

## EVOLUTIONARY ECOLOGY OF PLANT DEFENCES

# The multiple faces of indirect defences and their agents of natural selection

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## Summary

1. Plants commonly attract predatory and parasitoid organisms, and may thereby increase resistance against antagonistic herbivores. Mechanisms for indirect resistance include the provision of resources (e.g. food and shelter) for predators as well as the provision of information (e.g. herbivore-induced volatiles) on the location of hosts and prey that can facilitate the foraging behaviour of natural enemies of herbivores.

2. These ecologically divergent mechanisms for attracting bodyguards should also differ fundamentally in their evolution, particularly in how herbivores and their predators select on plant resistance traits. However, these different strategies are typically lumped together in theoretical discussions of indirect defences.

3. Here we highlight the fundamental differences between resource-mediated and information-mediated indirect resistance and discuss the relative evolutionary impacts of the interacting organisms as agents of natural selection in shaping indirect defence traits of plants.

4. We review clear evidence for a defensive function of resource-mediated indirect resistance, and recognize a significant lack of evidence for an adaptive function of information-mediated traits. A comparison of the underlying factors driving coevolution in each category of indirect defences, suggests that information-mediated indirect resistance is less likely to be subject to coevolution between plants and the third trophic level.

**Key-words:** extended phenotype, induced responses to herbivory, myrmecophyte, plant defences, plant–insect interactions, tritrophic interactions, volatile organic compounds

## Introduction

Plants produce a diverse array of physical and chemical traits that confer various types of resistance to insect pests, and can mediate complex interactions among the members of the plant-associated arthropod community (Kessler & Baldwin 2002b; Kessler & Halitschke 2007; Poelman, Van Loon & Dicke 2008). Among the most striking examples of such interactions are those between plants and species of the third trophic level – predators and parasitoids of herbivores. In a seminal paper, Price *et al.* (1980) highlighted that ‘...theory on insect–plant interactions cannot progress realistically without consideration of the third trophic level.... as part of a plant’s battery of defences against herbivores’. Since that time, researchers have gained insights into the expression of plant traits that facilitate top-down control of

herbivores. These traits have been termed ‘indirect defences’ to contrast them with plant traits such as toxic and anti-digestive compounds, leaf toughness or trichomes, that directly reduce herbivore fitness and thereby increase plant fitness (Duffey & Stout 1996). We follow the nomenclature of Karban & Baldwin (1997) and use the term resistance (e.g. indirect resistance) for traits which affect the preference and performance of herbivores (i.e. the herbivore’s perspective), and the term defence for traits that, through the reduction in herbivore performance, have a positive effect on plant fitness (i.e. the plant’s perspective). Accordingly, indirect defences are plant traits that (i) attract and improve foraging by natural enemies of herbivores, and thereby (ii) facilitate control of herbivore populations and (iii) ultimately increase plant fitness (Karbon & Baldwin 1997).

Indirect resistance can theoretically be mediated by a large spectrum of traits, including those that constitutively facilitate the residence of natural enemies on the plant, as well as

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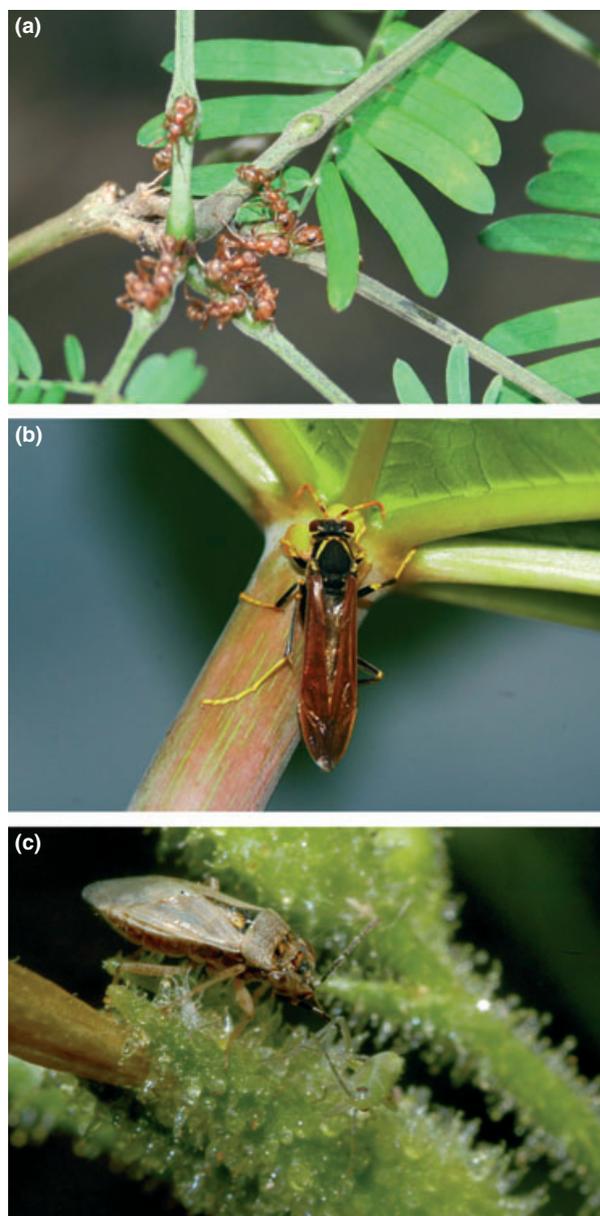
herbivore-induced traits that may be produced to recruit 'bodyguards' (Dicke & Sabelis 1988) in response to herbivore attack. These traits may provide some kind of resource to predatory insects, such as food and shelter, or provide information about the location and identity of herbivores in the form of altered visual and olfactory cues (Fig. 1).

