DOI: 10.1111/1365-2435.13884

REVIEW

Functional Ecology

The enemy of my enemy is not always my friend: Negative effects of carnivorous arthropods on plants

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Funding information

Early Postdoc Mobility fellowship from the Swiss National Science Foundation; Open Competition grant from the Netherlands Organization for Scientific Research, Grant/ Award Number: ALWOP.368

Handling Editor: Liza Holeski.

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Abstract

- 1. Plants are members of complex communities of which arthropods are the most speciose members. The role of carnivores in shaping the outcome of multi-trophic interactions by top-down control of herbivores has been well studied. Particularly, the positive impacts of natural enemies of herbivores on plants through direct (consumptive) and indirect (non-consumptive) effects on their prey and hosts have received considerable interest, while multi-trophic interactions that result in negative effects on plants have received little attention.
- 2. Negative impacts of carnivorous arthropods have been documented and arise when carnivores directly affect plants and/or their interactions with beneficial arthropods. In general, negative effects may be compensated by positive effects of other carnivorous arthropods, but their presence and significance is likely to be underestimated in tri-trophic interactions.
- 3. Recent studies have revealed that the composition and dynamics of the plant and arthropod community have a significant effect on plant fitness. Therefore, we encourage an approach that accounts for a larger community of species and interactions associated with plants, including interaction types in which carnivores may negatively affect plants.
- 4. This review highlights specific interaction types that ultimately lead to negative effects of carnivores on plants. This synthesis presents alternative hypotheses to those that predict that carnivores invariably benefit plants. Testing potential costs and benefits of carnivores to plants will advance our understanding of indirect plant defence.

KEYWORDS

community ecology, indirect defence, natural enemies, parasitoids, plant-insect interactions, predators, trophic cascade

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1 | INTRODUCTION

The importance of carnivorous arthropods in shaping plantherbivore interactions has been well investigated (Abdala-Roberts et al., 2019; Price et al., 1980). By "carnivorous", we mean the habit of feeding on other animals, which includes omnivores that feed on both plants and animals as well as intraguild predators (Boitani & Powell, 2012; Coll & Guershon, 2002; Polis et al., 1989). In addition to the direct suppression of herbivores by consumption (Gómez & Zamora, 1994), the landscape of fear by the presence of predators extends its effect on herbivores through non-consumptive effects (Abram et al., 2019). The benefit for plants of herbivore suppression by predators may also result in selection on plant traits that incidentally maximise predator performance as means of indirect plant defence (Price et al., 1980). There is extensive support that predators select for plant structures that offer housing to predators, as well as food bodies or extrafloral nectar to nourish predators. Moreover, herbivore-induced plant volatiles (HIPVs) reveal herbivores to predators and are hypothesized to function as a 'cry for help' (Dicke & Baldwin, 2010). So far, only a few studies have highlighted that the attraction of natural enemies of herbivores may lead to plant fitness benefits (Kergunteuil et al., 2019; Schuman et al., 2012). The principle of 'the enemy of my enemy is my friend', has stimulated fundamental research on the evolution of plant traits that maximise predator performance as well as applied research to use natural enemies as biological control agents in agriculture (Aartsma et al., 2017; Turlings & Erb, 2018).

However, predators may also have negative effects on plant performance. This is apparent when carnivorous arthropods directly feed on the plant, indirectly increase herbivory via non-consumptive effects or decrease plant pollination (Puentes & Björkman, 2017; Romero & Koricheva, 2011). In some cases, natural enemies of herbivores increase plant damage to maximize their own fitness, through direct feeding (omnivores; Puentes et al., 2018) or by increasing feeding by the host (koinobiont parasitoids; Rahman, 1970; Xi et al., 2015). This may result in an antagonistic relationship between plants and natural enemies of herbivores because of their opposed interests: plants are usually under selection to reduce herbivory (including from omnivores and parasitized herbivores) while natural enemies are under selection to increase their fitness, which may include feeding from the plant (Kaplan et al., 2016). In other cases, carnivores affect plant interactions with other members of the herbivore and carnivore communities via plant-mediated effects and intraguild predation (Polis et al., 1989; Stam et al., 2014). Hence, carnivore presence causes complex cascading effects on other arthropods which may result in negative feedback effects on the plant (Kessler & Halitschke, 2007; Poelman & Dicke, 2014). We hypothesize that such scenarios become especially apparent when tri-trophic interactions are placed in a wider plant and arthropod community context. Nevertheless, plant fitness costs resulting from the attraction of carnivores are rarely experimentally addressed or considered in concepts of plant defence (but see Ode, 2006; Romero & Koricheva, 2011).

As stated in Pearse et al. (2020), indirect plant defence traits as well as natural enemies of herbivores might come with costs, which have received considerably less attention than benefits. In the present review, it is not argued that the overall effect of all carnivores interacting with a plant during the whole season is negative. Instead, it is hypothesized that (1) depending on the context, not all carnivores have a positive effect on plants, (2) an apparent overall positive effect of all carnivores interacting with a plant could be the result of the sum of both positive and negative effects and (3) a large part of these negative effects of carnivores on plants are indirect (affecting the plant through other arthropods). Therefore, experiments that are not performed in natural environments, which include interactions with communities of arthropods, may underestimate the negative effects. In addition, negative effects of some carnivores on plant fitness could act as a balancing counter-selective force against some indirect plant defence traits. This implies that plant traits interacting with carnivores are not always positively selected by all carnivores but instead are influenced by the sum of positive and negative interactions with different carnivores, depending on the context.

Here, we review interaction types (Figure 1) in which the presence of a predator and/or parasitoid could lead to negative effects at the individual plant level, depending on plant and arthropod community composition.

2 | CARNIVORES INCREASING PLANT DAMAGE

2.1 | Direct effects of plant-feeding by omnivorous arthropods

The most apparent and direct effects of predators on plants are caused by omnivorous arthropods that feed on both herbivores and plants (Coll & Guershon, 2002; Figure 2). Despite the well documented positive role of omnivores on plants through pest suppression (van Lenteren et al., 2018), herbivory by omnivores may reduce plant performance as much as herbivory by true herbivores (Puentes & Björkman, 2017). Negative effects of omnivorous predators are even more extensive when these omnivores vector plant pathogens or specifically feed on plant reproductive structures (Albajes et al., 2006). In addition to tissue loss, direct plant feeding by omnivores also induces costly defences in the plant (Pérez-Hedo et al., 2015), which can result in a waste of resources and a negative effect on plant performance, depending on the context (Züst & Agrawal, 2017). Plant induction by omnivores is an efficient resistance strategy against some-but not all-subsequent herbivores (Pappas et al., 2015; Zhang et al., 2018). Such induction of a plant defence response against herbivores reduces plant growth, carbon fluxes and photosynthetic capacity (Züst & Agrawal, 2017).

Two of the most important factors affecting the dietary choice of omnivorous arthropods are plant quality and prey availability (Hunter, 2009; Kester & Jackson, 1996). Many omnivores prefer to feed on arthropod prey as a more nutritious food source than plants **FIGURE 1** Five interaction types in which carnivores may have negative effects on plants: (a) increased direct feeding damage done to the plant, by omnivorous arthropods (left) or by herbivores in response to parasitization by a gregarious koinobiont parasitoid (right), (b) reduction in plant pollination due to direct and indirect effects of carnivores on pollinators, (c) carnivorous aphidtending ants can increase hemipteran herbivore survival and herbivory, (d) carnivores alter plant response to herbivory early in the season and make plants more vulnerable to negative interactions with other arthropods arriving later in the season, (e) intraguild predators (feeding on both herbivores and predators) may negatively affect other predators, resulting in reduced control of herbivores

FIGURE 2 Overview of a four-trophiclevel food web with negative and positive carnivorous arthropod effects on plant fitness



(Moerkens et al., 2020), but this is not always the case (Eubanks & Denno, 1999). An increase in plant quality and/or a decrease in prey availability (or quality) leads to more omnivore plant damage (Agrawal et al., 1999). Hence, we hypothesize that in a context with good quality plants and limited arthropod prey, plant feeding by omnivores may lead to plant fitness reduction, although this remains to be demonstrated (Table 1; Adar et al., 2015; Puentes & Björkman, 2017).

