

REVIEWS AND SYNTHESES

Generalising indirect defence and resistance of plants

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Abstract

Indirect defence, the adaptive top-down control of herbivores by plant traits that enhance predation, is a central component of plant–herbivore interactions. However, the scope of interactions that comprise indirect defence and associated ecological and evolutionary processes has not been clearly defined. We argue that the range of plant traits that mediate indirect defence is much greater than previously thought, and we further organise major concepts surrounding their ecological functioning. Despite the wide range of plant traits and interacting organisms involved, indirect defences show commonalities when grouped. These categories are based on whether indirect defences boost natural enemy abundance via food or shelter resources, or, alternatively, increase natural enemy foraging efficiency via information or alteration of habitat complexity. The benefits of indirect defences to natural enemies should be further explored to establish the conditions in which indirect defence generates a plant–natural enemy mutualism. By considering the broader scope of plant–herbivore–natural enemy interactions that comprise indirect defence, we can better understand plant-based food webs, as well as the evolutionary processes that have shaped them.

Keywords

herbivory, indirect defense, plant–insect interactions, protective mutualism, tritrophic interactions, trophic cascade.

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INTRODUCTION

Indirect defence by plants occurs when plants interact with the enemies of their herbivores to reduce herbivory (Heil 2008; Kessler & Heil 2011). Plants can, for example, provide resources to attract and retain natural enemies. One of the best-known examples of this form of indirect defence involves interactions in which plants provide ants with food or shelter; these ants in turn attack herbivores, to the benefit of the plants (Rico-Gray & Oliveira 2007; Fig. 1a). In another well-known example, volatile odours emitted by plants following herbivore attack attract parasitic and predatory arthropods (natural enemies) that attack herbivores, to the benefit of the plants (Dicke & Baldwin 2010; Fig. 1b). Recent work suggests that indirect defence is probably ubiquitous in natural and managed systems. Yet, we know little about the breadth of plant traits that are involved in indirect defence and even less about their ecological and evolutionary consequences.

Our goals in this manuscript are to explore a broader range of traits that can be considered as indirect defence and to find commonalities in their ecological and evolutionary consequences among disparate systems. To do this, we provide a concise definition of indirect defence, as well as of related

concepts like indirect resistance. Within the scope of these definitions, we describe a wide range of plant traits that may be considered indirect defences, and highlight the main lines of evidence for demonstrating that a particular plant trait functions as an indirect defence. Finally, we synthesise ecological and evolutionary components of indirect defence to identify differences and commonalities among systems. We conclude that indirect defence is a nearly ubiquitous interaction in plants, even though the consequences and evolutionary histories of indirect defences vary considerably and have been thoroughly explored in very few systems to date.

HISTORY AND DEFINITIONS

The term ‘indirect defence’ was introduced in the late 1980s, primarily to describe plant volatile emissions (herbivore-induced plant volatiles, hereafter HIPVs) that attract natural enemies of herbivores (e.g. Fig. 1b; Dicke & Sabelis 1988; Turlings *et al.* 1990). However, the concept of a defensive tritrophic interaction initiated by plant traits is much older (Lundström 1887; Rico-Gray & Oliveira 2007, and references therein). Studies of plant–ant interactions repeatedly uncovered plant traits best explained as adaptations to attract ants

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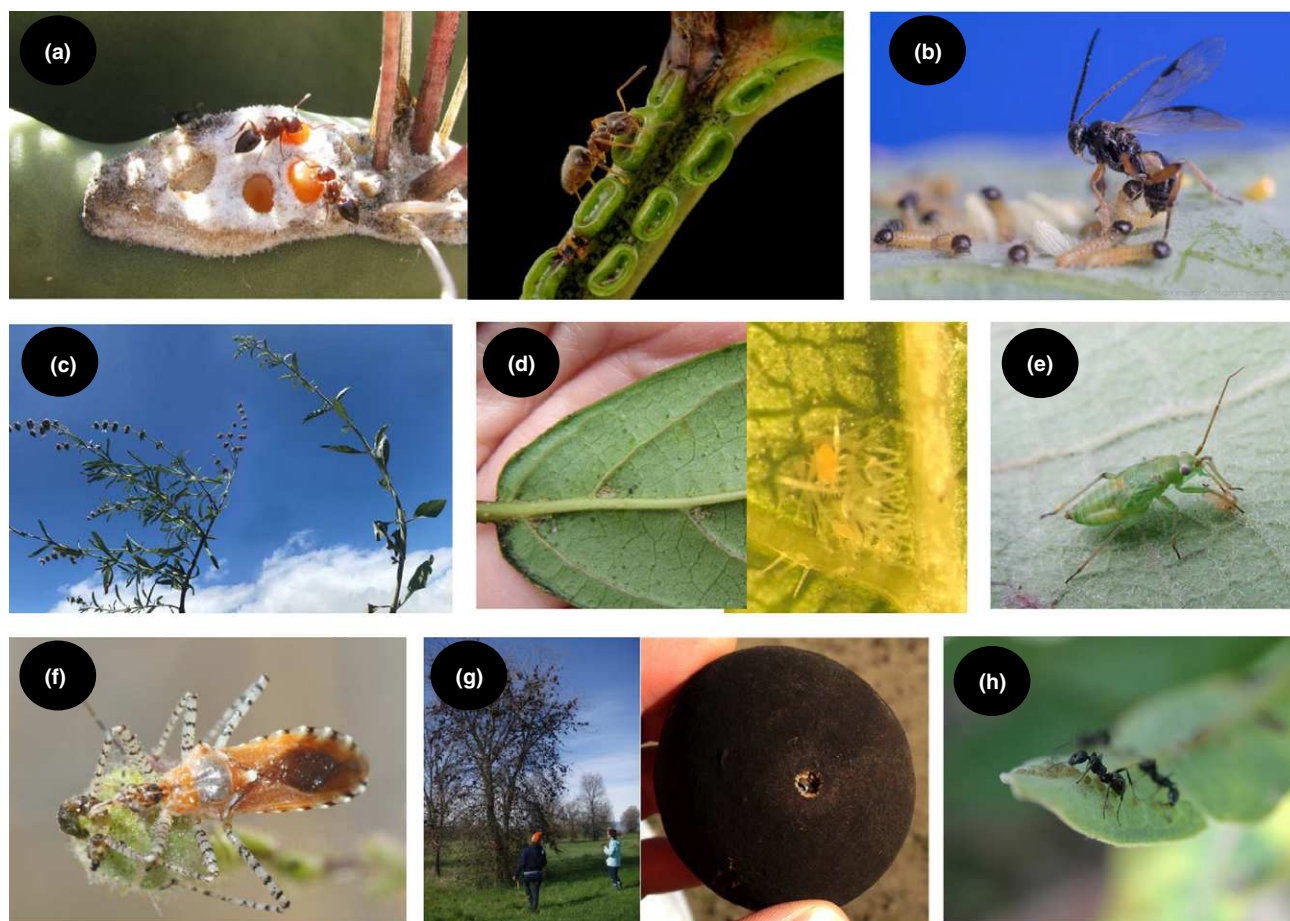


Figure 1 Examples of indirect defence and resistance. (a) Extrafloral nectaries on (left) barrel cactus and (right) *Viburnum* plants attract ants; (b) mustard plants attract *Cotesia glomerata* parasitoids that consume *Pieris brassicae* herbivores; (c) less bushy plant architectures facilitate greater attack rate of herbivores by birds; (d) acarodomatia (hair tufts) house predatory mites (left = full leaf, right – close up); (e) high-nitrogen leaf tissue retains omnivorous insects such as *Orthotylus marginalis* that consume other herbivores (f) carrion (dead insects) entrapped on the sticky hairs of *Madia elegans* is eaten by a predatory assassin bug (g) senesced gall structures on valley oak (*Quercus lobata*) house numerous predators such as spiders (left – tree with many galls; right – a spider hiding in a gall emergence hole); (h) plants that accumulate herbivorous aphids also attract ants that consume other herbivores to either the benefit or the detriment of the plant. Photograph credits: (a left) Michele Lanan; (a right) Marjorie Weber; (b) Hans Schmid; (c) Kailen Mooney; (d left and right) Marjorie Weber; (e) Karin Eklund; (f) Eric LoPresti; (g left and right) Will Wetzel; (h) Kailen Mooney.

that serve as ‘bodyguards’ (Fig. 1a, Bentley 1977). Around the same time, work with domatia that house mites (acarodomatia) revealed similar interactions (O’Dowd & Willson 1991). Recognising these similarities, Heil (2008) and Kessler & Heil (2011) synthesised ant–plant systems, predatory mite–plant systems and plant–natural enemy HIPV systems to generate a more general concept of indirect defence.