Conventional hypotheses for the evolution of plant defence suggest that these resource- and information-providing traits should be viewed collectively as indirect defences (Karban & Baldwin 1997). However, the phenotypic diversity of these traits suggests that they may be subject to quite different selective forces, and quite disparate ecological contexts, depending on variation in the herbivore and predator communities, and on the strength of the association between plants and their defenders (i.e. facultative vs. obligate). Indeed, we argue here that resource and information based recruitment represent two fundamentally different strategies. Moreover, we suggest that our theoretical and conceptual understanding of plant defence would be improved by a more detailed analysis of the adaptive value of these different traits in their natural ecological context. In this paper, we attempt such an analysis. We first review the current state of knowledge for the major indirect defence strategies, and then synthesize these findings to shed light on which traits actually contribute to a plant's 'indirect defence'.

#### ANT-PLANT INTERACTIONS COVER THE SPECTRUM FROM FACULTATIVE TO OBLIGATE AND SYMBIOTIC

Ant plants are prime examples of a plant-predator symbiotic mutualism (Fig. 1). Plants provide resources, largely constitutively produced (Heil & McKey 2003), to ant species that may be specialized to nest and feed on these plants (Fiala & Maschwitz 1990). The ants consume extrafloral nectar (EFN) and food bodies (FBs), and may nest in specialized plant parts in return for a protection of the plant from attackers and competitors. These systems can be obligate (myrmecophytes) and represent the association of one or a few plant species with one or very few ant species (Bronstein, Alarcon & Geber 2006) (Fig. 1a), or facultative (myrmecophiles), and may lack a close association (Fig. 1b). The production of ant food rewards increases predator visitations, and thus predation on herbivores may be higher on EFN-producing plants than on plants not producing EFN (O'Dowd 1982; Koptur 1992; Heil & McKey 2003). Similarly, physical shelters (domatia), such as hairy leaf pads or hollow shoots may increase predation pressure on plants with these traits (Agrawal, Karban & Colfer 2000; Heil 2008). Facultative plant associations with predators are often mediated via an inducible production of the rewards. For example, the secretion of EFN can increase in response to the presence of consumers and/or herbivory and lead to increased ant visitation (Heil *et al.* 2001).

Ant-plant associations mediated through the provision of food and/or shelter appear to be widely distributed and can involve up to one-third of all woody plant species in a given habitat (Schupp & Feener 1991). EFN is secreted by species in at least 332 plant genera from 93 Angiosperm families as



**Fig. 1.** Resource-mediated and information-mediated indirect resistance. (a) Obligate ant-ant plant associations: *Pseudomyrmex spinicola* ants feeding on *Acacia collinsii* extrafloral nectaries. Ants protect plants from herbivores and competitors. The plant invests in this indirect resistance through predators by providing food (extrafloral nectar, food bodies) and shelter (hollow thorns) [image (a) courtesy K. Poveda]. (b) Facultative attraction of generalist predators with extrafloral nectar: *Polistes* sp. wasp visiting extrafloral nectaries on *Ricinus communis*. (c) Herbivory-induced volatile organic compound (HIVOC) emission as predator-attracting cue: The predatory bug *Geocoris pallens* is attracted by HIVOCs emitted from herbivore damaged *Nicotiana attenuata* plants and preys on herbivorous insects, such as the mirid bug *Tupiocoris notatus* (image) [images (b) and (c) by A. Kessler].

well as in 11 genera of ferns (Koptur 1992; Keeler 2008). Domatia suitable for ants are found in at least 200 plant species and are particularly common and diverse in form and structure in the Rubiaceae (Beattie 1989). Moreover, very

close and specialized ant-plant associations are found in over 100 genera of tropical angiosperms in at least 20 plant families (O'Dowd 1982; Davidson & McKey 1993). The group of ant species engaged in specialized plant associations comprises five subfamilies of the Formicidae (Davidson 1997), while facultative ant plants often recruit a larger diversity of insect taxa into the indirect defensive arsenal.

