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The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry for help'

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Attacks by herbivores elicit changes in the bouquet of volatiles released by plants. These herbivore-induced plant volatiles (HIPVs) have been interpreted as being indirect defenses. However, given that no studies have yet investigated whether HIPVs benefit the fitness of a plant, their defensive function remains to be established. Moreover, herbivores, pathogens, pollinators and competitors also respond to HIPVs and, in addition, neighbouring plants in native populations also emit volatiles that provide a background odour. These considerations enrich the evolutionary context of HIPVs and complicate predictions about their adaptive value. Molecular advances in our understanding of HIPV signaling and biosynthesis is enabling the creation of HIPV-'mute' and possibly HIPV-'deaf' plants. As we discuss here, such plants could be used for unbiased examination of the fitness value of HIPV emissions under natural conditions.

The function of HIPVs in a multitrophic context

Plants are famous for their ability to produce a diversity of secondary metabolites [1], some of which are released into the air after attack or egg deposition by herbivores [2–5]. These herbivore-induced plant volatiles (HIPVs; see Glossary) mainly comprise terpenoids, fatty acid derivatives, phenyl propanoids and benzenoids [6,7] and can be emitted either at the site of damage or systemically from undamaged parts of affected plants [8]. The blends can be complex, comprising hundreds of compounds [9], some of which are not produced by intact or mechanically damaged plants and others of which are synthesised *de novo* in response to herbivore attack [10]. HIPVs can elicit behavioural changes in various community members, from carnivorous arthropods and parasitic nematodes to insectivorous birds and from conspecific neighbouring plants to parasitic plants [11–16]. Given that HIPVs can influence various community members (Figure 1), they can also influence community dynamics [17–20] and, therefore, food webs are overlaid with infochemical webs (Figure 2). The intricacies of these webs can confound simple interpretations of the fitness consequences of HIPVs for plants.

Most studies of the ecological functions of HIPVs address species interactions at the level of individuals,

and usually in simple linear agro-ecosystem food chains that involve one plant, one herbivore and one carnivore. However, the situation in agricultural and especially natural ecosystems is more complex. Herbivores are usually attacked by many different natural enemies and competition among these can obviate the top-down effects that are thought to be mediated by HIPVs [21,22]. It has been shown [23,24] that competition among insect herbivores is more pronounced than was previously thought, and HIPVs can also mediate such interactions [25–27]. Although HIPVs are thought to be an induced indirect plant defense, they can also attract herbivorous arthropods [28,29] or interfere with the attraction of pollinators by recruiting bodyguards [17,19]. During the 1980s, Peter Price and colleagues drew attention to carnivores as a component of the defense strategy of a plant [30], which was later coined 'indirect defense' [31]; the authors argued that plant–herbivore interactions should be studied in the context of the tri-trophic interactions in which they are embedded and that plant fitness should be the currency for determining whether a trait should be considered a defense [30]. Three decades later, limited progress has been made in testing the evolutionary framework that Price and his colleagues envisioned and, more specifically,

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Glossary

Direct plant defense: characteristics of a plant, such as thorns, thick cuticle or toxic secondary metabolites, that negatively affect the physiology or behaviour of herbivores.

Food web: all connections between species in a community that represent trophic interactions where one of the interactants consumes the other.

HIPVs (herbivore-induced plant volatiles): volatiles that a plant produces in response to herbivory. These can either be compounds that a plant does not biosynthesise unless it is damaged or compounds that are also synthesised by undamaged plants but in larger amounts by damaged plants. Because the information content of volatile blends is in the mixture of compounds, it is important to also consider compounds that are produced by plants but repressed when plants are attacked.

Indirect plant defense: characteristics of a plant that enhance the effectiveness of natural enemies of herbivores, such as alternative food for carnivores (extrafloral nectar, pollen) or HIPVs.

Infochemical: a chemical that, in the natural context, conveys information between two individuals evoking a behavioural or physiological response in the receiver that is adaptive to either one or both of the interactants [107].

Infochemical web: all connections between species in a community that represent interactions where one of the interactants affects the behaviour and/or physiology of the other.