Simultaneously, indirect defence was being studied in several other fields. One body of work concerning tritrophic interactions and herbivore regulation by plant defences and natural enemies focused on a broader array of plant–herbivore–natural enemy interactions (Price *et al.* 1980). Models exploring how plants might influence such predator–prey dynamics suggested that a plant’s influence on the third trophic level might be one of its most potent lines of defence against herbivores (Janssen *et al.* 1998; Sabelis *et al.* 1999a,b). Over the past decade, this work has stimulated empirical studies on how a diversity of plant traits affect natural enemies of herbivores. In agro-ecosystems, the burgeoning field of

integrated pest management sought to reduce herbivory and optimise crop yield while minimising pesticide use, in part by manipulating plant traits to better retain natural enemies in croplands (Janssen *et al.* 1998; Cortesero *et al.* 2000; Peterson *et al.* 2016; Stenberg, Heil, Åhman, & Björkman, 2015). Finally, the study of indirect defence was being developed in the mutualism literature, largely focusing on the role of reciprocal selection in ant–plant systems (Rico-Gray & Oliveira 2007; Mayer *et al.* 2014). Across these bodies of work over the past 10–15 years, an increasing number of studies has described a broad range of plant traits that might function as indirect defences (e.g. Styrsky & Eubanks 2007; Romero *et al.* 2008; Singer *et al.* 2012; Abdala-Roberts & Mooney 2013; Krimmel & Pearse 2013; Wetzel *et al.* 2016; Liman *et al.* 2017).

We define an indirect defence as a plant trait that increases plant fitness by reducing the negative consequences of herbivory or pathogen infection via changes in the local abundance or behaviour of predators, parasitoids, parasites or pathogens

(hereafter ‘natural enemies’). This definition is consistent with past use of the term (Kessler & Heil 2011), and with definitions of defence more generally (Karban & Baldwin 1997). Together, indirect and direct defence make up the total defence of a plant. However, it is important to recognise that direct and indirect defence can interact, and a single trait may operate as both a direct and an indirect defence. For example, a direct defence may slow the development of an herbivore and thereby increase its likelihood of attack by natural enemies (Benrey & Denno 1997; Uesugi 2015). Indirect defences increase plant fitness in the presence of herbivores and natural enemies. In contrast, ‘indirect resistance’ plant traits are those that have a negative impact on herbivore performance, host preference or foraging behaviour via their effects on natural enemies (Kessler & Heil 2011). Importantly, indirect defence is only a subset of indirect resistance. Herbivore preference or performance can be decreased with no benefit to the plant if the plant tolerates herbivore damage (Fornoni 2011), or if herbivores are killed or removed after they have already caused damage to the plant (Moran & Hamilton 1980). While indirect defence is the more commonly used term, most studies that use that term actually demonstrate indirect resistance. Of 17 plant traits described as affecting plant predators, most have been shown to mediate indirect resistance because they impact herbivore abundance, but only six have been shown to mediate indirect defence because they increase plant fitness (Table 1). For simplicity, we refer to plant traits as indirect defence if that defensive function has been demonstrated in at least one system at one point in time, while recognising that their consequences in each system likely vary.

Our definition of indirect defence provides clear boundaries to its scope. First, indirect defence is necessarily driven by plant traits that impact natural enemies. Thus, tritrophic interactions that occur irrespective of plant traits are not indirect defence, though we argue that it could be rare that *no* plant traits impact natural enemies. Importantly, our definition of indirect defence is agnostic to the evolutionary history of those traits (e.g. whether they arose or are maintained solely through selection as an indirect defence). However, while our definition of indirect defence does not focus on the role of adaptation in the trait’s evolutionary history, it does focus on its adaptive (fitness-increasing for the plant) function at present (*sensu* Reeve & Sherman 1993). Third, a reduction in plant damage because of indirect defence or resistance must occur due to natural enemies. Our definition thus precludes some interactions such as plant–plant signalling, in which volatile cues from a plant alert neighbouring plants to risk of herbivory, that are occasionally referred to as indirect defence, but includes others, such as the promotion of apparent competition between herbivores due to a shared natural enemy (Kaplan & Eubanks 2005; Mooney & Agrawal 2008; Kaser & Ode 2016), that have rarely been considered indirect defences.

The term indirect defence, both here and elsewhere, has typically focused on plant-based systems. However, the concepts derived from these systems have commonalities with a broader range of trophic interactions (e.g. Hay *et al.* 2004). Some cases may fit our definition of indirect defence. For example, aphid traits related to honeydew excretion attract ants, which defend aphids against other natural enemies

(Stadler & Dixon 2005). Other types of ‘bodyguard’ systems would not meet our definition of indirect defence because they do not involve three trophic levels, and they are not clearly promoted by traits of the first trophic level. For example, systems in which toxic bacteria protect aphids from parasitoids (Oliver *et al.* 2005) or epizootic sponges protecting scallops from marine predators (Pond 1992) have been described as protective mutualisms, but are not indirect defences because there are no three trophic levels involved. However, there are commonalities in the processes that link a lower trophic level (aphids and scallops respectively) with organisms that deter their predation.

SCOPE OF INDIRECT DEFENCE AND RESISTANCE

While the vast majority of indirect defence studies to date have involved (1) interactions between predatory ants and plants that attract them via rewards (Fig. 1a) or (2) attraction of natural enemies to plants via HIPVs (Fig. 1b), recent studies have pushed the boundaries of systems we would consider indirect defence (Fig. 1c–h).

All indirect defences described to date can be envisioned as interaction webs linked by consumptive or non-consumptive interactions between trophic levels; they include three or four links, starting with a plant trait and leading to plant fitness (Fig. 2). Below, we list the range of plant–herbivore–natural enemy interactions that can be considered indirect defence or resistance (Table 1) and describe them based on the structural characteristics of the food webs they form (Fig. 2 & below).

Direct shelter or food rewards to natural enemies

The most straightforward examples of indirect defence involve a plant reward offered directly to a natural enemy in the form of food or shelter (Chamberlain & Holland 2009; Rosumek *et al.* 2009) (Fig. 2a, Table 1). Overwhelmingly, studies have focused on plant traits that can attract or maintain populations of ants (Rico-Gray & Oliveira 2007), including domatia (living spaces), nutritional food bodies (lipid-rich rewards produced along leaf margins) and extrafloral nectar (EFN; carbohydrate rewards offered in organs located somewhere outside flowers; Fig. 1a, Table 1). Analogously, predatory mites and bugs are associated with acarodomatia (plant hair tufts and cavities) and suppress damage by small herbivores and pathogens of plants (O’Dowd & Willson 1991; Weber *et al.* 2012; Fig. 1d), increasing plant fitness as a result (Agrawal & Karban 1997).