2.2 | Herbivore feeding altered by parasitoids

Parasitoids are insects (usually wasps or flies) which lay their eggs on or in a host that will be killed upon parasitoid development (Godfray, 1994). Koinobiont parasitoids do not fully arrest their host from growing and feeding while the parasitoid larva is developing (as

TABLE 1 Positive and negative expected outcomes for plants in different plant-carnivore interaction types

Interactions type	Positive effects for plants	Hypothesized negative effects for plants	Current evidence for negative effects
Carnivores increasing plant damage (Figure 1a)	Omnivores reduce herbivore pressure and plant damage	Omnivore plant-feeding negatively affects plants, and induction of a plant defence response can be costly if useless	Reduced crop yield (Puentes et al., 2018)
	Herbivores parasitized by (koinobiont, mostly solitary) parasitoids grow and feed less	Some koinobiont parasitoids (mostly gregarious) enhance their host's growth, resulting in more plant damage	Reduced plant fitness (Xi et al., 2015) Increased plant damage (Ode, 2006)
Carnivore effects on pollinators (Figure 1b)	In general, predation by carnivores reduces plant damage via killing/repelling herbivores	When disrupting plant mutualism with pollinators, carnivores reduce plant pollination	Reduced plant fitness (Antiqueira & Romero, 2016)
Non-consumptive effects of carnivores on herbivores (Figure 1c)	Carnivores or aphid- tending ants repel most of the herbivores on the plant	Aphid-tending ants cause an outbreak of the tended herbivore	Reduced plant fitness (Canedo- Júnior et al., 2017; Ortega- Ramos et al., 2020; Renault et al., 2005)
		Negative effects may be increased when herbivores are vectors of pathgens and spread towards kin plants	/
Impact of carnivores on plant-mediated interactions (Figure 1d)	Plant-feeding by omnivores induces cross-resistance against herbivores, and volatiles that attract natural enemies of the herbivores	Volatiles produced by plant in response to omnivore feeding can also attract herbivores	Plant induction (reviewed by Pappas et al., 2017) Plant attraction of herbivores (Pérez- Hedo et al., 2015)
	Parasitized herbivores induce a lower plant resistance response, which could save some resources. Their HIPVs repel other parasitoids, preventing super-parasitism	Remaining unparasitized herbivores benefit from lower plant defence and repellence of parasitoids	Plant induction (Poelman et al., 2011; Tan et al., 2018)
		Altered HIPVs attract hyperparasitoids, whose presence can cause detrimental effects	Deterrence of parasitoids (Kafle et al., 2020) and attraction of hyperparasitoids (Zhu et al., 2015)
	Carnivores kill herbivores which limits plant damage and prevents/reduces plant induction	Killing of a first herbivore with low impact on plant fitness, prevents the plant from being induced and protected against a subsequent herbivore with high negative fitness consequence on plant	/
Intraguild predation (Figure 1e)	The presence of many carnivores can have a synergistic effect that reduces herbivore damage on the plant	A (dominant) carnivore can kill and repel other carnivores, resulting in a lower control of herbivores and a higher plant damage	Reduced plant biomass (Finke & Denno, 2005)

opposed to idiobiont parasitoids, that arrest their host growth after oviposition by paralyzing the host; Mackauer & Sequeira, 1993). Therefore, herbivores that are parasitized by a koinobiont parasitoid are still able to move and feed on plants for a certain amount of time. In most documented cases, herbivores parasitized by a solitary parasitoid grow and feed less compared to unparasitized ones, resulting in reduced plant damage (Bustos-Segura et al., 2019; Gols et al., 2015; Hoballah & Turlings, 2001). However, some koinobiont parasitoids enhance herbivore growth for their own benefit, leading to parasitized herbivores causing more damage than unparasitized ones (Ode, 2006; Rahman, 1970; Xi et al., 2015). Some parasitized aphids also increase feeding because of a reduced food assimilation efficiency (Cloutier & Mackauer, 1980). In addition, parasitized aphids are still able to reproduce and even increase their fecundity before death, producing heavier offspring with a higher fecundity, which could have positive immediate consequences for population growth (Kaiser & Heimpel, 2016). Parasitoids regulate the growth of their host according to their resource needs (Harvey, 2005). Accordingly, the feeding behaviour of a parasitized herbivore is more likely to increase when several parasitoids are developing inside (e.g. gregarious parasitoid and/or superparasitism) with potential negative effects on plant fitness (Smallegange et al., 2008). Solitary parasitoids can also increase their host feeding if the amount of resources available in the herbivorous host is not sufficient for the optimal development of one parasitoid larva (Harvey et al., 2010). Finally, we speculate that increased herbivory due to parasitism is particularly common in an ecological context with few hosts (increased superparasitism risks) and/or hosts of poor quality (increased need for host growth regulation by parasitoid to reach maximal development). When parasitoids enhance the feeding by their host this would lead to differential interests of the carnivore and the plant and may result in reduced plant fitness (Xi et al., 2015; Table 1).

3 | CARNIVORE EFFECTS ON POLLINATORS

Such different interests of plants and predators also arise when predators consume organisms that are beneficial to plants, such as pollinators (Knight et al., 2006; Romero et al., 2011). Plants in areas with a high density of predators suffer from reduced pollination and fitness, caused by pollinators avoiding these high-risk areas and/or direct predation of pollinators (Romero & Koricheva, 2011). The nonconsumptive effects of predators on pollination may be substantial. For example, crab spiders are generalist sit-and-wait ambush predators on flowers that can benefit the plant by feeding on herbivores (Romero & Vasconcellos-Neto, 2004); yet, they can also have negative effects by decreasing pollinator visits and seed set (Antiqueira & Romero, 2016; Gonçalves-Souza et al., 2008).

In addition, predators may affect pollinators by interfering with reward availability to pollinators. In rare cases, carnivores such as ants or wasps, feed on floral nectar without pollinating the flowers (Maloof & Inouye, 2000). Both nectar robbers, that make a hole in the petal tissue to have direct access to the nectar, and nectar thieves, that feed on nectar without pollinating the plant because of a morphological mismatch, reduce pollinator visitation time and efficiency (Irwin et al., 2001, 2010). Fitness costs of reduced pollination are particularly apparent for plants that solely depend on pollinators for reproduction or when pollen and pollinators are limited (Burkle et al., 2007; Ibarra-Isassi & Oliveira, 2018). When ants enter food-for-protection mutualisms with plants (see Section 4), their presence is not always beneficial. If plants fail to restrict ants to vegetative parts, their movement to inflorescences can lead to nectar robbing, predation or repellence of pollinators (Ibarra-Isassi & Oliveira, 2018; Levan & Holway, 2015; Ohm & Miller, 2014). In order to minimize these negative effects, flowers can produce ant-repellent compounds (Junker et al., 2011) and EFNs are hypothesized to localize ants (and other carnivores) at vegetative parts, distracting them from visiting flowers and lowering the negative effect on pollinators and reproductive fitness (Ness, 2006; Villamil et al., 2019).