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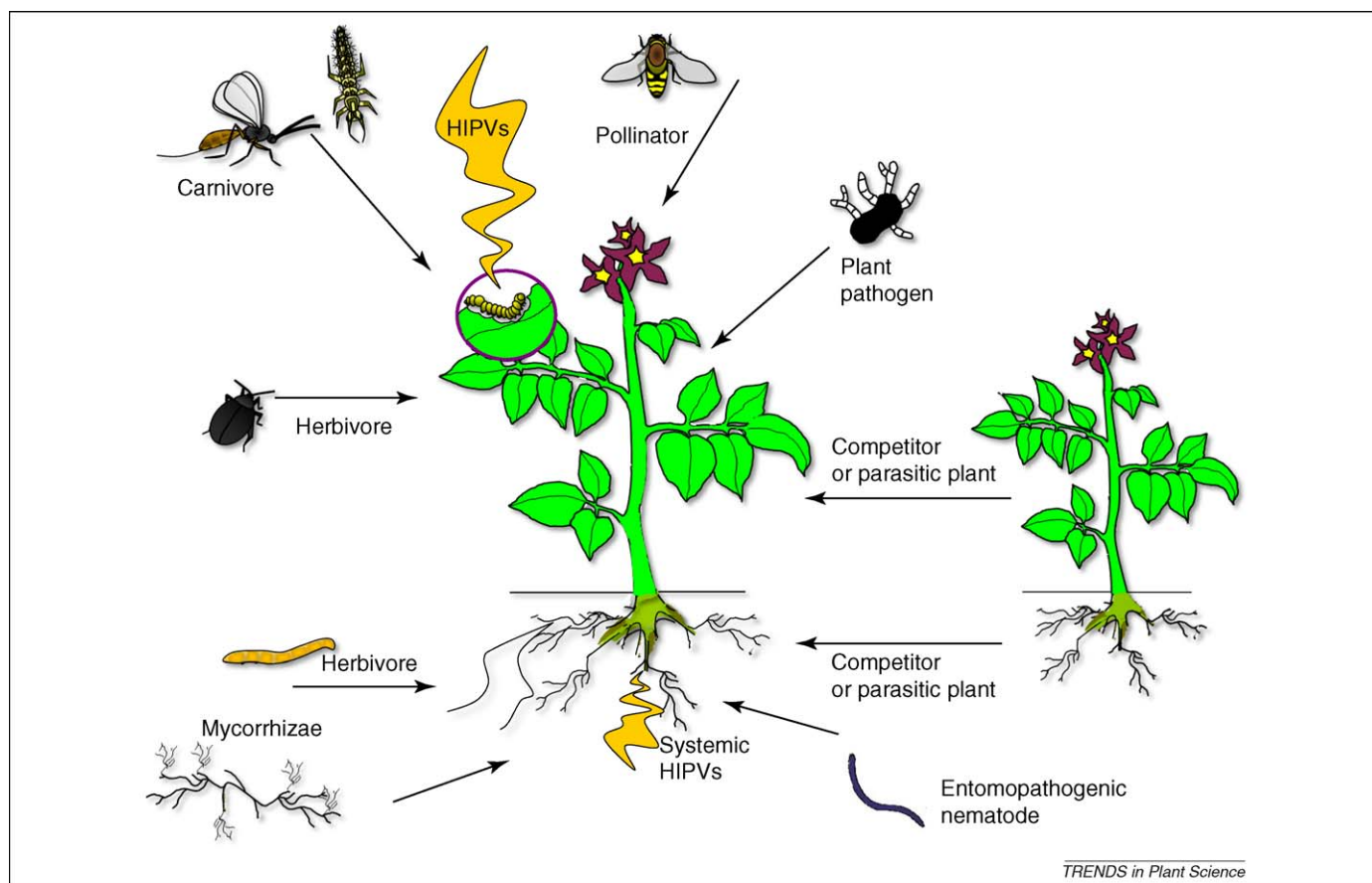
Figure 1. Plant damage and HIPVs. A plant that is locally damaged by a herbivore emits induced volatiles systemically, both above- and belowground. The HIPVs can affect various community members that each exert different selection pressures on the plant.

the hypothesis that HIPVs function as defenses that increase plant fitness has not been falsified.