#### PLANT VOLATILES MEDIATE FACULTATIVE INTERACTIONS WITH THE THIRD TROPHIC LEVEL

The close relationships between tropical ants and ant plants discovered in the nineteenth century were widely accepted as mutualistic by the 1970s (Janzen 1966; Bentley 1977; Bronstein 1998; Heil & McKey 2003; Bronstein, Alarcon & Geber 2006). In contrast, the emission of herbivory-induced volatile organic compounds (HIVOCs) was only recently identified as a trait that can attract predators and parasitoids to herbivore-damaged plants. Classic examples of HIVOC-mediated indirect resistance include the attraction of predatory mites to spider mite-attacked lima beans (Dicke & Sabelis 1988), and the attraction of the parasitoid braconid wasp, *Cotesia marginiventris*, to maize seedlings that are attacked by the beet armyworm, *Spodoptera exigua* (Turlings, Tumlinson & Lewis 1990). Meanwhile a whole range of folivorous mites (Dicke & Sabelis 1988; Dicke *et al.* 1990), insects (Turlings, Tumlinson & Lewis 1990; Drukker, Scutareanu & Sabelis 1995; Du *et al.* 1998; Halitschke *et al.* 2000; Kessler & Baldwin 2001), stem borers (Potting, Vet & Dicke 1995; Khan *et al.* 2008), seed feeders (Steidle, Fischer & Gantert 2005), and root feeders (Van Tol *et al.* 2001; Rasmann *et al.* 2005) have been shown to induce VOCs. They attract predators and parasitoids from at least five animal orders, including entomophagous nematodes (Rasmann *et al.* 2005), predaceous mites (Dicke *et al.* 1990), Heteroptera (Kessler & Baldwin 2001, 2004; Halitschke *et al.* 2008) (Fig. 1c) and Coleoptera, and particularly parasitoid Hymenoptera (Turlings, Tumlinson & Lewis 1990; Mattiacci, Dicke & Posthumus 1995; De Moraes *et al.* 1998). More recently birds have also been shown to be attracted to HIVOCs and use them to find their prey (Mantylä *et al.* 2008). Leaf injury caused by caterpillar movement (Peiffer *et al.* 2009) and insect oviposition (Hilker & Meiners 2006; Kopke *et al.* 2008) can also increase volatile emission and attract members of the third trophic level.

The composition and abundance of volatiles can change dramatically in response to herbivory, and such changes are likely ubiquitous among many, if not all, plant species. Many of these compounds can be perceived by insect olfactory receptors, thus they may provide cues for prey-searching predators and host-searching parasitoids. In contrast to direct resource provisioning, HIVOCs are information, and supposedly function in plant resistance only when inducible, since the HIVOC cue has to be associated with prey/host by the foraging natural enemies (Heil & Karban 2010).

Depending on whether or not predator attraction is primarily mediated through the provision of additional resources or through the provision of information, we should

expect significantly different natural selective forces directing their evolutionary trajectories. In the following paragraphs we try to identify the likely factors and agents influencing natural selection on resource- and information-mediated indirect defensive traits.

#### Plant defensive function of predator attraction

A defensive function of a plant trait is only evident if its expression increases the relative fitness of the plant under herbivory compared to a plant that does not express this trait growing in the same environment (Karban & Baldwin 1997). In order to prove that a trait has an indirect defensive function, we must present data that support the following three hypotheses: (a) Indirect defensive traits make plants more attractive to predators and parasitoids, and increase the residence time and/or number of the natural enemies on a plant compared to a plant not expressing the trait. (b) Increased enemy abundance decreases performance and survival of herbivores. (c) The difference in enemy abundance observed in (b) causes plant genotypes with these traits to show higher fitness compared to plant genotypes without the traits: that is, there is selection on heritable variation in indirect resistance traits. We review empirical support for these hypotheses as well as evidence for coevolution (i.e. reciprocal adaptation) between plants and third trophic level organisms.