4 | NON-CONSUMPTIVE EFFECTS OF CARNIVORES ON HERBIVORES

In addition to the landscape of fear that affects pollinators, the presence of predators affects herbivore behaviour. Herbivores adapt their dispersal behaviour according to predation risks (Lima & Dill, 1990). When prey are hiding, predator presence could reduce herbivore dispersal and increase herbivore density as well as plant damage (Sih & Wooster, 1994). On the other hand, carnivores can increase herbivore dispersal to neighbouring plants in several ways (e.g. escape behaviours or prophylactic feeding of herbivores). Herbivore dispersal has positive consequences for the "original" plant, which is released from herbivory (Sabelis et al., 1999). However, in cases where the direct neighbourhood consists of mostly kin plants, negative inclusive fitness consequences are expected; this effect is increased when herbivores are vectors of plant pathogens (Culshaw-Maurer et al., 2020).

Non-consumptive effects of predators extend to specific antmediated interactions that may enhance herbivore damage to plants. While carnivorous ants are able to directly feed on herbivores, they engage in non-consumptive, mutualistic relationships with honeydew-producing herbivores (mainly Hemiptera). In return for food, ants protect honeydew producers against their natural enemies and/or prey on competing herbivores (Ohm & Miller, 2014; Way, 1963). In most cases, plants benefit from these interactions (Styrsky & Eubanks, 2007), but ant presence can have a deleterious effect of on plant fitness (Canedo-Júnior et al., 2017; Ibarra-Isassi & Oliveira, 2018; Renault et al., 2005; Table 1). Aphid-tending ants can cause pest outbreaks of tended (Ortega-Ramos et al., 2020) and co-occurring hemipterans (Yoo et al., 2013) as they remove Hemiptera-produced honeydew, reducing their disease incidence (Nielsen et al., 2010). An increase in the hemipteran population is especially costly in a community context where herbivore pressure of non-hemipteran herbivores is low, because plants will benefit less from the predation services of ants (Ortega-Ramos et al., 2020; Styrsky & Eubanks, 2010). A negative effect on plant fitness arises when the presence of ants enables the negative effects of hemipterans to exceed the costs inflicted by the herbivore community in the absence of ants (Ortega-Ramos et al., 2020). In addition, the presence of ants can indirectly increase colonization by herbivores able to escape ant-attack, which profit from the deterrence of other local carnivores (Alves-Silva & Del-Claro, 2016).

5 | IMPACT OF CARNIVORES ON PLANT-MEDIATED INTERACTIONS

5.1 | Omnivorous predator effects on plantmediated interactions

Less apparent negative effects of predators come about by indirect trait-mediated interactions that may include networks of indirect species interactions. This cost is particularly high when induced defences are not effective against subsequent herbivores. For example, phloem feeders perform equally well on omnivore-induced plants compared to non-induced control plants (Pappas et al., 2015; Zhang et al., 2018). In addition to the cost of induction (Section 2.1), we hypothesize feeding damage of omnivores to be particularly costly when it causes induced susceptibility, facilitating subsequent herbivores (Underwood, 1998). This is particularly the case for omnivores using a piercing-sucking mode of plant feeding (e.g. mirids) because they secrete effectors responsible for induced susceptibility (Dong et al., 2020).

Plant volatiles induced by omnivores are hypothesized to result in a fitness cost when revealing the location of host plants to herbivores (Dicke & van Loon, 2000). Citrus plants infested with the omnivore phytoseiid Eusius stipulatus were found to be more attractive to the prey herbivore Tetranychus urticae, with no clear pattern of attraction to conspecifics of the phytoseiid omnivore (Cruz-Miralles et al., 2019). In a different system plant feeding by two different omnivores resulted in the attraction of the herbivorous pest Tuta absoluta (Pérez-Hedo et al., 2015). However, no studies quantified the plant fitness consequence of this attraction of herbivores. This negative effect could be increased in a community context where omnivore feeding attracts herbivores but the omnivores are not numerous enough to suppress the arriving herbivores. Furthermore, we speculate that if specialist natural enemies of common pests do not find hosts on plants damaged by omnivores, they may learn and avoid this type of cue (Stephens, 1993).

5.2 | Koinobiont parasitoid effects on plantmediated interactions

Koinobiont parasitoids developing inside their herbivorous host may negatively impact plant fitness when disrupting plant-mediated interactions with other community members. Physiological changes induced by parasitoids in their host mediate parasitoid-plant interactions (Poelman et al., 2011). Parasitized caterpillars have reduced levels of salivary elicitors, leading to a reduced plant induction response to herbivory (Cusumano et al., 2018; Tan et al., 2018) and may increase plant susceptibility to subsequent herbivores (Stam et al., 2014). We hypothesize that parasitoid larvae manipulate the plant response to increase their host's performance (but see Bukovinszky et al., 2009) and, thus, their own fitness, leading to a conflict of interest between parasitoid and plant. This may, however, strongly depend on the herbivore degree of specialization with the plant secondary compounds and its ability to detoxify or sequester them. In some cases, parasitized caterpillars and aphids induce a higher level of plant secondary compounds compared to unparasitized insects (Ode et al., 2016; Vaello et al., 2018). In cases where parasitoids reduce their host plant damage and increase plant response to herbivory (Tan et al., 2019), it could lead to a waste of plant resources.

In parallel to changes in direct defences, also indirect defences are also differentially affected by parasitized herbivores (Poelman et al., 2012; Zhu et al., 2015) and may cause a plant fitness cost by repelling beneficial carnivores from plants. Parasitoids detect their host's presence on plants through HIPVs and prefer those induced by unparasitized herbivores over those induced by parasitized herbivores (Fatouros et al., 2005; Kafle et al., 2020). How generalist predators respond to HIPVs elicited by plants hosting parasitized herbivores is mostly unknown. Plant volatiles induced by parasitized herbivores have likely been under selection to be less attractive or even repel other carnivores, because prevention of host death is critical to parasitoid fitness (Kaplan et al., 2016). This represents another example of conflicting interests of plant and parasitoid. Differential induction of HIPVs by parasitized and unparasitized herbivores are exploited by members of higher trophic levels, such as hyperparasitoids, to locate their host (Poelman et al., 2012; Zhu et al., 2018). Hyperparasitoids can reduce parasitoid efficacy through the production of allelochemicals. These induce parasitoid dispersal from environments with suitable hosts present, locally releasing herbivores from parasitoid pressure (Höller et al., 1994; Petersen et al., 2000). Additionally, if an individual plant is attacked by several generations of an herbivore, hyperparasitization of the first parasitoid generation may reduce parasitoid populations and increase herbivory during the next generations of the herbivore (Tougeron & Tena, 2019).

5.3 | Carnivores reduce herbivore-induced plant vaccination

When an herbivore induces plant cross-resistance against another herbivore, the suppression of the former by a carnivorous arthropod may result in a negative effect on plant fitness (McArt et al., 2013). So called "plant vaccination" (sensu Kessler & Baldwin, 2004) is a positive plant-mediated effect whereby an early-season herbivore with no or neglectable effects on plant fitness induces a plant defensive response effective against a subsequent herbivore with an important negative effect on plant fitness (Agrawal, 1998). For example, Kessler and Baldwin (2004) showed that mirid bugs *Tupiocoris notatus* induce the same resistance response in tobacco plants as *Manduca* larvae *Manduca quinquemaculata* but without plant fitness reduction. As a result, plants first induced by mirid bugs are still induced and protected when attacked by the subsequent herbivore and thereby realize a significant fitness benefit. We speculate that predation of the mirid bug could result in a higher likelihood of plant colonisation by *Manduca* with fitness consequences that are larger than the benefit of predation of the mirid. Finally, this may not apply to koinobiont parasitoids because their host can still feed and induce the plant during a certain period of time (Bustos-Segura et al., 2019).