Most studies of the function of HIPVs are laboratory based and only a few have demonstrated an HIPV-mediated increase in carnivore attack rates on herbivores under field conditions [26,32–35]. However, a recent study showed a correlation between carnivore attack rates in the laboratory and in the field [35]. Although no studies have yet rigorously tested the effects of HIPVs on plant fitness, it is likely that plants benefit from predator attraction, as predators remove herbivores by consuming them. The first studies of HIPVs [36,37] were instigated by modelling studies showing that the extermination of herbivorous spider-mite populations by a predatory mite could only be explained by a hypothesised factor that enhanced the colonisation of spider-mite colonies by the predator beyond random movements [38]. This factor appeared to consist of HIPVs [36,37]. To date, >25 predator species are known to be attracted to HIPVs [6]. That parasitoid activity benefits plant fitness is less self-evident (but see Ref. [39]) as parasitoids do not instantaneously kill their herbivorous host. However, two papers show that parasitoid activities can also benefit plant fitness [40,41]: these studies used pre-parasitised larvae and showed that the feeding of parasitised larvae does not reduce plant reproductive output in contrast to feeding by unparasitised larvae. However, because HIPVs and the attraction of parasitoids to feeding larvae were not examined in these studies, their relevance to the defensive value of HIPVs remains to be

elucidated. Moreover, most of the environmental variability was removed by growing the plants under controlled laboratory conditions. Many environmental factors, including light intensity, fertilisation and watering regimes, are known to influence how small differences in leaf damage are translated into differences in reproductive output [42], as well as HIPV emissions [43–45]. This environmental variability in HIPV emissions is likely to influence whether carnivores respond to HIPV emissions and locate feeding herbivores, and whether their feeding behaviour results in a top-down fitness benefit for plants under natural conditions.

Moreover, the importance of the community context for the evaluation of the effects on plant fitness makes it difficult to infer the selective pressures on the plant to release HIPVs. Here, we address these selection pressures and develop them in a community ecological context. First, we consider the different community members that react to HIPVs and how their responses could alter selective regimes for emissions. We then review what is known about the mechanisms responsible for the activation of HIPVs and consider how these mechanistic details will eventually enable definitive tests of the fitness consequences of HIPV emissions in the rich community context that occurs in the real world.

Carnivore attraction to HIPVs

Carnivorous arthropods are attracted to HIPVs and examples include mites as well as insects from five insect
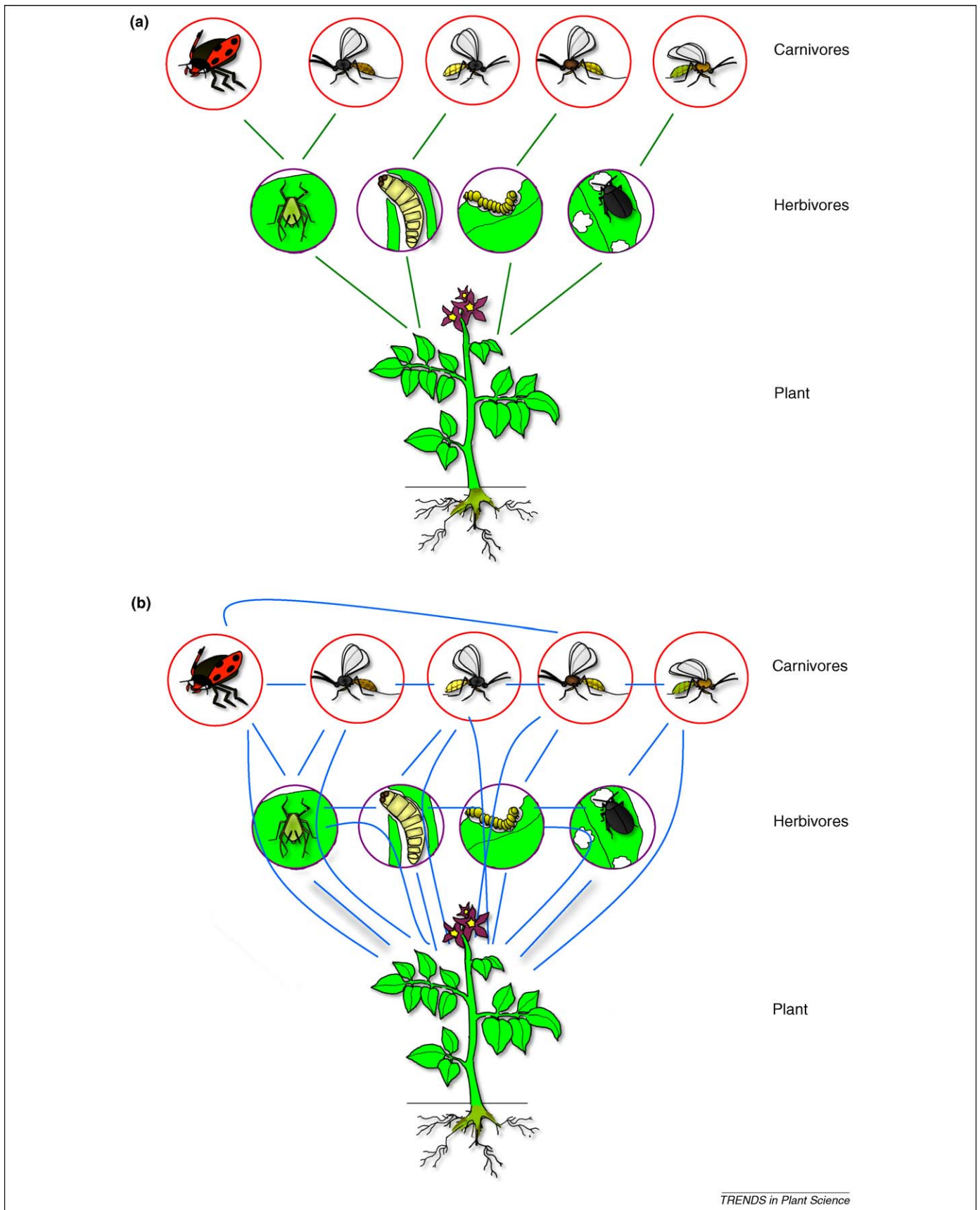
Figure 2. Food web and infochemical web. **(a)** A hypothetical food web represents trophic interactions (green lines) between members of a community, whereas **(b)** an associated hypothetical infochemical web represents the infochemically mediated interactions (blue lines) in a community.