#### DEFENSIVE FUNCTION OF RESOURCE-PROVIDING TRAITS

There is strong evidence that plants benefit from investing in resources for predators. The exclusion of ants from myrmecophytic plants almost always results in dramatic increases of herbivory on the plants (Heil & McKey 2003; Heil 2008). For myrmecophilic plants and their more diverse and ephemeral predator community, the benefits of investing in EFN or food body production are not always obvious. For example, studies on bracken fern (*Pteridium aquilinum*) and *Helichrysum* spp. could not find experimental evidence for an EFN-mediated resistance (O'Dowd & Catchpole 1983). The majority of ant-exclusion studies, however, clearly demonstrate a defensive effect of ants using extrafloral nectaries (Chamberlain & Holland 2009; Rosumek *et al.* 2009) and this interpretation is strongly supported by experimental manipulations of the quantity of EFN on *Macaranga* spp. (Heil *et al.* 2001) or lima bean (*Phaseolus lunatus*) plants (Kost & Heil 2005, 2008). Moreover, predatory ants were identified as the agents of selection in a definitive demonstration of the defensive function of EFN of wild cotton, *Gossypium thurberi*. When ant visitation was experimentally reduced, increased herbivore abundance caused greater damage and reduced plant fitness. Experimental reduction in EFN provision reduced ant recruitment, increased herbivory and decreased fitness. Moreover, natural variation in EFN production correlated positively with plant fitness (Rudgers & Strauss 2004).

## DEFENSIVE FUNCTION OF HIVOCS

In contrast to resource-mediated indirect resistance, natural selection on HIVOC traits has never been demonstrated. There are some studies that collectively imply a defensive function of plant volatiles and support hypotheses (a) and (b) above. For example, differential HIVOC emission results in differential attraction of predators and parasitoids (Rasmann *et al.* 2005; Halitschke *et al.* 2008). These predators and parasitoids can in turn have significant effects on herbivore performance, herbivore populations and herbivory (De Moraes *et al.* 1998; Thaler 1999; Kessler & Baldwin 2001, 2004). However, observations of plant fitness benefits of volatile traits are rare (Kost & Heil 2008; Allison & Hare 2009). We propose two major reasons why HIVOC-mediated reductions in herbivory may not result in increased plant fitness. First, the effects of HIVOC-attracted predators or parasitoids on herbivores may not influence plant fitness, perhaps because many of these natural enemies do not immediately kill their hosts (e.g. parasitoids), which results in continued damage to the plant. In addition, plants may simply have a high tolerance for herbivory, which overrides potential fitness effects mediated by attracted predators. Secondly, because of the facultative nature of the attraction, complex interactions within the arthropod community may result in no net effect.

A synthesis of the available studies is difficult because the data are often from simplified agro-ecosystems, where natural selection by natural enemies of herbivores is less likely, because there is usually virtually no genetic variation within a single agricultural field. In other cases, there are missing causal links. For example, in wild tobacco *Nicotiana attenuata*, the major herbivore, tomato hornworm (*Manduca quinque-maculata*) has significant negative effects on plant fitness (Kessler & Baldwin 2002a, 2004). Plants emit HIVOCs that are attractive to a major heteropteran predator, *Geocoris pallens* (Kessler & Baldwin 2001; Halitschke *et al.* 2008) (Fig. 1c). The predator has significant positive fitness effects for the plant, suggesting that HIVOCs function as indirect defences in this system (Kessler & Baldwin 2001, 2004). However, it is unclear if natural genetic variation in HIVOC emission (Halitschke *et al.* 2000) is correlated with predator effects on plant fitness. Allison & Hare (2009) proposed and reviewed a number of additional requirements to demonstrate that HIVOCs are adaptive as predator signals (synomones). Specifically, natural enemies should (a) preferentially learn a subset of HIVOCs associated with their host/prey and (b) respond innately to the particular HIVOCs induced by their prey/host. A review of over 450 studies revealed no study testing hypothesis (a) and weak evidence for (b) (Allison & Hare 2009). The latter hypothesis is based on the expectation that a more intimate association (higher dietary specialization) of natural enemies with the plant (here through the herbivore) should result in a higher specialization of the traits mediating the interaction. However, a review of 140 papers on 95 species of parasitoids and herbivores revealed only weak evidence that specialist natural enemies use more specialized volatile cues than generalists, and no sig-

nificant difference of innate responses between specialists and generalists was found (Steidle & Van Loon 2003).

In conclusion, although we know of a large number of plant species specifically emitting HIVOCs in response to herbivore damage, and an equally large number of natural enemy species responding to these signals, evidence is weak that these HIVOCs in fact function as signals or as indirect defences by the above definitions. One emerging theme however is that the probability of reciprocal natural selection on plant traits that attract natural enemies of their herbivores, and on predators to utilize those resources and/or information, may be higher the more intimate the interaction between plants and the predators/parasitoid of their herbivores.