6 | INTRAGUILD PREDATION

A wide range of carnivorous arthropods is commonly present in natural and agricultural systems (Gagnon et al., 2011) and while they individually suppress pest pressure, their co-occurrence can lead to synergistic or antagonistic effects on each other. This has the potential to affect prey populations and plant fitness (Finke & Denno, 2002; Müller & Brodeur, 2002). Intraguild predation (IGP) is described as an interaction in which two predators have the same food source (extraguild prey), but also have a direct trophic interaction between them (Polis et al., 1989; Figure 2). This leads to a combination of competition and predation between carnivores. IGP causes a variety of direct and indirect ecological effects (Finke & Denno, 2002), which result in alleviation of predator pressure on herbivores when intraguild interactions dominate (Müller & Brodeur, 2002). Negative effects of IGP through an increase of herbivore populations appear to be strongest in simple habitats with low biodiversity. Increased structural complexity of a habitat reduces the chance of IGP taking place, due to the availability of refuges and alternative prey for subordinate carnivores (Snyder, 2019). In community contexts with low plant diversity (such as agroecosystems) and carnivorous arthropods with overlapping traits, the negative effects of (direct and indirect) IGP are expected to impact herbivore suppression and plant fitness.

Direct interactions between carnivores are often asymmetrical: one carnivore feeds on the other but not vice versa. Asymmetrical IGP can be negative for plant fitness and pest suppression. The outcome of this interaction is mostly dependent on the size, mobility and feeding style of the carnivores involved (Müller & Brodeur, 2002; Snyder, 2019). Plant fitness suffers the most when the more vulnerable carnivore is the main pest regulator (Vance-Chalcraft et al., 2007) or in the presence of an aggressive intraguild predator (Rosenheim et al., 1993). Additionally, carnivores interact indirectly through IGP by trait-mediated effects when a carnivore affects the (foraging) behaviour, activity or habitat choice of other guild members, with consequences for their prey (Schmitz et al., 2004). Behavioural alterations through enemy-associated cues (e.g. frass, aggregation pheromones, contact infochemicals) impact complex community dynamics, alleviating carnivore pressure and ultimately leading to larger herbivore populations on the focal patch (Culshaw-Maurer et al., 2020). For example, the presence of an intraguild predator can repel other carnivores (Raymond et al., 2000) and affect their oviposition site selection (Pineda et al., 2007). These trait-mediated effects can reduce the foraging efficiency of other carnivores or result in leaving the focal patch, without contacting the intraguild predator (Mouratidis et al., 2021). We hypothesize that

negative effects on plants due to IGP mainly arise in the presence of a strong intraguild predator dominating other carnivores and poorly (or sub-optimally) controlling pests, which are strengthened through its trait-mediated effects.

7 | CONCLUSIONS AND FUTURE DIRECTIONS

Some plant traits, such as domatia for ants or mites, facilitate a mutualistic interaction between carnivorous arthropods and plants. As discussed by Pearse et al. (2020), other plant traits involved in indirect plant defence are multifunctional, suggesting that other factors select on them. This prevents these traits from becoming more specialized towards indirect plant defence functions. Furthermore, we hypothesize that the specificity of carnivore-plant interactions can be an important factor in the specialization of plant traits toward an indirect defence role. In this review, we argue that negative effects of some carnivorous arthropods may also play an important role as a counter-selection force against the indirect defence function of some plant traits. This is possible in a situation where a plant trait favours herbivore suppression by some carnivores (indirect defence function) but also favours, to a lesser extent, negative interactions with other carnivores. In addition, we stress that antagonistic plantcarnivore interactions should be considered along mutualistic and commensal plant-carnivore interactions in order to have a better understanding of selection forces driving indirect plant defence traits.

Although some of the negative effects of predators, such as omnivory or predation on pollinators, are well characterized (Puentes et al., 2018; Romero et al., 2011), indirect negative effects resulting from plant-mediated interactions initiated by predators or parasitoids have been largely overlooked. The notion that predators may directly or indirectly induce plant responses that lead to changes in the interaction of plants with other community members has resulted in identification of a range of interaction types in several plant species that are initiated by natural enemies (Stam et al., 2014). These studies have provided evidence that these interactions can result in negative consequences for plants such as the attraction of new herbivores or enhanced plant damage. Major challenges for future studies will be to unravel whether the negative effects of carnivores on plants indeed translate into negative effects on plant fitness and whether this fitness cost is still present when the indirect interactions initiated by natural enemies are studied in the natural context of the interacting community. This can only be achieved through field experiments exposing plants to the arthropod communities naturally present in their environment. Furthermore, our study focused on carnivorous arthropods, but similar interactions may take place with non-arthropod carnivores aboveground (e.g. lizards, birds) and belowground (e.g. nematodes; Mäntylä et al., 2011; Rasmann et al., 2005).

Negative effects of predators on plant fitness may result in selection on plant traits to reduce these costs. Arguing from this perspective, we earlier presented examples of such selective forces in the deterrence of ants from flowers (Section 3). Alternatively, some of the interaction types may be largely driven by the benefit of natural enemies, with neutral effects on plant fitness or with limited potential for plants to control for these interactions. For example, after parasitism koinobiont parasitoids manipulate their insect host and host plant to create a suitable environment for their offspring (e.g. increased herbivore feeding, deterrence of conspecifics through HIPVs), which can ultimately result in negative effects on plants (van der Meijden & Klinkhamer, 2000). However, plants may not be able to counter the negative effects of interacting with natural enemies of their herbivores, for example, when parasitoids affect elicitors in herbivore oral secretions that are critical for plants to recognize herbivory in the first place.

In conclusion, by summarising the current knowledge about the negative effects of carnivores on plants we urge future work to quantify the potential of these interactions for selecting on plant traits. We recommend the study of plants in their natural environments where the interaction with natural arthropod communities can lead to negative effects.

ACKNOWLEDGEMENTS

We thank three anonymous reviewers for their insightful suggestions to a previous version of this manuscript. Our research was funded by Early Postdoc Mobility fellowship from the Swiss National Science Foundation to M.A.C.C. and Open Competition grant from the Netherlands Organization for Scientific Research (NWO) ALWOP.368 to E.H.P.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

M.A.C.C., M.E.B., and E.H.P. had the original idea for this review, M.A.C.C. and M.E.B. wrote the first version of the manuscript; E.H.P. and M.D. edited the manuscript and all authors contributed substantially to the final version.

DATA AVAILABILITY STATEMENT

No new data are associated with this manuscript.