orders (Hymenoptera, Neuroptera, Diptera, Coleoptera and Heteroptera) [6]. In some studies, a positive correlation was found between the degree of attraction and the amount of HIPVs emitted by a plant [46,47]. However, when different maize (*Zea mays*) accessions were compared for their ability to attract the parasitoid *Cotesia marginiventris,* it was clear that the quality of the HIPV blend was as important as its quantity. Indeed, not all HIPV constituents emitted elicit a response in carnivores. Gas chromatography–electroantennography (GC-EAG) can be used to reveal which compounds within a blend of HIPVs elicit a response in the chemoreceptors of the carnivore and such studies have shown that the compounds that dominate the HIPV blend are not necessarily the most important components for the carnivore [48–50]. This is not surprising, given that carnivores must evaluate how reliably the compound predicts the presence of a feeding herbivore [51].

The observation that the quantity of HIPV is positively correlated with carnivore attraction implies that there is a positive selection on plants to increase rates of HIPV emission. However, these emissions are frequently orders of magnitude lower than other plant emissions used to attract insects, such as those emitted from flowers [52]. This suggests that ecological, rather than biosynthetic costs of emission, set upper boundaries to emission rates [52,53]. Moreover, it is not clear how to quantitate the emission rate. Although some studies have shown that enhancing individual components of HIPV blends increases predator attraction under field conditions [26], others suggest that individual HIPV components function independently. For instance, the predatory mite *Phytoseiulus persimilis* is not attracted to the homoterpene (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene when it is offered as a pure compound [37]. However, when this compound, which is emitted from prey-infested lima bean plants (*Phaseolus lunatus*), is added to a blend of compounds emitted from a plant infested by non-prey caterpillars, it becomes more attractive to the predatory mite [54,55]. Thus, to understand the selection pressure exerted by carnivores on HIPV emission, one needs to know which combination of compounds is used by the carnivores.

Additional complications come from the observation that some HIPVs are not attractive to carnivores or can even be repellent or mask the attractive compounds [46,56]. When combined with a recent report that herbivore elicitation not only increases the emission of certain compounds, but can also suppress the release of certain wound-elicited constituents [9], these observations suggest that plants have the tools to fine-tune the attractiveness to carnivores, and could alter the role that certain compounds have in interactions that the plant has with other members of its community.