Several other plant traits provide direct rewards to natural enemies but have rarely been conceptualised in terms of indirect defence. First, floral nectar, while primarily considered in relation to its role in animal-mediated pollination, is also consumed by many natural enemies (some of which are also pollinators; Table 1). Floral nectar can boost natural enemy abundance and reduce herbivore abundance on some plants (Wäckers *et al.* 2007; Lee & Heimpel 2008; van Rijn & Wäckers 2016), but has never been documented to increase plant fitness via these effects. Second, plant traits other than domatia may help retain natural enemies on a plant (Table 1). For example, marcescent leaves (dead leaves retained over winter)

Table 1 Plant traits involved in indirect defense and resistance

Plant trait	Description of interaction	Predator	Herbivore	Plant	Structure*	Resistance	Defence	Inducible	Interaction links	Specialist predator
Extrafloral nectaries	Nectary visitation by predators	Ants	Insects; mammals	Many	a	Yes	Yes	Sometimes	3	No
Plant VOCs	Attraction of natural enemies to VOCs	VARIOUS	Various insects and mites	Most	b	Yes	Yes	Usually	3	Sometimes
Acarodomatia	Domation-containing predatory mites	Mites; thrips	Mites; pathogens; small insects	Many	a	Yes	Yes	No	3	?
Ant domatia	Domatia-containing predatory ants	Ants	Insect; mammal	Acacia;	a	Yes	Yes	No	3	No
Food bodies	Proteinaceous food rewards used by ants	Ants	Insect	Acacia; macaranga	a	Yes	No	sometimes	3	No
Susceptibility to minor herbivore	Susceptibility to a minor herbivore promotes apparent competition due to shared predator	Ants; other predatory arthropods	Weevils; caterpillars	Cotton	c	Yes	Yes	No	4	No
Sticky resins; entrapped carrion	Sticky resins entrap carrion and boost predator abundance	Assassin bugs; stilt bugs; spiders	Caterpillar; weevil	Tarweeds; tobacco; columbine	e	Yes	Yes	Sometimes	4	No
Susceptibility to ecosystem engineer herbivore	Susceptibility to a minor herbivore that makes structures used later by predators	Spiders	Various insect	Valley oak	c	Yes	No	No	4	No
Greater defensive traits that delay herbivore development	Slow growth high mortality'; nonlethal defences slow herbivore growth, increasing per capita attack rate of predators	Various	Various insect	?	d	Yes	No	No	4	Sometimes
Floral nectar	Floral nectar attracts predators	Various	Various insect	Many	a	Yes	No	No	3	Sometimes
Less of a sequestered defense	Reduction of a plant compound that is sequestered by an herbivore that renders them unpalatable to predators	Various	Specialist (sequestering) herbivore	?	d	Yes	No	No	4	Sometimes
Wooly trichomes that entrap pollen	wooly trichomes entrap pollen that is consumed by omnivores that act primarily as predators	mites; thrips; spiders; bugs	mites; thrips; lepidopteran	<i>Croton</i>	e	Yes	No	No	4	No
Marcescent leaves that retain predators	Dead (marcescent) leaves that are retained over winter provide overwintering habitat for predators	Spiders	Various insect	Oak	a	Yes	No	No	3	No
Canopy structure open to birds	Open canopies promote bird foraging of herbivores on plant	Birds	Various insect	?	b	Yes	No	No	3	No
Lack of traits that repel predators	Reduction of a plant trait (such as dense hairs) that impedes the foraging of predators	Lady beetles;	Various insect	<i>Datura</i>	b	Yes	No	?	3	Sometimes
Less (or greater) palatability to omnivorous predator**	More palatable plants increase the abundance of an omnivore, but less palatable plants may shift omnivore behavior to predation	Thrips, hemipterans	Varous insect and mite		a	Yes	No	Sometimes	3	No

*From Figure 2, **Technically, extrafloral and floral nectaries act in this way, though nectar feeding is typically thought of differently than herbivory.

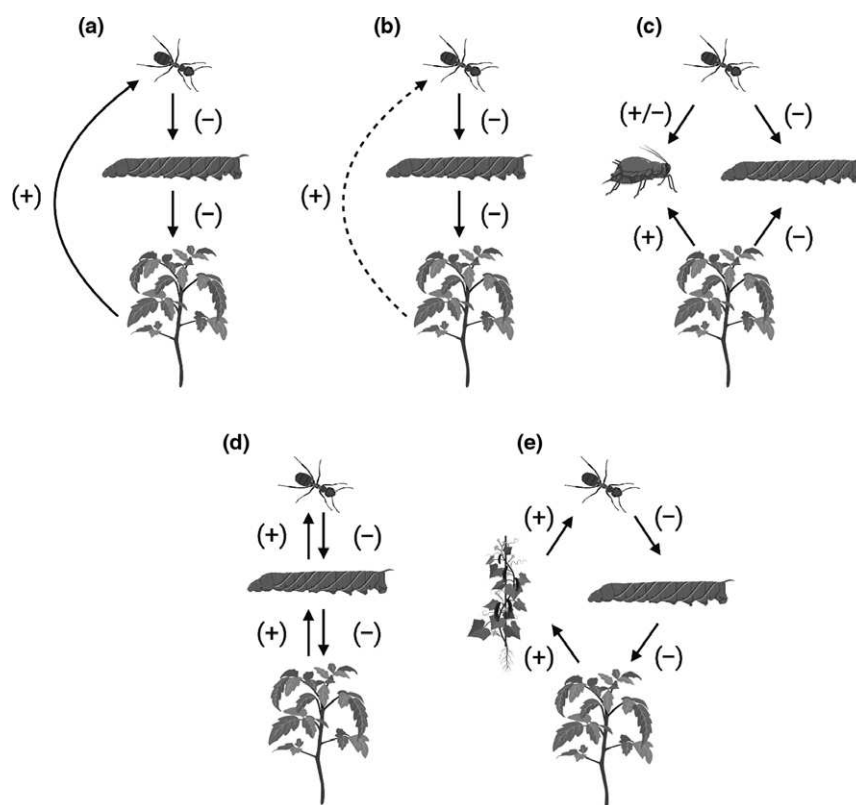


Figure 2 Interaction webs for five types of indirect defence. Links in the web may be consumptive or non-consumptive and can either affect an organism's abundance or behaviour. Interactions can be either positive (increasing abundance or foraging rate) or negative. Dashed lines indicate completely non-consumptive interactions. Examples of indirect defences illustrate the links in (a) food or shelter interactions such as plant extrafloral nectaries or domatia, (b) informational or habitat complexity differences that allow natural enemy foraging, (c) plant traits that modulate apparent competition between herbivores via a shared natural enemy or 'bodyguard' mutualist of one herbivore, (d) plant traits that decrease the growth rate or defence of herbivores, increasing the risk of predation and (e) plant traits that increase the amount of a natural enemy's alternate resource, such as carrion or heterospecific pollen.

on oak trees can increase spider abundance in early spring (I. Pearse, unpublished data). Finally, omnivorous natural enemies often consume plant resources other than nectar (Eubanks & Denno 1999), and their presence at those resources can suppress herbivores (Table 1, Fig. 1e). For example, willows whose leaves are higher in nitrogen (N) maintain more stable populations of omnivores, which reduce long-term herbivore populations (Liman *et al.* 2017). In each of these cases, the extent to which plant–natural enemy interactions benefit the plant remains unclear.

Plant traits that directly increase natural enemy foraging efficiency

Other plant traits affect the efficiency of natural enemies when they attack herbivores (Fig. 2b). The classic interactions in this category involve HIPVs that are attractive to predatory and parasitic arthropods (Turlings *et al.* 1990; De Moraes *et al.* 1998; Dicke & Baldwin 2010; Fig. 1b), nematodes (Rasman *et al.* 2005; Ali *et al.* 2011) and vertebrates (Amo *et al.* 2013). Volatile cues are induced by herbivory. They contain no direct reward to natural enemies outside the information they provide about their prey, the plants' herbivores (Table 1). HIPV blends have been shown to increase natural enemy abundance, decrease herbivore damage and increase plant fitness, providing evidence for their function as

an indirect defence (Kessler & Baldwin 2001; Schuman *et al.* 2012).