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REFERENCES

- Aartsma, Y., Bianchi, F. J. J. A., van der Werf, W., Poelman, E. H., & Dicke, M. (2017). Herbivore-induced plant volatiles and tritrophic interactions across spatial scales. New Phytologist, 216(4), 1054–1063. https://doi.org/10.1111/nph.14475
- Abdala-Roberts, L., Puentes, A., Finke, D. L., Marquis, R. J., Montserrat, M., Poelman, E. H., Rasmann, S., Sentis, A., Dam, N. M., Wimp, G., Mooney, K., & Björkman, C. (2019). Tri-trophic interactions: Bridging

species, communities and ecosystems. *Ecology Letters*, 22, 2151-2167. https://doi.org/10.1111/ele.13392

- Abram, P. K., Brodeur, J., Urbaneja, A., & Tena, A. (2019). Nonreproductive effects of insect parasitoids on their hosts. *Annual Review of Entomology*, 64(1), 259–276. https://doi.org/10.1146/annurevento-011118-111753
- Adar, E., Inbar, M., Gal, S., Issman, L., & Palevsky, E. (2015). Plant cell piercing by a predatory mite: Evidence and implications. *Experimental* and Applied Acarology, 65(2), 181–193. https://doi.org/10.1007/ s10493-014-9860-5
- Agrawal, A. A. (1998). Induced responses to herbivory and increased plant performance. *Science*, 279(5354), 1201–1202. https://doi. org/10.1126/science.279.5354.1201
- Agrawal, A. A., Kobayashi, C., & Thaler, J. S. (1999). Influence of prey availability and induced host-plant resistance on omnivory by western flower thrips. *Ecology*, 80(2), 518–523. https://doi. org/10.1890/0012-9658(1999)080[0518:IOPAAI]2.0.CO;2
- Albajes, R., Castañé, C., Gabarra, R., & Alomar, O. (2006). Risks of plant damage caused by natural enemies introduced for arthropod biological control. In F. Bigler, D. Babendreier, & U. Kuhlmann (Eds.), Environmental impact of invertebrates for biological control of arthropods: Methods and risk assessment (pp. 132–144). CABI Publishing Oxon.
- Alves-Silva, E., & Del-Claro, K. (2016). On the inability of ants to protect their plant partners and the effect of herbivores on different stages of plant reproduction: Ant-Plant-Thrips Interactions. Austral Ecology, 41(3), 263–272. https://doi.org/10.1111/aec.12307
- Antiqueira, P. A. P., & Romero, G. Q. (2016). Floral asymmetry and predation risk modify pollinator behavior, but only predation risk decreases plant fitness. *Oecologia*, 181(2), 475–485. https://doi.org/10.1007/ s00442-016-3564-y
- Boitani, L., & Powell, R. A. (Eds.). (2012). Carnivore Ecology and Conservation: A handbook of techniques. Oxford University Press.
- Bukovinszky, T., Poelman, E. H., Gols, R., Prekatsakis, G., Vet, L. E., Harvey, J. A., & Dicke, M. (2009). Consequences of constitutive and induced variation in plant nutritional quality for immune defence of a herbivore against parasitism. *Oecologia*, 160(2), 299–308. https://doi. org/10.1007/s00442-009-1308-y
- Burkle, L. A., Irwin, R. E., & Newman, D. A. (2007). Predicting the effects of nectar robbing on plant reproduction: Implications of pollen limitation and plant mating system. *American Journal of Botany*, 94(12), 1935–1943. https://doi.org/10.3732/ajb.94.12.1935
- Bustos-Segura, C., Cuny, M. A. C., & Benrey, B. (2019). Parasitoids of leaf herbivores enhance plant fitness and do not alter caterpillar-induced resistance against seed beetles. *Functional Ecology*, 34(3), 586–596. https://doi.org/10.1016/s0740-5472(96)90021-5
- Canedo-Júnior, E. O., Santiago, G. S., Zurlo, L. F., Ribas, C. R., Carvalho, R. P., Alves, G. P., Carvalho, M. C. S., & Souza, B. (2017). Isolated and community contexts produce distinct responses by host plants to the presence of ant-aphid interaction: Plant productivity and seed viability. *PLoS ONE*, 12(1), e0170915. https://doi.org/10.1371/journ al.pone.0170915
- Cloutier, C., & Mackauer, M. (1980). The effect of superparasitism by Aphidius smithi (Hymenoptera: Aphidiidae) on the food budget of the pea aphid, Acyrthosiphon pisum (Homoptera: Aphididae). Canadian Journal of Zoology, 58(2), 241–244. https://doi.org/10.1139/ z80-028
- Coll, M., & Guershon, M. (2002). Omnivory in terrestrial arthropods: Mixing plant and prey diets. *Annual Review of Entomology*, 47(1), 267– 297. https://doi.org/10.1146/annurev.ento.47.091201.145209
- Cruz-Miralles, J., Cabedo-López, M., Pérez-Hedo, M., Flors, V., & Jaques, J. A. (2019). Zoophytophagous mites can trigger plant-genotype specific defensive responses affecting potential prey beyond predation: The case of *Euseius stipulatus* and *Tetranychus urticae* in citrus. *Pest Management Science*, 75(7), 1962–1970.

- Cusumano, A., Zhu, F., Volkoff, A. N., Verbaarschot, P., Bloem, J., Vogel, H., Dicke, M., & Poelman, E. H. (2018). Parasitic wasp-associated symbiont affects plant-mediated species interactions between herbivores. *Ecology Letters*, 21(7), 957–967. https://doi.org/10.1111/ ele.12952
- Dicke, M., & Baldwin, I. T. (2010). The evolutionary context for herbivore-induced plant volatiles: Beyond the 'cry for help'. *Trends in Plant Science*, 15(3), 167–175. https://doi.org/10.1016/j.tplan ts.2009.12.002
- Dicke, M., & van Loon, J. J. A. (2000). Multitrophic effects of herbivore-induced plant volatiles in an evolutionary context. *Entomologia Experimentalis et Applicata*, 97(3), 237–249. https://doi. org/10.1046/j.1570-7458.2000.00736.x
- Dong, Y., Jing, M., Shen, D., Wang, C., Zhang, M., Liang, D., Nyawira, K. T., Xia, Q., Zuo, K., Wu, S., Wu, Y., Dou, D., & Xia, A. (2020). The mirid bug *Apolygus lucorum* deploys a glutathione peroxidase as a candidate effector to enhance plant susceptibility. *Journal of Experimental Botany*, 71(9), 2701–2712. https://doi.org/10.1093/jxb/eraa015
- Eubanks, M. D., & Denno, R. F. (1999). The ecological consequences of variation in plants and prey for an omnivorous insect. *Ecology*, 80(4), 1253–1266. https://doi.org/10.1890/0012-9658(1999)080[1253:TE COVI]2.0.CO;2
- Fatouros, N. E., van Loon, J. J. A., Hordijk, K. A., Smid, H. M., & Dicke, M. (2005). Herbivore-induced plant volatiles mediate in-flight host discrimination by parasitoids. *Journal of Chemical Ecology*, 31(9), 2033– 2047. https://doi.org/10.1007/s10886-005-6076-5
- Finke, D. L., & Denno, R. F. (2002). Intraguild predation diminished in complex-structured vegetation: Implications for prey suppression. *Ecology*, 83(3), 643-652. https://doi. org/10.1890/0012-9658(2002)083[0643:IPDICS]2.0.CO;2
- Finke, D. L., & Denno, R. F. (2005). Predator diversity and the functioning of ecosystems: The role of intraguild predation in dampening trophic cascades. *Ecology Letters*, 8(12), 1299–1306. https://doi. org/10.1111/j.1461-0248.2005.00832.x
- Gagnon, A.-È., Heimpel, G. E., & Brodeur, J. (2011). The ubiquity of intraguild predation among predatory arthropods. *PLoS ONE*, 6(11), e28061. https://doi.org/10.1371/journal.pone.0028061
- Godfray, H. C. J. (1994). Parasitoids: Behavioral and Evolutionary Ecology (P. U. Press, Ed.; Vol. 67). Princeton University Press. https://doi. org/10.1016/0169-5347(94)90089-2
- Gols, R., Wagenaar, R., Poelman, E. H., Kruidhof, H. M., van Loon, J. J. A., & Harvey, J. A. (2015). Fitness consequences of indirect plant defence in the annual weed, *Sinapis arvensis*. *Functional Ecology*, 29(8), 1019–1025. https://doi.org/10.1111/1365-2435.12415
- Gómez, J. M., & Zamora, R. (1994). Top-down effects in a tritrophic system: Parasitoids enhance plant fitness. *Ecology*, 75(4), 1023–1030. https://doi.org/10.2307/1939426
- Gonçalves-Souza, T., Omena, P. M., Souza, J. C., & Romero, G. Q. (2008). Trait-mediated effects on flowers: Artificial spiders deceive pollinators and decrease plant fitness. *Ecology*, 89(9), 2407–2413. https:// doi.org/10.1890/07-1881.1
- Harvey, J. A. (2005). Factors affecting the evolution of development strategies in parasitoid wasps: The importance of functional constraints and incorporating complexity. *Entomologia Experimentalis et Applicata*, 117(1), 1–13. https://doi.org/10.1111/j.1570-7458.2005.00348.x
- Harvey, J. A., Sano, T., & Tanaka, T. (2010). Differential host growth regulation by the solitary endoparasitoid, *Meteorus pulchricornis* in two hosts of greatly differing mass. *Journal of Insect Physiology*, 56(9), 1178–1183. https://doi.org/10.1016/j.jinsphys.2010.03.018
- Hoballah, M. E. F., & Turlings, T. C. J. (2001). Experimental evidence that plants under caterpillar attack may benefit from attracting parasitoids. Evolutionary Ecology Research, 3, 553–565.