EVIDENCE FOR RECIPROCAL NATURAL SELECTION:  
HIGH INTIMACY AND HIGH SPECIALIZATION

The broad taxonomic distribution and the ontogenetic diversity of resource traits, such as EFN, domatia and FBs (see above) suggest multiple gains and losses of those traits over evolutionary time. For example, in the Southeast Asian genus *Macaranga*, the ant-associations range from highly specialized to generalized (Fiala *et al.* 1994). Highly specialized associations have likely evolved two to four times and been lost one to three times (Blattner *et al.* 2001; Davies *et al.* 2001). In contrast, a study on 13 Central American *Acacia* spp. and related genera suggested that specialized myrmecophytes are monophyletic and obligatory ant-ant plant interactions have only evolved once (Heil *et al.* 2004). However, anatomical and functional differences make independent origins of myrmecophytes within the African *Acacia* spp. likely (Palmer *et al.* 2000). Moreover, myrmecophytes are known from plant genera that belong to many different plant families (*Cecropia*: Moraceae; *Piper*: Piperaceae etc.). In short, available evidence supports multiple origins and perhaps also multiple losses of obligate myrmecophytism in the angiosperms.

It has been hypothesized that more long-lived, constant and exclusive associations between ants and ant plants are more likely when the ants reside within the plant, which may result in higher specialization of both partners (Heil & McKey 2003). Such higher specialization would include a larger allocation of resources to supply the ants with food and shelter and a higher level of protection by the ants. Both trends have been found in phylogenetic comparisons. For example, myrmecophytic *Macaranga* species produce more lipids and proteins in their food bodies, while facultative myrmecophiles produce carbohydrate-rich food bodies (Heil *et al.* 1998). EFN also tends to have a more complex composition in myrmecophytes than in myrmecophilic plants and is secreted constitutively by the obligate Central American *Acacia* myrmecophytes, whereas the myrmecophilic species of the same group secrete EFN only in response to herbivory (Heil *et al.* 2004; Heil, Rattke & Boland 2005; Gonzalez-Teuber & Heil 2009). All these observations indirectly support the hypothesis that more intimate mutualistic interactions result in more specialized traits.

In addition to the altered provision of food via food bodies and EFN along a gradient from obligate to facultative ant-plant associations, selection has likely acted on morphological and chemical traits. Prominent examples include preformed domatia in hollow thorns and stems, petioles and leaf pouches, but also olfactory cues that allow a rapid recruitment of ants and, in at least some cases, alternative chemical defence traits (Bronstein, Alarcon & Geber 2006). Although there are some examples of facultatively defended ant plants producing domatia (Maschwitz & Fiala 1995) and/or food bodies (O'Dowd 1982), there is broad support for the hypothesis that a more intimate interaction between ant plants and their ant partners resulted in the evolution of highly specialized traits and a greater investment in these traits. Accordingly, there is far greater evidence for reciprocal natural selection in myrmecophyte than in myrmecophile systems (Bronstein, Alarcon & Geber 2006).

Similarly, the broad taxonomic distribution of HIVOC predator attractants suggests either a very ancient origin or multiple phylogenetic origins of the ability to produce certain compounds and the ability to change relative rates of their emission. HIVOC emission has been shown in at least 13 plant families (Dicke, Van Poecke & De Boer 2003). However, there are a number of significant differences between HIVOC-mediated and resource-mediated indirect resistance. HIVOC emission has been found in virtually every plant species tested. Part of the reason that HIVOCs are universally produced by probably all plant species is that some of the herbivore-induced volatiles are emitted as a direct consequence of chemical breakdown processes in plant tissue ruptured by feeding herbivores (Noordermeer, Veldink & Vliegenthart 2001). Moreover, even the compounds specifically induced and produced *de novo* after herbivore damage derive from compound classes (e.g. terpenoids and phenylpropanoids) that are commonly expressed in all plant taxa. Therefore HIVOC emission represents a suite of traits that are diverse, ubiquitous and which may be utilized by any organism with an appropriate perception system. Moreover, in contrast to resource-mediated indirect resistance, HIVOCs can have multiple functions other than indirect resistance (e.g. coping with physiological stresses, direct resistance, plant-plant signaling). This potentially increases the number of agents of selection, which would result in more diffuse natural selection. The analysis of the costs of producing a defensive trait can help to evaluate its functionality and reveal evolutionary processes. Therefore we compare potential costs of resource and signal-mediate indirect resistance in the following paragraphs.