Apart from HIPVs, many other plant traits might directly impact natural enemy foraging, though these traits have other clear functions outside the herbivory. Plant architecture is one example: plants with open canopies or perch sites enable higher attack rates of herbivores by birds (Marquis & Whelan 1996; Whelan 2001; Fig. 1c; Table 1). Similarly, traits that enhance natural enemy movement can increase attack rates on herbivores (Kareiva & Sahakian 1990; Table 1). Researchers have often framed traits that impede predator movement, such as leaf trichomes, as costly to the plant (Eisner *et al.* 1998; Gassmann & Hare 2005). However, the lack of traits like these (e.g. smooth leaves that lack trichomes) might be considered indirect resistance, as non-glandular leaves increase natural enemy movement and consequently decrease herbivore abundance (Gassmann & Hare 2005).

Plant traits that attract a 'bodyguard' mutualist of one herbivore or modulate apparent competition between herbivores via a shared natural enemy

Susceptibility to an herbivore can actually benefit a plant, if that herbivore attracts a natural enemy that controls a different, more damaging herbivore (Eubanks 2001). Indeed,

apparent competition (Holt 1977) among herbivores due to shared natural enemies appears to be one of the most common antagonistic interactions among herbivores (Kaplan & Denno 2007), and 'bodyguard' mutualists of one herbivore are often voracious predators of other herbivores. For example, cotton and milkweed plants that have a higher abundance of aphids attract honeydew-consuming ants, which subsequently attack and suppress more detrimental herbivores such as lepidopteran pests, resulting in higher plant fitness (Fig. 1h, Kaplan & Eubanks 2005; Styrsky *et al.* 2006; Mooney & Agrawal 2008). In milkweed, ant–aphid interactions are under clear genetic control of the plant, suggesting that a plant trait mediates this interaction (Fig. 1h; Mooney & Agrawal 2008; Züst & Agrawal 2016).

In other cases, herbivores may act as ecosystem engineers, changing the habitat structure in which natural enemies live without necessarily being preyed upon by those natural enemies. For example, the senescent twig galls made by *Andricus quercuscalifornicus* house predatory arthropods over the winter and reduce herbivore abundance in the following spring (Wetzel *et al.* 2016, Fig. 1g). Again, it is unknown what plant traits affect the susceptibility of trees to twig galls, but plants show heritable variation in their susceptibility to other gall-makers, suggesting a role of heritable plant traits in this interaction (Bailey *et al.* 2006). Similarly, herbivores may affect other resources of predators. For example, genetic lines of maize that are more susceptible to aphids accumulate honeydew that is consumed by parasitic wasps that attack lepidopteran herbivores (Faria *et al.* 2007).

Plant traits that affect the growth, behaviour or defence of an herbivore, altering its rate of attack by natural enemies

As pointed out above, the line between direct defence and indirect defence can be blurry (Poelman *et al.* 2008). For example, plant traits that extend the development of an herbivore and expose it to an increased chance of predation (plant traits involved in the slow-growth high-mortality hypothesis e.g. Benrey & Denno 1997) might act in part as indirect defences because they increase the per capita attack rate by natural enemies (Singer *et al.* 2012; Kaplan *et al.* 2016). In such cases, some of the fitness benefit to the plant conveyed by a defensive trait may be mediated by greater natural enemy attack, while another portion of that benefit may be due to the direct negative effect of the trait on the herbivore (Kaplan *et al.* 2016). Nevertheless, support for the slow-growth high-mortality hypothesis is mixed, and, to date, *no* studies have clearly demonstrated a benefit to plant fitness due to slow-growth high mortality of herbivores. Whether direct defences of a plant that expose an herbivore to greater risk of predation ever act as indirect defences remains an open question. We explore this idea further in the section 'Food web ecology', considering new work on non-consumptive effects of predators and potential synergies between different defence mechanisms.

In other cases, direct and indirect defences may interact antagonistically because a plant trait offers direct defence against an herbivore, but simultaneously makes that herbivore better defended against its own natural enemies (Table 1). For

example, lower amounts of a direct chemical defence plant trait may cause indirect resistance or defence in cases when plants are attacked by herbivores that sequester those chemicals for their own defence (Stamp 2001; Nishida 2002), or in cases when those chemicals impede natural enemies for other reasons (Ode 2006; Singer *et al.* 2009). Top-down suppression of herbivores has not been demonstrated to select for the reduction in an herbivore-sequestered defence. However, plant defences affect herbivore–natural enemy interactions differently for sequestering and non-sequestering herbivores (Stamp & Bowers 1992; Harvey *et al.* 2005). Demonstrating when and how a plant trait affects direct and indirect suppression of herbivores is particularly important for understanding how natural enemies alter selection for and against plant direct defence traits.

Plant traits that indirectly increase other resources of natural enemies

Plants can indirectly provide resources to natural enemies (Table 1). For example, various plant species have glandular trichomes that entrap small insects, which are consumed as carrion by scavenging predators (Fig. 1f; Romero *et al.* 2008; Krimmel & Pearse 2013; LoPresti *et al.* 2015). Those predators also consume herbivores of the glandular plants. This interaction has been shown to increase plant fitness in at least three plant species (Krimmel & Pearse 2013; LoPresti *et al.* 2015, 2018). Moreover, glandular residues can be induced by damage to leaves, increasing visitation by natural enemies (Karban *et al.* 2019). Plant trichomes also entrap pollen from the environment. This pollen increases the abundance of predatory arthropods, subsequently decreasing herbivore abundance (van Rijn *et al.* 2002; Van Wyk *et al.* 2019). Because alternate resources such as pollen and insect carrion are very common in the environment, accumulating those resources may be an important and largely overlooked way in which plants attract natural enemies. Alternate resource entrapment is now being tested as a way to retain predators in agricultural systems (Nelson *et al.* 2019).

Pathogens and microbes as frontiers in indirect defence

The concept of indirect defence has been traditionally confined to herbivores and their natural enemies that are animals, but this need not be the case. In each of the categories of interactions described above, pathogens can function analogously to 'herbivore' or 'natural enemy'. In several cases, plant traits mediate top-down control of plant fungal pathogens. For example, mycophagous mites inhabit leaf domatia and reduce the incidence of grape powdery mildew (Norton *et al.* 2000), and volatiles emitted from powdery mildew-infested leaves attract mycophagous ladybird beetles (Tabata *et al.* 2011).

Plant traits might increase the incidence of herbivore infection with entomopathogenic microbes (Cory & Hoover 2006; Gasmi *et al.* 2019). For example, cuticular waxes and glucosinolate compounds on leaves of some Brassicaceae affect germination of the entomopathogenic fungus, *Metarhizium anisopliae*, and can alter its ability to attack a chrysomelid herbivore of those plants (Inyang *et al.* 1999, b). In a

remarkable case, the plant even accrues nutrients from herbivores killed by entomopathogens. Plants provision *Laccaria bicolor*, a mycorrhizal fungal associate, with carbon resources (Behie *et al.* 2017). This fungus also kills and derives nutrients from soil-dwelling insect herbivores, and traces of those nutrients can be found in associated plant tissues (Behie *et al.* 2012). In another case, volatile compounds from mite-damaged cassava plants induce the sporulation of entomopathogenic fungi that are known to attack mites (Hountondji *et al.* 2005). Plant defensive metabolites can compromise the immune system of herbivores, making them more susceptible to pathogens (Elder *et al.* 2013; Rosa *et al.* 2018); in other cases, plant defensive metabolites promote herbivore immune responses (Gowler *et al.* 2015). Thus, selection may favour defensive metabolites because of their impacts on herbivore–pathogen interactions. To date, the fitness consequences of plant traits that promote entomopathogenic microbes have not been clearly demonstrated. This is an exciting avenue for exploring a novel form of indirect defence.