- Höller, C., Micha, S. G., Schulz, S., Francke, W., & Pickett, J. A. (1994). Enemy-induced dispersal in a parasitic wasp. *Experientia*, 50(2), 182– 185. https://doi.org/10.1007/BF01984961
- Hunter, M. D. (2009). Trophic promiscuity, intraguild predation and the problem of omnivores. Agricultural and Forest Entomology, 11(2), 125– 131. https://doi.org/10.1111/j.1461-9563.2008.00427.x
- Ibarra-Isassi, J., & Oliveira, P. S. (2018). Indirect effects of mutualism: Ant-treehopper associations deter pollinators and reduce reproduction in a tropical shrub. *Oecologia*, 186(3), 691–701. https://doi. org/10.1007/s00442-017-4045-7
- Irwin, R. E., Brody, A. K., & Waser, N. M. (2001). The impact of floral larceny on individuals, populations, and communities. *Oecologia*, 129(2), 161–168. https://doi.org/10.1007/s004420100739
- Irwin, R. E., Bronstein, J. L., Manson, J. S., & Richardson, L. (2010). Nectar robbing: Ecological and evolutionary perspectives. Annual Review of Ecology, Evolution, and Systematics, 41(1), 271–292. https://doi. org/10.1146/annurev.ecolsys.110308.120330
- Junker, R. R., Gershenzon, J., & Unsicker, S. B. (2011). Floral odor bouquet loses its ant repellent properties after inhibition of terpene biosynthesis. *Journal of Chemical Ecology*, 37(12), 1323–1331. https://doi. org/10.1007/s10886-011-0043-0
- Kafle, B. D., Morawo, T., & Fadamiro, H. (2020). Host-induced plant volatiles mediate ability of the parasitoid *Microplitis croceipes* to discriminate between unparasitized and parasitized *Heliothis virescens* larvae and avoid superparasitism. *Journal of Chemical Ecology*, 46(10), 967– 977. https://doi.org/10.1007/s10886-020-01218-x
- Kaiser, M. C., & Heimpel, G. E. (2016). Parasitoid-induced transgenerational fecundity compensation in an aphid. *Entomologia Experimentalis* et Applicata, 159(2), 197–206. https://doi.org/10.1111/eea.12431
- Kaplan, I., Carrillo, J., Garvey, M., & Ode, P. J. (2016). Indirect plantparasitoid interactions mediated by changes in herbivore physiology. *Current Opinion in Insect Science*, 14, 112–119. https://doi. org/10.1016/j.cois.2016.03.004
- Kergunteuil, A., Röder, G., & Rasmann, S. (2019). Environmental gradients and the evolution of tri-trophic interactions. *Ecology Letters*, 22(2), 292–301. https://doi.org/10.1111/ele.13190
- Kessler, A., & Baldwin, I. T. (2004). Herbivore-induced plant vaccination. Part I. The orchestration of plant defenses in nature and their fitness consequences in the wild tobacco Nicotiana attenuata. Plant Journal, 38(4), 639–649. https://doi.org/10.1111/j.1365-313X.2004.02076.x
- Kessler, A., & Halitschke, R. (2007). Specificity and complexity: The impact of herbivore-induced plant responses on arthropod community structure. *Current Opinion in Plant Biology*, 10(4), 409–414. https://doi.org/10.1016/j.pbi.2007.06.001
- Kester, K. M., & Jackson, D. M. (1996). When good bugs go bad: Intraguild predation by Jalysus wickhami on the parasitoid, Cotesia congregata. Entomologia Experimentalis et Applicata, 81(3), 271–276. https://doi. org/10.1046/j.1570-7458.1996.00096.x
- Knight, T. M., Chase, J. M., Hillebrand, H., & Holt, R. D. (2006). Predation on mutualists can reduce the strength of trophic cascades. *Ecology Letters*, 9(11), 1173–1178. https://doi. org/10.1111/j.1461-0248.2006.00967.x
- Levan, K. E., & Holway, D. A. (2015). Ant-aphid interactions increase ant floral visitation and reduce plant reproduction via decreased pollinator visitation. *Ecology*, 96(6), 1620–1630. https://doi. org/10.1890/14-0058.1
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68(4), 619–640. https://doi.org/10.1139/z90-092
- Mackauer, M., & Sequeira, R. (1993). Patterns of development in insect parasites. In N. E. Beckage, S. N. Thompson, & B. A. Federici (Eds.), *Parasites and pathogens of insects* (pp. 1–23). Academic Press.
- Maloof, J. E., & Inouye, D. W. (2000). Are nectar robbers cheaters or mutualists? *Ecology*, 81(10), 2651–2661.https://doi.org/10.1890/0012-9658(2000)081[2651:ANRCOM]2.0.CO;2

