology (sped-up development from flower to fruit) [44•]. Hence, it is important to evaluate benefits and costs of omnivore plant-feeding for the target system in question. Long-term population dynamics studies of omnivores, pests and other natural enemies will be needed. Both experimental and modelling approaches can be used to tackle these knowledge gaps.

Conclusions

Considering their wide distribution and ability to stabilize food webs, omnivores may have potential to mitigate new threats in plant protection due to global change. Our literature review shows there is increasing evidence that omnivores can provide predatory and plant-defence induction services, and there are likely other unexplored benefits to uncover. Plant protection can be strengthened by considering the multiple functions that omnivores provide in ecosystems, and these can be complemented with other pest management measures (Box 3). Some important knowledge gaps to address are: a) understanding how simultaneous damage by omnivores and herbivores changes plant induced responses, b) how interactions of omnivores with other predators can affect pest control, c) if omnivore-induced responses enhance or diminish resistance to other pests, and d) if the extent of omnivore plant-feeding occurs at low and economically acceptable levels. Moreover, there is a strong need to examine plant-herbivore-omnivore interactions in non-herbaceous crops and open field settings.

Conflict of interest statement

Nothing declared.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.cois.2021.06.001.

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The authors show that two omnivorous predators *Macrolophus pygmaeus* and *Nesidiocoris tenuis* induce plant volatiles through plant-feeding. These plant volatiles make sweetpepper plants less attractive for two herbivorous prey (western flower strips and sweetpotato whitefly), and more attractive for the whitefly parasitoid *Encarsia formosa.*

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This study shows that the omnivorous predator *Macrolophus pygmaeus* induces plant defences in sweetpepper plants. More specifically, jasmonic acid and abscisic acid defence pathways, which negatively affect herbivorous prey (two spotted spider mites, western flower thrips, but not green peach aphids).

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This systemic literature review focuses on how often levels of omnivore damage and its consequences for plants are considered or quantified. The authors found that measures of omnivore plant-feeding are occasionally reported, but seldom are the direct consequences of such damage also considered. Thus, the direct costs to plants of omnivore-inflicted damage are often neglected. Furthermore, the effects reported were disproportionally based on studies examining tomato plants and its omnivorous biocontrol agents. Publication trends suggested that more studies are evaluating costs to plants, but a paradigm shift is still needed.

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In this study, the authors examine how omnivore-induced plant responses affect other natural enemies in the *Vicia faba* plants and the omnivore *Podisus maculiventris* (Hemiptera: Pentatomidae) system. The parasitoid *Telenomus podisi* was shown to be more attracted to plants that had both been damaged by the feeding activity of *P. maculiventris* and on which host egg masses had been laid. However, the parasitoid was not attracted to plants only damaged by omnivore feeding activity or undamaged plants.

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This is the first study showing that zoophytophagous phytoseiid mites can induce plant defences through feeding. Authors show that the omnivorous predatory mite *Euseius stipulatus* can trigger plant-genotype specific defences and plant volatiles in citrus plants. Herbivorous spider mites are attracted to citrus plants induced by the predatory mites *E. stipulatus*, while conspecifics are attracted to less-defended plants that are induced by *E. stipulatus*.

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