TYPES OF EVIDENCE FOR INDIRECT DEFENCE AND RESISTANCE

Three types of evidence have been used to test whether a plant trait is an indirect defence (Fig. 3). First, and most commonly, a trait is manipulated (Fig. 3b) either phenotypically, such as by adding artificial domatia-like structures to a plant

(Agrawal & Karban 1997), or genetically, such as by creating genetically altered plant lines differing in volatile components (Schumann *et al.* 2012). Evidence for indirect defence comes from a concomitant increase in natural enemy abundance, decrease in herbivory and increase in plant fitness in the presence of the putative trait. Experiments alternatively may remove a putative indirect defence trait, such as by blocking EFNs (Koptur *et al.* 2015), or may add a plant trait, such as ‘glandular’ traits bred into a non-glandular plant genetic background (Elle *et al.* 1999).

Second, piecewise evidence can connect a plant trait to plant fitness by exploring the set of interactions between plants, herbivores and natural enemies (Fig. 3c). This information can be incorporated into population models (Sabelis *et al.* 1999) and structural equation models (Karbon *et al.* 2019) to define the circumstances under which a trait may function as indirect defence. This line of evidence does not provide as strong support for the fitness-increasing function of the putative indirect defence traits, but it is particularly useful in cases where the plant trait is difficult to manipulate. For example, the first studies providing evidence for fitness benefits of carrion entrapment (Krimmel & Pearse 2013), ant-aphid–plant interactions (Styrsky & Eubanks 2010) and HIPVs (van Loon *et al.* 2000; Hoballah & Turlings 2001; Smallegange *et al.* 2008; Gols *et al.* 2015) did not manipulate plant traits (glandularity, aphid susceptibility and HIPVs); rather, they manipulated the interactions that these traits have

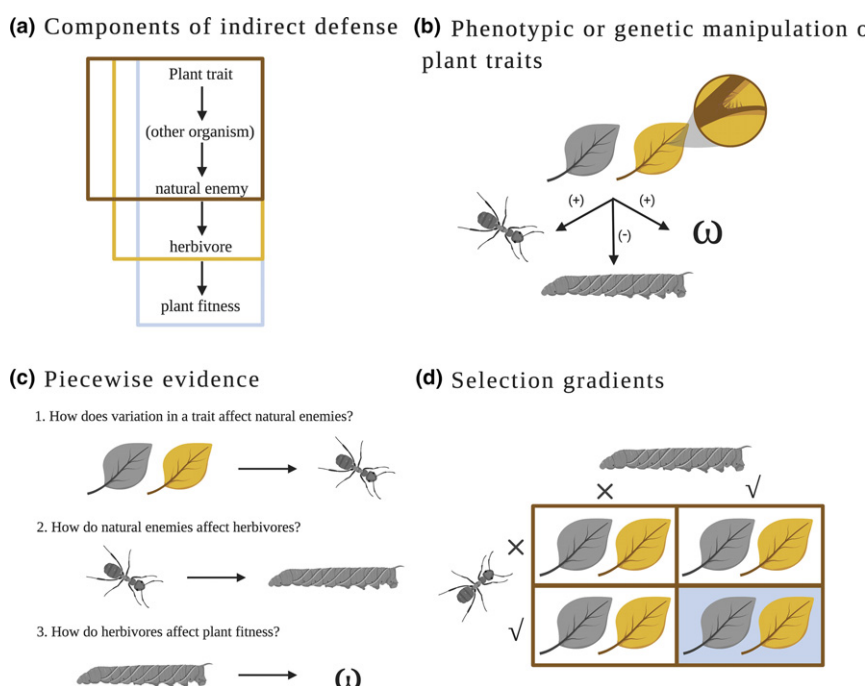


Figure 3 Evidence for indirect defence. (a) Indirect defence involves multiple interactions. We refer to plant traits that increase predator abundance or feeding, either directly or via their impact on other organisms, as ‘predator enhancement traits’ (red box). When those predators reduce herbivore abundance or damage, those traits are ‘indirect resistance traits’ (yellow box), when a reduction of those herbivores or that herbivore damage results in increased plant fitness, those are ‘indirect defence traits’ (blue box). Evidence for indirect defence comes from (b) a response of (+) predators, (-) herbivores and (+) plant fitness to genetic or phenotypic manipulation of plant traits, from (c) piecewise evidence in which a trait enhances predators, predators decrease herbivores/herbivory and herbivory decreases plant fitness, and from (d) selection gradients where selection on a trait (or shifts in trait values/frequencies due to selection) is more positive in the presence of both herbivores and predators than in other situations. An ‘ ω ’ indicates plant fitness. A ‘✓’ indicates presence and an ‘X’ indicates absence.

been shown to mediate. In each of these cases, complementary work succeeded in directly manipulating the plant trait in question (Mooney & Agrawal 2008; Schumann *et al.* 2012; LoPresti *et al.* 2015).

Third, while rare in practice, selection experiments can provide the clearest evidence for the adaptive function of putative indirect defence traits (Rudgers, 2004; Rudgers & Strauss 2004; Rutter & Rausher 2004; English-Loeb *et al.* 2005). In this case, indirect defences are those traits under more positive selection in an environment with both herbivores and natural enemies than in environments lacking either or both trophic levels (Fig. 3d). A disadvantage of this approach is that it is difficult to independently manipulate herbivores and natural enemies over a timescale relevant for selection. However, there are at least two substantial advantages. This approach uses natural variation in plant traits, mirroring the process of natural selection. By following populations of plants under manipulated herbivore and natural enemy environments for multiple generations, a study could not only observe selection gradients, but also shifts in plant traits due to selection. Furthermore, this approach could also be used to screen many plant traits or genomic regions to find new indirect defences whose functions have not yet been hypothesised. Such a selection gradient 'omics' study has not yet been used to test for traits under selection by indirect defence. It may be highly valuable in identifying new plant traits that operate as indirect defence, as well as for better describing evolutionary processes that shape indirect defence. It has the potential to uncover fitness costs of indirect defences in the absence of herbivores or natural enemies, and might be able to identify instances in which an indirect defence trait cannot evolve due to a lack of standing genetic variation.

ECOLOGY AND EVOLUTION OF INDIRECT DEFENCE

Given the wide scope of systems in which indirect defence or resistance may occur, it is important to evaluate how these interactions can be studied. Below, we outline three major concepts (food web ecology, context-dependent mutualisms and macroevolution) that apply to the study of indirect defence, highlighting the ways in which they can be extended to encompass a broader scope and definition.

Food web ecology

In the examples above, we characterised potential indirect defences based on the structure of their tritrophic interaction (Figure 2). Here, we explore this idea further by considering their broader food web attributes.

Consumptive and non-consumptive interactions

The non-consumptive effects of natural enemies promoted by plant indirect defences may be important. It is likely that many interactions among plants, herbivores and natural enemies are non-consumptive, in which nothing is eaten, but natural enemies alter the behaviour of herbivores (Schmitz *et al.* 1997; Preisser *et al.* 2005). For example, when herbivorous *Manduca sexta* larvae are exposed to the predatory hemipteran *Podisus maculiventris*, the herbivores feed substantially

less, even in cases where the predators are unable to attack them (Thaler & Griffin 2008). Plant traits can shift the relative importance of consumptive and non-consumptive effects of natural enemies on their prey (Kersch-Becker & Thaler 2015; Kersch-Becker *et al.* 2017). For example, plant traits that slow the growth of herbivores may also promote the predation of those herbivores (Benrey & Denno 1997). However, unless herbivores undergo multiple generations on the same plant, the consumptive effect is unlikely to benefit the plant if predation comes late in the life of the herbivore. In contrast, if the herbivore avoids plants on which it will grow slowly and perceives risk of predation or parasitism (a non-consumptive effect), the plant may benefit considerably. Non-consumptive effects of indirect resistance may even play an important role in the evolution of host specificity of herbivores, if herbivores actively avoid plants that have high predation risk (Murphy 2004).