- Mäntylä, E., Klemola, T., & Laaksonen, T. (2011). Birds help plants: A meta-analysis of top-down trophic cascades caused by avian predators. *Oecologia*, 165(1), 143–151. https://doi.org/10.1007/s0044 2-010-1774-2
- McArt, S. H., Halitschke, R., Salminen, J. P., & Thaler, J. S. (2013). Leaf herbivory increases plant fitness via induced resistance to seed predators. *Ecology*, 94(4), 966–975. https://doi.org/10.1890/12-1664.1
- Moerkens, R., Pekas, A., Bellinkx, S., Hanssen, I., Huysmans, M., Bosmans, L., & Wäckers, F. (2020). Nesidiocoris tenuis as a pest in Northwest Europe: Intervention threshold and influence of Pepino mosaic virus. Journal of Applied Entomology, 144(7), 566–577. https:// doi.org/10.1111/jen.12789
- Mouratidis, A., Vacas, S., Herrero, J., Navarro-Llopis, V., Dicke, M., & Tena, A. (2021). Parasitic wasps avoid ant-protected hemipteran hosts via the detection of ant cuticular hydrocarbons. *Proceedings of the Royal Society B: Biological Sciences*, 288(1942), 20201684. https:// doi.org/10.1098/rspb.2020.1684
- Müller, C. B., & Brodeur, J. (2002). Intraguild predation in biological control and conservation biology. *Biological Control*, 25(3), 216–223. https://doi.org/10.1016/S1049-9644(02)00102-0
- Ness, J. H. (2006). A mutualism's indirect costs: The most aggressive plant bodyguards also deter pollinators. *Oikos*, 113(3), 506–514. https://doi.org/10.1111/j.2006.0030-1299.14143.x
- Nielsen, C., Agrawal, A. A., & Hajek, A. E. (2010). Ants defend aphids against lethal disease. *Biology Letters*, 6(2), 205–208. https://doi. org/10.1098/rsbl.2009.0743
- Ode, P. J. (2006). Plant chemistry and natural enemy fitness: Effects on herbivore and natural enemy interactions. *Annual Review of Entomology*, *51*(1), 163–185. https://doi.org/10.1146/annur ev.ento.51.110104.151110
- Ode, P. J., Harvey, J. A., Reichelt, M., Gershenzon, J., & Gols, R. (2016). Differential induction of plant chemical defenses by parasitized and unparasitized herbivores: Consequences for reciprocal, multitrophic interactions. *Oikos*, 125(10), 1398–1407. https://doi.org/10.1111/oik.03076
- Ohm, J. R., & Miller, T. E. X. (2014). Balancing anti-herbivore benefits and anti-pollinator costs of defensive mutualists. *Ecology*, 95(10), 2924– 2935. https://doi.org/10.1890/13-2309.1
- Ortega-Ramos, P. A., Mezquida, E. T., & Acebes, P. (2020). Ants indirectly reduce the reproductive performance of a leafless shrub by benefiting aphids through predator deterrence. *Plant Ecology*, 221(2), 91– 101. https://doi.org/10.1007/s11258-019-00995-0
- Pappas, M. L., Broekgaarden, C., Broufas, G. D., Kant, M. R., Messelink, G. J., Steppuhn, A., Wäckers, F., & van Dam, N. M. (2017). Induced plant defences in biological control of arthropod pests: A doubleedged sword. *Pest Management Science*, *73*(9), 1780–1788. https:// doi.org/10.1002/ps.4587
- Pappas, M. L., Steppuhn, A., Geuss, D., Topalidou, N., Zografou, A., Sabelis, M. W., & Broufas, G. D. (2015). Beyond predation: The zoophytophagous predator *Macrolophus pygmaeus* induces tomato resistance against spider mites. *PLoS ONE*, 10(5), 1–18. https://doi. org/10.1371/journal.pone.0127251
- Pearse, I. S., LoPresti, E., Schaeffer, R. N., Wetzel, W. C., Mooney, K. A., Ali, J. G., Ode, P. J., Eubanks, M. D., Bronstein, J. L., & Weber, M. G. (2020). Generalising indirect defence and resistance of plants. *Ecology Letters*, 23(7), 1137–1152. https://doi.org/10.1111/ele.13512
- Pérez-Hedo, M., Urbaneja-Bernat, P., Jaques, J. A., Flors, V., & Urbaneja, A. (2015). Defensive plant responses induced by *Nesidiocoris tenuis* (Hemiptera: Miridae) on tomato plants. *Journal of Pest Science*, 88(3), 543–554. https://doi.org/10.1007/s10340-014-0640-0
- Petersen, G., Matthiesen, C., Francke, W., & Wyss, U. (2000). Hyperparasitoid volatiles as possible foraging behaviour determinants in the aphid parasitoid *Aphidius uzbekistanicus* (Hymenoptera: Aphidiidae). *European Journal of Entomology*, 97(4), 545–550. https:// doi.org/10.14411/eje.2000.084

- Pineda, A., Morales, I., Marcos-García, M. A., & Fereres, A. (2007). Oviposition avoidance of parasitized aphid colonies by the syrphid predator *Episyrphus balteatus* mediated by different cues. *Biological Control*, 42(3), 274–280. https://doi.org/10.1016/j.bioco ntrol.2007.05.017
- Poelman, E. H., Bruinsma, M., Zhu, F., Weldegergis, B. T., Boursault, A. E., Jongema, Y., van Loon, J. J. A., Vet, L. E. M., Harvey, J. A., & Dicke, M. (2012). Hyperparasitoids use herbivore-induced plant volatiles to locate their parasitoid host. *PLoS Biology*, 10(11). https://doi. org/10.1371/journal.pbio.1001435
- Poelman, E. H., & Dicke, M. (2014). Plant-mediated interactions among insects within a community ecological perspective. Annual Plant Reviews: Insect-plant Interactions, 47, 309–337. https://doi. org/10.1002/9781118829783.ch9
- Poelman, E. H., Gols, R., Snoeren, T. A. L., Muru, D., Smid, H. M., & Dicke, M. (2011). Indirect plant-mediated interactions among parasitoid larvae. *Ecology Letters*, 14(7), 670–676. https://doi. org/10.1111/j.1461-0248.2011.01629.x
- Polis, G. A., Myers, C. A., & Holt, R. D. (1989). The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annual Review of Ecology and Systematics*, 20(1), 297–330. https://doi. org/10.1146/annurev.es.20.110189.001501
- Price, P. W., Bouton, C. E., Gross, P., McPheron, B. A., Thompson, J. N., & Weis, A. E. (1980). Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, 11(1), 41–65. https:// doi.org/10.1146/annurev.es.11.110180.000353
- Puentes, A., & Björkman, C. (2017). Costs and benefits of omnivoremediated plant protection: Effects of plant-feeding on Salix growth more detrimental than expected. Oecologia, 184(2), 485–496. https://doi.org/10.1007/s00442-017-3878-4
- Puentes, A., Stephan, J. G., & Björkman, C. (2018). A systematic review on the effects of plant-feeding by omnivorous arthropods: Time to catch-up with the Mirid-Tomato bias? *Frontiers in Ecology and Evolution*, 6. https://doi.org/10.3389/fevo.2018.00218
- Rahman, M. (1970). Effect of parasitism on food consumption of Pieris rapae larvae. Journal of Economic Entomology, 63(3), 820–821.
- Rasmann, S., Köllner, T. G., Degenhardt, J., Hiltpold, I., Toepfer, S., Kuhlmann, U., Gershenzon, J., & Turlings, T. C. J. (2005). Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature*, 434(7034), 732–737. https://doi.org/10.1038/ nature03451
- Raymond, B., Darby, A. C., & Douglas, A. E. (2000). Intraguild predators and the spatial distribution of a parasitoid. *Oecologia*, 124(3), 367– 372. https://doi.org/10.1007/s004420000396
- Renault, C. K., Buffa, L. M., & Delfino, M. A. (2005). An aphid-ant interaction: Effects on different trophic levels. *Ecological Research*, 20(1), 71–74. https://doi.org/10.1007/s11284-004-0015-8
- Romero, G. Q., Antiqueira, P. A. P., & Koricheva, J. (2011). A meta-analysis of predation risk effects on pollinator behaviour. *PLoS ONE*, 6(6), https://doi.org/10.1371/journal.pone.0020689
- Romero, G. Q., & Koricheva, J. (2011). Contrasting cascade effects of carnivores on plant fitness: A meta-analysis. *Journal of Animal Ecology*, 80(3), 696–704. https://doi. org/10.1111/j.1365-2656.2011.01808.x
- Romero, G. Q., & Vasconcellos-Neto, J. (2004). Spatial distribution patterns of jumping spiders associated with terrestrial Bromeliads. *Biotropica*, 36(4), 596–601. https://doi.org/10.1111/ j.1744-7429.2004.tb00353.x
- Rosenheim, J. A., Wilhoit, L. R., & Armer, C. A. (1993). Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia*, 96(3), 439–449. https:// doi.org/10.1007/BF00317517
- Sabelis, M. W., Baalen, M. V., Bakker, F., Bruin, J., Egas, M., Janssen, A. R. M., Lesna, I. K., Pels, B., Rijn, V. P. C. J., & Scutareanu, P. (1999). The

evolution of direct and indirect plant defence against herbivorous arthropods. In H. Olff, V. K. Brown, & R. H. Drent (Eds.), *Herbivores: Between plants and predators* (pp. 109–166). Blackwell Science.