### Multiple functions, multiple costs

The benefits that plants obtain from interactions with herbivore enemies should broadly depend on the strength of the association, which varies depending in part on whether the interaction-mediating trait provides a private channel for interaction or not. Moreover, the strength of association seemingly varies depending on whether or not the predator-

attractive trait is a resource (and what type of resource) or simply information. Obligate myrmecophytes generally obtain stronger benefits from ant-mediated protection than myrmecophilic plants (Chamberlain & Holland 2009; Rosumek *et al.* 2009). Similar comparisons for HIVOCs are not possible because we are not aware of any study reporting HIVOC-mediated resistance as obligate for plant survival, leaving information-mediated indirect defences at the extreme facultative end of the interaction spectrum. From our previous analysis of indirect defence strategies, however, we conclude that obligate, specialized defensive mutualisms in general confer a much stronger benefit to both partners than facultative ones. Does this also mean that the potential costs associated with expressing an indirect resistance trait are different between obligate and facultative interactions?

Producing defence traits is assumed to be costly (and indirect defences are no exception) but how the expression of plant defences affects the allocation of resources away from reproductive success is still hotly debated (Agrawal 2011). In part, this debate stems from the fact that costs of resistance are measured in various ways, and evaluating costs of defence has proven difficult. Karban (2011) argues that costs of resistance should always be measured in terms of fitness to be interpreted in an evolutionary sense. Measuring costs by accounting for metabolite budgets can often not be interpreted in a coevolutionary framework, but represents most of the available data in the literature. Being aware of the limitations, and based on the available data and the associated theoretical frameworks, we predict that the type and strength of the costs likely vary between obligate and facultative interactions.

### PHYSIOLOGICAL AND ALLOCATION COSTS OF INDIRECT RESISTANCE

Allocation costs occur when a limited resource is used for defence, at the expense of primary metabolism, growth or reproduction. Evidence exists that resource-providing indirect resistance can impose substantial allocation costs. For example, FB production in the obligate ant-plant, *Macaranga bancana* represents almost 10% of overall aboveground tissue construction costs and 7% of the proteins that are invested into aboveground growth (Heil *et al.* 1997). The high costs of maintaining an ant colony are further emphasized by the observation that ant-related traits are plastic, and show reduced expression when such plants are released from their herbivores (Janzen 1973; Koptur 1985; Huntzinger *et al.* 2004; Palmer *et al.* 2008). The need to produce these costly resources throughout the whole year likely represents the main reason for the restriction of obligate ant-plant mutualisms to the tropics.

At the other extreme of the scale, physiological costs of HIVOC synthesis are assumed to be low due to the low molecular weight and quantity of VOCs that are typically induced (Dicke & Sabelis 1989; Halitschke *et al.* 2000). However, no study has rigorously quantified the direct metabolic costs of the release of HIVOCs or EFN. Circumstantial evidence for

the existence of allocation costs stems from the fact that EFN (Heil *et al.* 2000; Holland, Chamberlain & Horn 2009), and in some cases HIVOCs (Rostás & Eggert 2008), appear to be preferentially produced or released from young leaves. Both traits thus conform to the 'optimal defence' hypothesis (McKey 1974, 1979), which states that plants should preferably defend their young, still developing organs. Assuming a debated trade-off between growth and secondary metabolism (Herms & Mattson 1992), which should restrict the equal allocation of defensive traits, these optimal allocation patterns suggest costs of EFN secretion and HIVOCs release. Alternatively, two studies comparing the release of HIVOCs from cultivated and wild types of *Brassica* and *Phaseolus* species did not find evidence for a trade-off between growth and the production of secondary metabolites in the cultivated forms (Benrey *et al.* 1998; Ballhorn *et al.* 2008), despite the common but rarely tested hypothesis that costly resistance traits tend to be lost when relieved from natural selection during the domestication process (Karban 2011). Studies comparing elicitor-induced and control plants in the absence of herbivory have also failed to demonstrate significant fitness costs of HIVOC release, although there was some evidence for a transient cost to growth (Hoballah *et al.* 2004). Nectary-rich cotton cultivars exhibited similar growth and fitness as near-isogenic nectary-less ones under enemy-free conditions (Adjei-Maafa *et al.* 1983), which was further supported by the study of EFNs in *Chamaecrista fasciculata* (Rutter & Rausher 2004). In conclusion, the balance of empirical evidence supports the assumption that facultative indirect resistance, mediated by EFN or HIVOCs, will have negligible allocation costs, in contrast to comparatively high allocation costs of obligate, resource-based indirect resistance.