It is likely that multiple plant traits operate in concert to create a situation in which an herbivore perceives high predation risk and avoids a plant. For example, wild tobacco induces defences that slow the growth of *Manduca* larvae (and expose them to a longer duration of predator attack). At the same time, induction increases plant volatile production, increasing predator attack rate on these herbivores (Kessler & Baldwin 2004). Similarly, oviposition on plant leaves induces chemical responses that slow the development of larvae or eggs, while inducing plant volatiles that increase their attack rate (Hilker & Fatouros 2015; Pashalidou *et al.* 2015). Do these or other plants advertise their high predation risk so that herbivores might choose to avoid them?

Numerical and functional responses of natural enemies to indirect defence traits

Kessler & Heil (2011) point out that some indirect defences are based on direct food or shelter rewards to natural enemies, whereas others are based on the provision of information. We expand upon this idea by distinguishing between plant traits that act as direct rewards to increase natural enemy numbers, and plant traits that heighten natural enemy functional responses (Fig. 4). This distinction allows us to make predictions about how plant traits affect natural enemy–herbivore interactions. Indirect defences involving direct rewards (traits such as domatia and EFNs) are expected to increase natural enemy numbers irrespective of herbivore abundance, a demographic or aggregative numerical response to the plant trait (Fig. 4). In contrast, indirect defences involving increased foraging efficiency (e.g. traits like HIPVs that orient parasitoids to herbivores, or canopy openness, which increases movement of predators, Fig. 4) are expected to increase herbivore suppression via altered per capita effects of natural enemies.

Some plant traits alter both predator abundance and behaviour. Natural enemies may aggregate in habitats where foraging is efficient, as is suggested by increased natural enemy abundance in the presence of plant HIPVs (e.g. Kariyat *et al.* 2012). Likewise, direct rewards, such as sugar-rich extrafloral nectaries, alter the aggressiveness, and likely functional response, of natural enemies (Ness *et al.* 2009, Fig. 4, dashed line). Similarly, N-rich plant tissues are consumed by

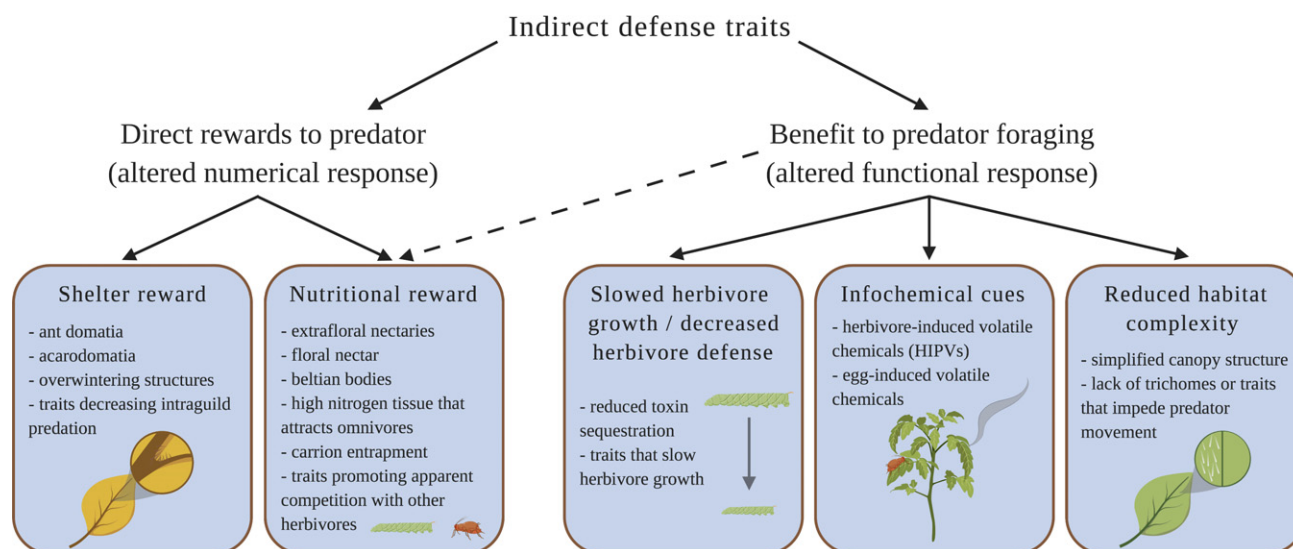


Figure 4 A categorisation tree of indirect defences based on the nature of plant interactions with natural enemies. Most examples of putative indirect defences can be categorised based on their benefits as a direct reward to a predator or based on benefits to predator foraging. However, in one example (depicted as a dashed line), extrafloral nectar acts as a direct reward to predators and also affects how predators forage for prey (Ness *et al.* 2009). Are there other, yet unnoticed, ways in which plant traits both directly reward predators and also change how they forage?

omnivorous mirids, and those same tissues shift mirids to a more carnivorous diet (Liman *et al.* 2017, Fig. 1e).

In most cases, we have little information about *how* indirect defences alter natural enemy behaviour. Mathematical models focus on search time of natural enemies with and without an indirect defence (Vos *et al.* 2001), and empirical examples seem to suggest that search time is indeed shortened by some indirect defences (Soler *et al.* 2007). In other cases, such as when plant defences alter herbivore development and behaviour, it is possible that indirect defences might also shorten handling times, although we have found no examples in the literature.

The details of natural enemy foraging and herbivore damage may be crucial in determining whether a plant trait is an indirect defence or resistance trait (Sabelis *et al.* 1999a, Fig. 5). For example, herbivore suppression by birds is greater for plant species that are relatively palatable to herbivores, because birds preferentially attack high densities of herbivores (Singer *et al.* 2012; Nell & Mooney 2019; Fig. 5 path 4). However, when herbivore density is constant, the per capita attack rate of herbivores by birds is higher on well-defended tree species, likely due to slow-growth, high-mortality mechanisms (Singer *et al.* 2012, Fig. 5 path 2). In this case, then, tissue palatability likely acts as a direct defence reducing the abundance of herbivores. However, the shape of the relationship between tissue palatability and damage is determined by the complicated interactions between herbivores and natural enemies that are also mediated by that same trait.

Specificity/generality of interactions

Most indirect defences seem to promote a generalised response of natural enemies. One way to quantify the response of natural enemies to a plant trait is to either tally the abundance or describe the behaviour of all natural

enemies in response to that trait. Another way to measure a natural enemy response would be to consider the effect of a plant trait on the composition of natural enemies, with the expectation that plant traits will promote more effective natural enemy communities. In this response, certain functional groups of natural enemies become more abundant, sometimes at the expense of other groups. For instance, in diverse systems, EFNs, domatia and honeydew-producing herbivores all increase the abundance of ant species on plants (Janzen 1966; Kaplan & Eubanks 2005; Mooney & Agrawal 2008; but see Heil *et al.* 2005 as an example of EFN-ant specificity), often at the expense of other predatory arthropods that are also preyed upon by ants (Eubanks 2001; Styrsky & Eubanks 2007). In some cases, interactions disproportionately promote the abundance of the most effective predators, such as large-bodied ants in ant-aphid-plant interactions (Clark & Singer 2018). In other cases, it is less clear whether the most effective predators are those most favoured by an indirect defence trait. For instance, many parasitoids are gregarious koinobionts (those that allow their host to continue developing and growing); these can induce their host to consume *more* plant tissue than unparasitised hosts (Harvey 2005; Ode *et al.* 2016). At present, it is not clear how often such parasitoids play a dominant role in plant-herbivore-natural enemy interactions, though in a case study that surveyed parasitoid communities, two solitary koinobionts (which reduce host feeding relative to unparasitised herbivores) were also more common (Hoballah *et al.* 2004).