- Schmitz, O. J., Krivan, V., & Ovadia, O. (2004). Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecology Letters*, 7(2), 153–163. https://doi.org/10.1111/j.1461-0248.2003.00560.x
- Schuman, M. C., Barthel, K., & Baldwin, I. T. (2012). Herbivory-induced volatiles function as defenses increasing fitness of the native plant *Nicotiana attenuata* in nature. *Elife*, 1, e00007.
- Sih, A., & Wooster, D. E. (1994). Prey behavior, prey dispersal, and predator impacts on stream prey. *Ecology*, 75(5), 1199–1207. https://doi.org/10.2307/1937446
- Smallegange, R. C., van Loon, J. J. A., Blatt, S. E., Harvey, J. A., & Dicke, M. (2008). Parasitoid load affects plant fitness in a tritrophic system. *Entomologia Experimentalis et Applicata*, 128(1), 172–183. https://doi.org/10.1111/j.1570-7458.2008.00693.x
- Snyder, W. E. (2019). Give predators a complement: Conserving natural enemy biodiversity to improve biocontrol. *Biological Control*, 135, 73– 82. https://doi.org/10.1016/j.biocontrol.2019.04.017
- Stam, J. M., Kroes, A., Li, Y., Gols, R., van Loon, J. J. A., Poelman, E. H., & Dicke, M. (2014). Plant interactions with multiple insect herbivores: From community to genes. *Annual Review of Plant Biology*, 65(1), 689– 713. https://doi.org/10.1146/annurev-arplant-050213-035937
- Stephens, D. W. (1993). Learning and behavioral ecology: Incomplete information and environmental predictability. In D. R. Papaj & A. C. Lewis (Eds.), *Insect learning* (pp. 195–218). Springer.
- Styrsky, J. D., & Eubanks, M. D. (2007). Ecological consequences of interactions between ants and honeydew-producing insects. *Proceedings of the Royal Society B: Biological Sciences*, 274(1607), 151–164. https://doi.org/10.1098/rspb.2006.3701
- Styrsky, J. D., & Eubanks, M. D. (2010). A facultative mutualism between aphids and an invasive ant increases plant reproduction. *Ecological Entomology*, 35(2), 190–199. https://doi. org/10.1111/j.1365-2311.2009.01172.x
- Tan, C.-W., Peiffer, M., Hoover, K., Rosa, C., Acevedo, F. E., & Felton, G. W. (2018). Symbiotic polydnavirus of a parasite manipulates caterpillar and plant immunity. *Proceedings of the National Academy* of Sciences of the United States of America, 115(20), 5199–5204. https://doi.org/10.1073/pnas.1717934115
- Tan, C. W., Peiffer, M., Hoover, K., Rosa, C., & Felton, G. W. (2019). Parasitic wasp mediates plant perception of insect herbivores. *Journal of Chemical Ecology*, 45(11-12), 972-981. https://doi. org/10.1007/s10886-019-01120-1
- Tougeron, K., & Tena, A. (2019). Hyperparasitoids as new targets in biological control in a global change context. *Biological Control*, 130, 164–171. https://doi.org/10.1016/j.biocontrol.2018.09.003
- Turlings, T. C. J., & Erb, M. (2018). Tritrophic interactions mediated by herbivore-induced plant volatiles: Mechanisms, ecological relevance, and application potential. *Annual Review of Entomology*, 63(1), 433–452. https://doi.org/10.1146/annurev-ento-020117-043507
- Underwood, N. C. (1998). The timing of induced resistance and induced susceptibility in the soybean-Mexican bean beetle system. *Oecologia*, 114(3), 376-381. https://doi.org/10.1007/s0044 20050460
- Vaello, T., Sarde, S. J., Marcos-García, M. Á., de Boer, J. G., & Pineda, A. (2018). Modulation of plant-mediated interactions between herbivores of different feeding guilds: Effects of parasitism and belowground interactions. *Scientific Reports*, 8, 14424. https://doi. org/10.1038/s41598-018-32131-9

- van der Meijden, E., & Klinkhamer, P. G. L. (2000). Conflicting interests of plants and the natural enemies of herbivores. *Oikos*, *89*(1), 202–208. https://doi.org/10.1034/j.1600-0706.2000.890123.x
- van Lenteren, J. C., Bolckmans, K., Köhl, J., Ravensberg, W. J., & Urbaneja, A. (2018). Biological control using invertebrates and microorganisms: Plenty of new opportunities. *BioControl*, 63(1), 39–59. https://doi. org/10.1007/s10526-017-9801-4
- Vance-Chalcraft, H. D., Rosenheim, J. A., Vonesh, J. R., Osenberg, C. W., & Sih, A. (2007). The influence of intraguild predation on prey suppression and prey release: A meta-analysis. *Ecology*, 88(11), 2689– 2696. https://doi.org/10.1890/06-1869.1
- Villamil, N., Boege, K., & Stone, G. N. (2019). Testing the distraction hypothesis: Do extrafloral nectaries reduce ant-pollinator conflict? *Journal of Ecology*, 107(3), 1377–1391. https://doi. org/10.1111/1365-2745.13135
- Way, M. J. (1963). Mutualism between ants and honeydew-producing Homoptera. Annual Review of Entomology, 8(1), 307–344. https://doi. org/10.1146/annurev.en.08.010163.001515
- Xi, X., Eisenhauer, N., & Sun, S. (2015). Parasitoid wasps indirectly suppress seed production by stimulating consumption rates of their seed-feeding hosts. *Journal of Animal Ecology*, 84(4), 1103–1111. https://doi.org/10.1111/1365-2656.12361
- Yoo, H. J. S., Kizner, M. C., & Holway, D. A. (2013). Ecological effects of multi-species, ant-hemipteran mutualisms in citrus. *Ecological Entomology*, 38(5), 505–514. https://doi.org/10.1111/een.12042
- Zhang, N. X., Messelink, G. J., Alba, J. M., Schuurink, R. C., Kant, M. R., & Janssen, A. (2018). Phytophagy of omnivorous predator *Macrolophus pygmaeus* affects performance of herbivores through induced plant defences. *Oecologia*, 186(1), 101–113. https://doi.org/10.1007/s0044 2-017-4000-7
- Zhu, F., Broekgaarden, C., Weldegergis, B. T., Harvey, J. A., Vosman, B., Dicke, M., & Poelman, E. H. (2015). Parasitism overrides herbivore identity allowing hyperparasitoids to locate their parasitoid host using herbivore-induced plant volatiles. *Molecular Ecology*, 24(11), 2886– 2899. https://doi.org/10.1111/mec.13164
- Zhu, F., Cusumano, A., Bloem, J., Weldegergis, B. T., Villela, A., Fatouros, N. E., van Loon, J. J. A., Dicke, M., Harvey, J. A., Vogel, H., & Poelman, E. H. (2018). Symbiotic polydnavirus and venom reveal parasitoid to its hyperparasitoids. *Proceedings of the National Academy of Sciences* of the United States of America, 115(20), 5205–5210. https://doi. org/10.1073/pnas.1717904115
- Züst, T., & Agrawal, A. A. (2017). Trade-offs between plant growth and defense against insect herbivory: An ermerging mechanistic synthesis. Annual Review of Plant Biology, 68(1), 513–534. https://doi. org/10.1146/annurev-arplant-042916-040856

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Cuny, M. A. C., Bourne, M. E., Dicke, M., & Poelman, E. H. (2021). The enemy of my enemy is not always my friend: Negative effects of carnivorous arthropods on plants. *Functional Ecology*, 00, 1–11. <u>https://doi.</u> org/10.1111/1365-2435.13884