#### DIFFERENTIAL EFFECTS OF ECOLOGICAL COSTS

Negative fitness effects caused by the influence of a resistance trait (including indirect resistance) on a plant's interaction with its biotic or abiotic environment are referred to as 'ecological' costs (Felton *et al.* 1999; Heil 2002; Strauss *et al.* 2002). Intuitively, information-based strategies are expected to have a higher potential for ecological costs than resource-based strategies, because of the widely broadcast information and the lower specificity (see also Karban 2011). For example, plant viruses can manipulate the VOC spectrum that is released from their host plant and thereby attract their vectors (Mauck, De Moraes & Mescher 2010) – a strategy that is assumed to improve virus mobility and clearly causes significant ecological costs for the VOC-emitting plant. The expression of induced resistance to one attacker may also have a positive effect on a non-target attacker, as is the case for specialist herbivores that use HIVOCs as oviposition cues (Agrawal 2000). Indeed, there is abundant evidence that herbivores use HIVOCs to localize their host plants (Kessler & Baldwin 2001; Frati *et al.* 2008, 2009; Garcia-Robledo & Horvitz 2009; Jordan *et al.* 2009; Mooney, Robertson & Wanner 2009). Several adult insects with herbivorous larvae feed on ant-attracting EFN (Beach, Todd & Baker 1985; Koptur

1992), which might explain reduced herbivore populations on nectary-less vs. nectaried cotton cultivars (Adjei-Maafa *et al.* 1983). Even parasitic plants such as *Cuscuta* can use volatiles to localize their host plant (Runyon, Mescher & De Moraes 2006).

Ecological costs that result from the attraction of plant enemies by HIVOCs clearly exist. In addition, EFN-producing plants can also experience ecological costs when ants reduce pollinator visits to flowers (Ness 2006). Interestingly, plants may counter-adapt to reduce these problems. *Citrus* plants attract entomopathogenic nematodes via HIVOCs that are released from the roots (Ali, Alborn & Stelinski 2011). However, the release of these attractants by various *Citrus* cultivars may vary depending on their susceptibility to plant parasitic nematodes, which may also respond to the 'cry for help'. Apparently, lines that are resistant to nematodes emit the nematode attractants constitutively, whereas susceptible lines take the risk only when being under attack by beetle larvae (Ali, Alborn & Stelinski 2011). In the context of EFN, the ecological costs of pollinator deterrence by ants can be counterbalanced by positive effects if EFN attract or benefit the pollinators themselves (Hernández-Cumplido, Benrey & Heil 2010). Plants can also offset the ecological costs by releasing ant-repellent odours from flowers (Ghazoul 2001), or by spatially or temporally separating ant defenders and floral pollinators (Raine, Willmer & Stone 2002; Nicklen & Wagner 2006). For EFN, the danger of attracting herbivores appears low (but see the case of cotton noted above: Adjei-Maafa *et al.* 1983), because ants usually show territorial behaviour and protect access to extrafloral nectaries.

Plants emitting HIVOCs, can also experience costs in their interactions with neighbouring, competing plants. This occurs when undamaged plants receive the HIVOCs that are released from damaged neighbours and improve their defensive status, which in turn could give them a competitive advantage over their attacked neighbour (Karban 2011). Plant–plant signaling was first described for herbivore resistance (Baldwin & Schultz 1983; Rhoades 1983; Karban *et al.* 2000), but it can also affect resistance to pathogens (Shulaev, Silverman & Raskin 1997; Yi *et al.* 2009). The strength of 'plant communication' costs should depend in part on the relatedness of the emitter and receiver (Karban & Shiojiri 2009). It should be noted that in just considering plant communication costs and benefits, there may also be benefits to the emitter if HIVOCs also function as within-plant signals to expedite defence induction (Farmer 2001), as found for sagebrush (*Artemisia tridentata*), lima bean (*Phaseolus lunatus*), poplar (*Populus deltoides* × *nigra*) and blueberry (*Vaccinium corymbosum*) (Karban *et al.* 2006; Frost *et al.* 2007; Heil & Silva Bueno 2007; Rodríguez-Saona, Rodríguez-Saona & Frost 2009). Plant–plant communication (eavesdropping) apparently represents information parasitism and thus may be further ecological costs of HIVOC release.