For some plant-natural enemy interactions, there is evidence for high specialisation. In a remarkable example, the EFNs of one plant species reward specific ant taxa because the nectar contains sugars that are a unique match to the ant's digestive physiology (Heil *et al.* 2005). Likewise, some interactions involving HIPVs are highly specialised (McCorrick *et al.* 2012). HIPV cues, on the one hand, have been

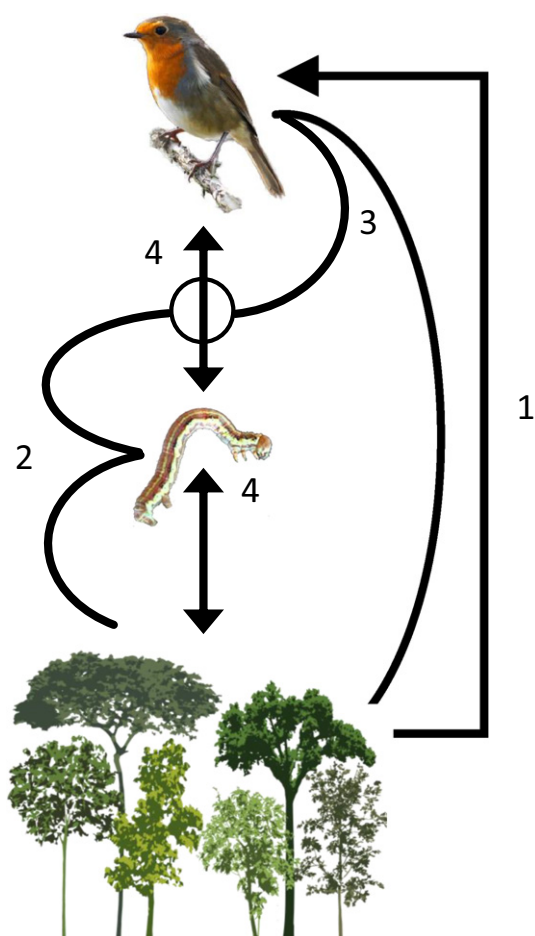


Figure 5 Indirect defence or resistance can occur by a number of interrelated, non-mutually exclusive mechanisms. Straight-line arrows represent density-mediated effects, curved lines represent trait-mediated effects. (1) Density-mediated indirect effects, where plants alter predator abundance and this suppresses herbivore abundance to the benefit of plants (e.g. EFNs). (2) Plant modification of herbivore traits that mediate predator–herbivore interactions to increase the per capita effect of predators on herbivores (e.g. traits causing slow herbivore growth). (3) Plant modification of predator traits that mediate predator–herbivore interactions to increase the per capita effect of predators on herbivores (e.g. Ness *et al.* 2009 where EFN increases protein demands of predatory ants). (4) Plant effects on herbivore density where predator–herbivore interactions are positively density dependent (nonlinear), such that an increase in herbivore abundance results in an increase in the per capita effects of a predator on herbivores (e.g. Singer *et al.* 2012). Photograph credits: John Avise and Colleen Nell.

shown to convey very detailed information about an herbivore, including its species identity (McCormick *et al.* 2012; Stam *et al.* 2014), age (Yoneya *et al.* 2009) and parasitism status (Poelman *et al.* 2011). On the other hand, HIPV cues provide general information to a wide variety of organisms and may be perceived by natural enemies, other herbivores and by other organisms such as hyperparasitoids (Halitschke *et al.* 2008; Poelman *et al.* 2012). It is currently unclear whether indirect defence involving HIPVs tends towards greater specialisation than other systems or whether specialised systems are simply those that we have focused on thus far.

The importance of specificity is particularly striking in indirect defence systems involving introduced species. For example, exotic plants with EFNs and that host honeydew-producing herbivores attract both native and introduced ant bodyguards (Eubanks 2001; Kaplan & Eubanks 2005; Ludka *et al.* 2015). Similarly, exotic plants with glandular trichomes entrap carrion that attracts predatory insects (LoPresti *et al.* 2015), and exotic plants with acarodomatia house predatory mites (Weber *et al.* 2012). To date, there have only been anecdotal examples of a loss of indirect defence with novel sets of organisms due to altered biogeographies of those organisms (Desurmont *et al.* 2014). Understanding the circumstances under which novel interactions between introduced plants, herbivores and natural enemies do or do not result in indirect defence or resistance is an important and active area of research.

Context-dependent mutualism

Above, we focused on the tritrophic interaction as a defining component of indirect defence and resistance. Here, we focus on the positive fitness consequences for plants (which are required for indirect defence) and natural enemies (which are not required for indirect defence or resistance, but which are central to the idea that plant–predator interactions are protective mutualisms). We find that, perhaps surprisingly, a better understanding of natural enemy fitness is needed to demonstrate the circumstances under which indirect defence is a protective mutualism.

Fitness consequences for the plant

The search for benefits to plants has been a long-running priority in the study of indirect defence, but benefits have been notoriously difficult to demonstrate (Kessler & Heil 2011; Poelman 2015). At present, we find convincing evidence for fitness benefits to a plant in six of the 17 categories of potential indirect defences described in Table 1.

Studies have begun to test how putative indirect defences affect plant fitness across gradients. These studies suggest that indirect defence is context dependent, because the outcomes of interactions caused by plant traits vary predictably as a function of local ecological context. As with many positive interactions (Brooker *et al.* 2008), we might expect that plants benefit more from indirect defence when under greater environmental stress. For example, in a Mesoamerican ant–plant association, drought-stressed plants provided more carbohydrate provisions to ants via EFNs, despite a projected increase in cost of these provisions under drought (Pringle *et al.* 2013). This trend has been found in many other ant–plant interactions as well (Leal & Peixoto 2017). The ‘context’ of context dependency can also be biotic. For example, canopy structure affects how birds forage on herbivorous insects (Nell & Mooney 2019), but the diversity of nearby trees also affects bird foraging (Letourneau *et al.* 2009; Nell *et al.* 2018). Further work will be needed to determine when these interactions benefit the plant.

One reason why indirect defence should be context dependent is that indirect defences are adaptive only when the benefits of indirect defence outweigh the costs associated with

those traits. The costs of indirect defence traits have received considerably less attention than their benefits. The emerging trend of this work is that costs are often based on biotic interactions (*sensu* Strauss *et al.* 2002) as opposed to direct resource costs, although direct resource costs to the plant can be considerable in some cases (Pringle 2016).

Many indirect defences might inflict costs because they repel some natural enemies while attracting others. For example, trichomes attract a suite of sticky plant-associated insects, but also exclude other predators such as lady beetles (Eisner *et al.* 1998; Gassmann & Hare 2005; Krimmel & Pearse 2013). Likewise, investment in an indirect defence trait may have limiting returns because of negative interactions between predators (Styrsky *et al.* 2006; LoPresti *et al.* 2018), and the recruitment of a fourth trophic level (Poelman *et al.* 2012).

Other traits might increase natural enemy abundance in some cases, but herbivore abundance in others. For example, many plant traits, such as domatia, trichomes and architecture, promote natural enemy abundance by increasing habitat complexity (Agrawal & Karban 1997; Norton *et al.* 2001). However, habitat complexity within a plant can also provide habitat for herbivores (Lill & Marquis 2003) and reduce predation of insects by birds (Grof-Tisza *et al.* 2017). Information about damage conveyed by HIPVs may attract natural enemies, but it can also attract gregarious or search-limited herbivores (Halitschke *et al.* 2008; Ali *et al.* 2011; Mescher & Pearse 2016).

Natural enemies also inflict costs by disrupting other mutualisms in which plants engage. For example, ants attracted to EFNs attack or deter pollinators in several systems, apparently favouring the evolution of traits that reduce the likelihood that ants will forage near flowers (Ness 2006; Cembrowski *et al.* 2013). Similarly, volatile cues involved in indirect defence reduce the attractiveness of flowers to pollinators (Kessler *et al.* 2011; Schiestl *et al.* 2014; Glaum & Kessler 2017).