Herbivore responses to HIPVs
The behavioural responses of herbivores to HIPVs have been investigated less intensively than have those of carnivores. Some herbivores, such as spider mites [25], aphids [57] or moths [26], are repelled by HIPVs, whereas others are attracted, such as beetles [28,29,58], aphids [59] and moths [60,61]. Thus, the infestation of a plant by a herbi-

vore can result in differential responses in different community members; this has been shown with tobacco (*Nicotiana attenuata*) plants in their native habitats in the southwestern USA. Genetically silencing the production of fatty-acid derived green leaf volatiles (GLVs), a major component of the HIPVs of *N. attenuata* [26], reduces herbivore loads on these transformed plants when they are planted into native populations [28,62]. These results underscore the double-edged sword of HIPV emissions. The net selective consequences for a plant of releasing HIPVs probably depend on the composition of the herbivorous insect community associated with it as well as the relative fitness consequences that result from attack by each of these herbivores [63]. For instance, although attack of an *N. attenuata* plant by the mirid bug *Tupiocoris notatus* leads to some damage, it also leads to an increased resistance to caterpillars of the more damaging specialist herbivore *Manduca sexta* [64]. Thus, the selection pressures exerted by these two herbivore species are quite different. In an environment where *M. sexta* is present, selection is likely to favour the emission of those HIPVs that attract the bug as its presence is likely to be beneficial for the plant.

Effects of HIPVs on plant pathogens
Other GLVs, such as C6-aldehydes, have been reported to interfere with the germination of plant pathogen conidia [65] and can also protect plants from infection by plant pathogens [66,67]. Interfering with the biosynthesis of GLVs can affect plant fitness; for example, in glasshouse studies, antisense-mediated silencing of the hydroperoxide lyase *HPL* gene increased the susceptibility of *Arabidopsis thaliana* plants to the fungal necrotrophic pathogen *Botrytis cinerea*, whereas overexpression of the gene resulted in enhanced protection from the fungus. Application of synthetic (*Z*)-3-hexen-1-ol also interfered with fungal infection [66]. Therefore, the emission of some HIPVs will be under positive selection in environments that are rich in plant pathogens, such as *B. cinerea,* that might invade wounds made by herbivores. However, the effects of GLVs on fungal resistance are not universal, as planting *HPL*-silenced *N. attenuata* plants into their native habitats over three field seasons revealed no evidence for increased susceptibility to fungal or bacterial attack, even when other plants, silenced in other pathogen resistance genes, were more susceptible (I.T. Baldwin, unpublished results, [68]).

Pollinator responses to HIPVs
The responses of pollinators to flower volatiles are well studied [69] and leaf herbivory can alter the emission of volatiles by flowers of the same plant [70]. Moreover, much anecdotal evidence suggests that some predators use flower volatiles to hide themselves within inflorescences to predate on flower-visiting insects. However, few studies have examined the responses of pollinators to HIPVs [11,17]. If these compounds are indicators of a plant under herbivore attack and increase the influx of predators, their emissions should signify a risk of low food availability or enhanced predator presence to pollinators. Given that pollinators use plant volatiles to optimise food intake, HIPVs might interfere with pollinator attraction when

better quality plants are present [71]. If HIPVs do result in a reduced attraction of pollinators [19], this implies that the emission of those HIPVs is under negative selection pressure during flowering, a possibility that requires more scrutiny.

Plant responses to HIPVs

The role of HIPVs in eliciting responses from neighbouring plants, both con-and heterospecifics, has been discussed for almost four decades and, although evidence from laboratory and field experiments continues to accumulate that is consistent with the notion that plants respond to the volatile emissions of their neighbours, the biological significance of these responses remains unclear [15,72]. Although plants have the potential to respond, the response distance was found to be short under field conditions in a study on interactions between plants from two different plant species (sagebrush *Artemisia tridentata* and *N. attenuata*) [73].

How plants perceive the emissions also remains unknown. HIPVs exposure can prime plant neighbours to respond faster or more intensely to subsequent herbivory, and priming can also mediate systemic responses within a damaged plant [8,74]. However, it is not clear what signals plants respond to. In laboratory studies with GLV-silenced *N. attenuata* plants located upwind of neighbouring wild-type plants, transcriptional responses were elicited in the downwind wild-type plants [75], suggesting that, for conspecifics, it is the absence of a volatile signal, rather than its presence, that provides biologically relevant information. This study, combined with a recent report that herbivore elicitation not only increases the emission of certain compounds, but can also suppress the release of certain wound-elicited constituents [9], suggests that researchers should be open minded about the nature of the signal in a volatile blend.