Obligate ant-plants can be challenged by ecologically costly parasites as well. Certain ant species make use of host-derived resources but either fail to defend their host (Janzen 1975; Raine *et al.* 2004; Clement *et al.* 2008) or show a 'castration'

behaviour, consuming reproductive tissue in order to redirect host investment towards vegetative structures (Yu & Pierce 1998; Gaume, Zacharias & Borges 2005). Specialized ant-plants have evolved numerous strategies to exclude such parasites (Brouat *et al.* 2001; Izzo & Vasconcelos 2002; Heil, Rattke & Boland 2005), including increasing the resources provided to specialized ants, which evidently raises the costs of the mutualism (Heil *et al.* 2009).

Costs can also arise when the expression of one defensive trait is negatively correlated with another trait. Trade-offs between direct and indirect resistance are possible and have also been observed in obligate ant-plants, which often show reduced direct resistance (Heil *et al.* 1999; Heil, Staehelin & McKey 2000; Dyer *et al.* 2001), and also in plants with information-based strategies. For example, a negative correlation between HIVOC release and direct resistance by cyanogenesis was found in a comparison of different lines of lima bean, *Phaseolus lunatus* (Ballhorn *et al.* 2008). Such trade-offs are difficult to interpret, because they might be caused by genetic or allocation costs or simply represent adaptations to different environmental stresses. Nevertheless, there is at least some evidence that plants with a high capacity for information-based resistance strategies may exhibit lower direct resistance to herbivores.

We conclude that obligate mutualisms likely cause higher allocation costs than information-based strategies, whereas the latter type of indirect resistance shows a higher risk of ecological costs, possibly because plants have limited control over the receivers of HIVOCs. The diversity of potential ecological costs of information-based indirect defence strategies is congruent with the potential multiple functions that have been identified with HIVOC emissions. In addition to an indirect resistance function, within-plant signaling, direct resistance against herbivores and pathogens and the alleviation of physiological stress, have all been demonstrated as potential functions of HIVOC emission. As a consequence, there are apparently multiple agents of selection on HIVOC traits, likely resulting in diffuse and potentially conflicting natural selection. Resource-mediated indirect defences appear to have only a defensive function, such that increased intimacy of the interaction results in increased specialization and likely decreased probability of compromising selection.

## Conclusions

There exists broad evidence for the hypothesis that both resource-mediated and information-mediated indirect resistance strategies efficiently attract natural enemies of herbivores to the plant. Resource-mediated attraction of natural enemies generally results in a clear top-down control of the herbivore population, with positive fitness effects for the plant. Specifically, experiments that manipulated either predator access to plants or the amount of rewards, have established a causal link between resource provision and plant fitness benefits under predator (ant) protection. Although direct tests are still rare, the limited evidence suggests that

obligate ant-plant interactions (at least) may be the result of reciprocal natural selection and perhaps coevolution (Bronstein, Alarcon & Geber 2006). In addition, interactions with a higher level of intimacy (e.g. residency on a plant) may result in higher specialization, reduced ecological costs, and a reduced potential for conflicting selection by organism other than the mutualists.

In contrast, information-mediated HIVOC interactions of plants with members of the third trophic level are inherently less intimate, with a reduction in the consistency of enemy presence and a lower likelihood of direct selection on the volatile traits by predators and parasitoids. Natural enemies, with either high or low diet specialization, can learn and associate almost any HIVOC signal with their prey, and naïve predators/parasitoids show no strong innate preferences for HIVOCs induced by their hosts. In contrast to resource-mediated tritrophic associations, HIVOCs also have a large number of putative functions in addition to their proposed function as indirect defences. Those include within- and between plant signaling, direct herbivore resistance, and alleviation of physiological stresses, all of which have more direct effects on plant fitness than plant-mediated predator attraction. Moreover, information encoded in HIVOC cues is universally available for every organism that is able to perceive them, which inherently broadens the spectrum of potential selective agents (diffuse natural selection) and increases the probability of ecological costs and conflicting selection on those traits. We thus conclude that the absence of experimental evidence for an indirect defensive function of HIVOCs is likely not due only to the difficulty of the appropriate experiments. Rather, we argue that HIVOC production is inherently less closely associated with plant fitness via the top-down control of the herbivore population, and suggest that defence may be a relatively rare reason for the evolution of HIVOC traits. To be clear, we appreciate and value the overwhelming evidence that HIVOCs can specifically attract natural enemies to the plant, but emphasize the fact that we still lack evidence that this attraction influences plant fitness. Finally, a clear defensive function of HIVOC traits seems most likely to be found in systems where herbivory has significant negative impacts on plant fitness and where the herbivore species with the strongest impact is controlled by a HIVOC responsive natural enemy. Future research should thus focus on the study of tritrophic interactions involving key-stone herbivores that have significant effects on plant fitness and when testing these 'defences' should explicitly consider potential additional functions of HIVOC cues as alternative hypotheses.

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