Fitness consequences for the natural enemy

Even before the term was defined, indirect defence was closely tied to the concept of mutualism between plants and natural enemies (Janzen 1966; Dicke & Sabelis 1988; Agrawal & Karban 1997). More recently, models suggest that stable mutualism can evolve between plants and natural enemies (Sabelis *et al.* 2011). However, the evidence for mutualism is still elusive in most systems because benefits of an indirect defence trait to both natural enemies and plants have not been jointly demonstrated.

In many cases, indirect defences may be inconsequential for a natural enemy. For example, open canopies or those with ideal perch sites increase bird predation of arthropods (Marquis & Whelan 1996; Whelan 2001; Nell & Mooney 2019); however, it is unclear whether those bird populations are increased because of better access to prey.

In other cases, there is substantial evidence for mutualism. For example, predatory mite associations with acarodomatia (Fig. 1d) confer positive fitness effects to both plants and predators (Romero & Benson 2005), and lynx spiders benefit from carrion entrapped on sticky plants (Romero *et al.* 2008). Plants can experience increased fitness due to increased

predatory mite abundance and reduced herbivory, while the predatory mites that facultatively inhabit domatia experience reduced predation and hence higher fitness themselves (Norton *et al.* 2001). In the best-studied indirect defence, a group of *Pseudomyrmex* ant species is associated with a group of acacias that provide shelter and food to the ants (Heil & McKey 2003). This near-obligate, mutualistic association has been central to our thinking about plant–natural enemy mutualisms. However, it may be even more valuable to explore facultative associations in which we can realistically explore the fitness of each partner in the presence and absence of the other and in different environments. This work can explore the conditions under which both partners or only one partner receives a benefit.

Macroevolution

How have plant, herbivore and natural enemy traits been shaped by tritrophic interactions during the tens of millions of years in which these interactions have occurred? We are far from answering this question. However, research over the past decade has reshaped how we think about the evolution of indirect defence. Our definition of indirect defence focuses only on the fitness benefit of the interaction at present, and does not consider the history of the traits or interactions that result in indirect defence. However, an important feature of indirect defence is that the indirect trophic connection between a plant and a natural enemy can be shaped by the evolution of plant and natural enemy traits.

From a macroevolutionary perspective, we can demonstrate both evolutionary lability and an ancient origin of indirect defences. In specialised ant-domatia systems, patterns of ancient origins of indirect defence traits, along with lability in their gain and loss, appear to be a common pattern (Chomicki *et al.* 2015). The oldest origins of ant domatia appear to be around 20 MYA (Chomicki & Renner 2015). These structures have evolved independently at least 158 times (and have been lost 43 times), arising from diverse ontogenic origins, including modified thorns, leaves and roots (Chomicki & Renner 2015). EFNs have an ancient origin in some plant groups; fossil EFNs have been found that date back to the Oligocene (Pemberton 1992). Estimates of their origin range from the early Palaeogene to the late Cretaceous (Rico-Gray & Oliveira 2007; Weber & Keeler 2012). While sometimes ancient, within the vascular plants, EFNs are also estimated to have evolved at least 457 times (Weber & Keeler 2012). Likewise, acarodomatia are present in Cretaceous fossils (MacCracken *et al.* 2019), but have been gained and lost in numerous plant clades (O'Dowd & Willson 1991). At a narrower phylogenetic scale, carrion-entrapping plants in the Madiinae, a tribe of Asteraceae, have sticky stem surfaces caused by dense glandular trichomes that show phylogenetic signal, where some taxonomic groups are highly glandular, while others are not. However, within various glandular species, some populations largely lack glandular trichomes (Krimmel & Pearse 2016).

We should hypothesise that indirect defence traits are key innovations that allow plants to diversify by overcoming trade-offs that are otherwise inherent to coping with

herbivores, opening up ecological opportunity. In a macroevolutionary context, evidence of this idea comes from comparing lineage diversification rates of plant groups with and without an indirect defence trait. In support of this, plant groups with extrafloral nectaries have diversified faster than groups without them (Weber & Agrawal 2014). In contrast, the evolution of ant domatia is not associated with higher diversification rates (Chomicki & Renner 2015).

Macroevolutionary patterns in natural enemy traits may also reflect the consequences of indirect defence. In ants, arboreal nesting (a behaviour associated with the use of domatia and plant-derived food bodies) has evolved numerous times (Nelsen *et al.* 2018), and there are relatively few reversions away from close association with domatia (Chomicki *et al.* 2015). Even in this well-studied case, we know relatively little about the ant traits that cause their close association with domatia. We know even less about the evolution of traits in other natural enemy groups that interact with indirect defences. However, there are hints that they have evolved traits that are critical to their role in indirect defence. For example, predatory insects that live on glandular plants often have specialised leg traits that allow them to navigate on sticky surfaces (Voigt & Gorb 2010). Whether these or other natural enemy traits arose in concert with a transition to their role in indirect defence is unknown, as are the macroevolutionary consequences of that transition.

Macroevolutionary patterns of gain and loss in indirect defence can generate hypotheses about the factors shaping indirect defence evolution. For example, an outstanding question in these and other examples is the degree to which selection, based on either the costs and benefits of indirect defence or other functions of those traits, has shaped the current phylogenetic distribution of indirect defence traits. Some indirect defence traits, such as canopy architecture, have obvious functions outside the indirect defence. It is reasonable to hypothesise that their potential role in indirect defence is an exaptation; that is, a case in which selection due to indirect defence was not the primary driver of evolution of that trait. Other traits, such as domatia or EFNs, have few hypothesised functions outside the indirect defence, so it is reasonable to hypothesise that selection due to indirect defence may have shaped (and will continue to shape) their evolutionary gains and losses. Some indirect defence traits, such as a single metabolite that is attractive to predators, likely have simpler genetic determination than other traits such as ant domatia that are probably highly polygenic. Do multifunctional and genetically complicated indirect defence traits show different evolutionary patterns than traits that have fewer functions outside the indirect defence and simpler genetic determination? This remains an important outstanding question.

CONCLUSIONS

The concept of indirect defence encompasses so many plant traits and plant–natural enemy interactions that it is probably ubiquitous among plants. Nevertheless, the most ubiquitous forms of indirect defence and resistance may be still go unnoticed. We have only begun to explore the ways in which plant traits attract natural enemies and facilitate their attack of

herbivores. To date, no studies have demonstrated a benefit to plant fitness because of plant metabolites that reduce herbivore growth and raise their mortality, because of natural enemy attraction to floral nectar, or because of plant traits that limit the ability of an herbivore to sequester toxins for its own defence. Likewise, the study of pathogens and other microbes in indirect defence is still in its infancy.

We may find commonalities among indirect defences based on food webs: how directly plant traits enhance predation and the degree of specificity for each of the links in the plant–natural enemy–herbivore interaction. Moreover, selection on the process of indirect defence is an important evolutionary driver of some indirect defence traits, whereas the multifunctional nature of other indirect defence traits suggests that other aspects of the environment may select more strongly on those traits. Some indirect defences comprise a mutualism between plants and natural enemies, although more work on the benefits of plant traits to natural enemy fitness is needed to understand when plant–predator interactions are truly mutualistic rather than commensal. By considering the full scope of interactions that encompass how plant traits reduce herbivory through promotion of natural enemies, we will better understand the intertangled role of top-down and bottom-up control of herbivores in wild and managed systems.

In conclusion, we reiterate the statement by Price *et al.* (1980) that ‘theory on insect–plant interactions cannot progress realistically without consideration of the third trophic level’. We emphasise that we cannot reasonably understand interactions with the third trophic level without considering the role of a broad suite of plant traits.

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AUTHORSHIP

All the authors contributed novel ideas and synthesis, wrote and edited the manuscript. ISP synthesised those ideas in manuscript drafts.

DATA AVAILABILITY STATEMENT

No new data are presented in the manuscript.

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