Exploiting HIPVs for systemically induced responses within the attacked plant implies that there is a positive selection pressure to increase HIPV emissions, but not if the signal is the absence of a volatile signal, or, in other words, the 'sound of silence'. Given that most phytohormone signaling cascades are negatively regulated signaling systems in which the perception of the phytohormone results in the removal of repressors, the absence of signals would be relatively easy to perceive and respond to. Preliminary evidence from field work with *A. tridentata* suggests that the degree of genetic relatedness influences the response of 'receiver' conspecifics [76]; when neighbouring plants use HIPVs to prime the defenses of genetically related neighbours, the inclusive fitness of the HIPV 'emitter' can also increase. However, when the neighbouring plants are not genetically related, valuable information could be co-opted by an eavesdropping competitor and plants would be under strong selection to reduce HIPV emissions. Clearly, the response of neighbouring plants to HIPV emissions is another complicating selection pressure that requires more scrutiny if researchers are to understand more fully the fitness consequences of HIPV emissions.

Community effects on HIPVs effectiveness

In most laboratory studies of the effects of HIPVs on community members, the HIPVs are presented to the insects against an odour-free background (but see Ref. [77]). However, in nature, the HIPV blend is present among a multitude of volatiles from other plants, which can influence the responses of insects to HIPVs [78]. An interesting observation from a laboratory study was that HIPVs from *Arabidopsis* or Brussels sprouts (*Brassica oleracea*) plants infested with caterpillars of the diamondback moth attracted fewer *Diadegma semiclausum* parasitoid wasps in the presence of isoprene than in its absence [79]. This effect was already clear at low isoprene concentration and isoprene was also shown to be perceived by the chemoreceptors of the wasp. Isoprene is one of the abundantly released volatiles from particular plant species, such as poplar *Populus* spp., and functions in protection against certain abiotic stresses [80]. The interference with parasitoid attraction in the laboratory suggests that HIPVs are less effective in attracting *D. semiclausum* parasitoids in habitats with elevated isoprene levels.

Given the previously mentioned large environmental influence on the HIPV emission of a plant, when this variance is embedded in a dynamic background of volatile organic compounds (VOCs) contributed by other members of the community, it is clear that special tools will be required to come to grips with the diversity of selective pressures that influence HIPV emissions under natural conditions. Specifically, researchers must be able to manipulate the ability of a plant to produce or respond to HIPVs or, in other words, to produce plants that are HIPV 'mute' or 'deaf', so that they can understand the fitness consequences of not producing or not responding to (components of) these emissions [15]. However, to produce such 'deaf' or 'mute' plants, researchers must understand the mechanisms by which they are produced and perceived, as the genes that encode the proteins mediating these mechanisms provide targets for manipulations such as post-transcriptional gene silencing or genetic transformation.

Mechanisms underlying the induction of HIPVs

Induced plant responses are mediated by a network of signal perception and transduction, ranging from the perception of cell damage through changes in plasma transmembrane potential and cytosolic Ca^{2+} concentration, through protein kinase responses to phytohormone signaling [81–83]. In *N. attenuata*, in which the relevance of HIPVs has been firmly established in field experiments [26], the signaling cascades responsible for the elicitation of HIPVs are understood in great detail. Moreover, many of the key regulatory loci in the signaling cascade have been genetically silenced and the ability of the plant to attract predators after elicitation has been tested in the field. When *M. sexta* larvae attacked *N. attenuata*, fatty acid-amino acid conjugates found in the oral secretions (OS) of the larvae were introduced into plant wounds during feeding [84]. These conjugates elicited a signal transduction cascade starting with a suite of mitogen-activated protein kinases (MAPKs), including a SIPK (salicylic acid induced protein kinase) and a WIPK (wound induced protein kinase) [85], both of which activate transcription factors of the WRKY family [86]. These transcription factors then orchestrate the induction pattern of three main

phytohormones [i.e. salicylic acid (SA), jasmonic acid (JA) and ethylene] that are involved in eliciting a suite of induced plant responses that include HIPV emissions [87]. *Nicotiana attenuata* plants transformed to silence JA [88], SIPK and WIPK [62], or WRKY transcription factors [86] were unable to release key constituents of the HIPVs blend and failed to attract predatory *Geocoris pallens* when planted into native populations.

The herbivore-induced signal-transduction pathways are characterised by extensive crosstalk [89], which can result in interference with HIPVs emission, as shown for the effect of whitefly *Bemisia tabaci* infestation on spidermite induced lima bean volatile emission [90]. However, compounds that are under the control of either signal-transduction pathway can also result together in the attraction of a carnivore species [91]. For instance, JA induces most spider-mite inducible volatiles in lima bean plants [92] and several of these JA-inducible compounds attract the predatory mite *P. persimilis* [37]. However, a major HIPV involved in the attraction of this predator is methyl salicylate (MeSA), which is not JA inducible in lima bean [54,55,92].

Genetically manipulated plants in which certain genes were introduced or silenced have been instrumental in elucidating mechanisms underlying HIPV-mediated plant-insect interactions [62,79,85,86,93–95] or in demonstrating the effects of gene function under field conditions [88,96].

Natural variation in HIPVs emission

Most research on HIPVs has used cultivated plants, such as maize, lima bean, tomato (*Solanum lycopersicum*), cabbage (*Brassica oleracea*) or gerbera daisies (*Gerbera jamesonii*) [6]. Some studies have addressed variation among accessions. For instance, among maize cultivars, the emission of HIPVs varied up to a factor of eight, and a similar variation was recorded for the total amounts emitted by different wild relatives of maize (i.e. different teosinte species) [45,97,98]. Also among *Gerbera* cultivars [99], apple (*Malus domesticus*) cultivars [100] and cotton (*Gossypium hirsutum*) accessions [101], variation in HIPV emissions has been reported. In addition to quantitative variation, there is also variation in the composition of the blend.

These studies show that there is variation in HIPV emissions among different plant genotypes. The first studies addressing natural variation in HIPV emissions are emerging for solanaceous plants, such as *Datura wrightii* [102] or *N. attenuata* [103] and for the brassicaceous plant *Brassica nigra* [104]. For instance, accessions obtained from *N. attenuata* plants located <1 m apart in a native population in Utah differed in their HIPV composition. Variation was recorded for several terpenes and a green leaf volatile, as well as for total detectable VOCs. In these experiments, the effect of environmental variation was minimised so that the variation recorded is probably genetic variation [103].

Thus, evidence for variation among conspecific plants exists for cultivated as well as wild plants. To understand the evolutionary importance of HIPVs, it will be relevant to expand the studies of natural variation in HIPV emission, both in terms of quantity and in blend composition. Such knowledge will provide information about the range of variation that other community members are exposed to and will be essential for an understanding of the selective forces that affect HIPV emission.

Conclusion and future perspectives

Although there is substantial evidence from laboratory and field studies that HIPVs can attract carnivores, it remains unclear whether their release results in a net fitness benefit for the plant. It is clear that there is considerable intraspecific variation in the emission of HIPVs and that some of this variation has a genetic basis [98,103,104]. This intraspecific variation and the presumed variation in degree of attraction of carnivorous 'bodyguards', especially when recorded for non-cultivated plants [103,104], might indicate that natural selection on this plant trait mediating indirect defense has not been strong. However, an alternative conclusion is that this variation reflects the different selection pressures on the emission of HIPVs, the mosaic of selection pressures and, thus, a mosaic of HIPV emission characteristics analogous to the geographical mosaic of coevolution [105]. The expression of defense traits represents a balance of their selective benefits tempered by their costs, and if HIPVs are a component of the indirect defenses of a plant, one might expect that their emissions have not been driven to extreme rates [106], unless HIPV emissions also function allelopathically as a competitive agent against neighbours, a special circumstance under which extreme emission rates might be selected for.

HIPVs have more functions than just as carnivore attractants and should be seen in the context of an infochemical web that overlays the food webs of a community (Figure 2). Plants are under selection to maximise fitness and this involves more than just defense against attackers. Plants should also maximise their competitive ability, by being a better forager than neighbouring plants and by interacting with synergists such as mycorrhizal fungi; they should also maximise reproductive output through effective interactions with pollinators. Thus, an understanding of the evolutionary ecology of HIPVs should concentrate on the role of HIPVs in a community context rather than on the role of HIPVs in individual tritrophic interactions. Rather than searching for the role of HIPVs, researchers should focus on the various effects, and relative selective strengths, of HIPVs on the reproductive output of the plant. This is likely to complicate the study of HIPVs but we remain optimistic that the rapid molecular advances in current understanding of the mechanisms of HIPV emissions will provide the tools to create HIPV 'deaf' and 'mute' plants in many different taxa. When such plants are planted into native habitats, they could provide the means to integrate all of the complicated HIPV-mediated interactions in a common currency of plant fitness, just as Price and colleagues [30] envisioned 30 years ago.

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