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Citation for final published version:

Sobhy, Islam S. and Bruce, Toby J.A. 2021. Evolutionary ecology: Plant volatile profile changes after escaping specialist insects. *Current Biology* 31 (15) , PR969-R971. 10.1016/j.cub.2021.06.043 Item availability restricted. file

Publishers page: <http://dx.doi.org/10.1016/j.cub.2021.06.043>
<<http://dx.doi.org/10.1016/j.cub.2021.06.043>>

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DISPATCH

Evolutionary ecology: Plant volatile profile changes after escaping specialist insects

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Considerable debate surrounds the role of plant volatiles in plant defence against insects. A new study provides evidence for evolutionary changes in an invasive plant that support the defensive role of plant volatiles.

Coevolution between insects and plants has been theorised as a major factor driving plant chemistry, with plants evolving herbivore-detering chemicals to which specialist herbivorous insects subsequently adapt. A classic paper by Ehrlich and Raven¹ drew attention to how certain butterfly phylogenies are associated with particular plant phylogenies and these authors suggested that plant chemistry could explain this association, with specialist insects being adapted to the chemistry of their host plants. Furthermore, the existence of a plant 'cry for help' signal when attacked by herbivores, with the aim of calling in natural enemy 'bodyguards' for protection, was first suggested over 30 years ago²⁻⁵. While there are many examples of natural enemies responding to herbivore-induced plant volatiles (HIPVs)⁶, there has been considerable debate regarding whether HIPVs are actually coevolved signals of the tritrophic (plant–herbivore–parasitoid) system or merely foraging cues^{7,8}. A key question relates to whether plant fitness is improved by releasing HIPVs to attract natural enemies of herbivores

In this issue of *Current Biology*, Turlings, Lin and colleagues⁹ provide evidence using the tritrophic study system of the common ragwort (*Jacobaea vulgaris*) as a host plant model, the specialist herbivore *Tyria jacobaeae* (cinnabar moth) and its specialist parasitoid *Cotesia popularis*; they also studied the generalist herbivore *Mamestra brassicae* (cabbage moth) for comparison. These authors looked at differences in volatile emission between ragwort plants from the native range in Europe and plants from other parts of the world (Australia, New Zealand and North America) where they are invasive. The invasion of ragwort took place 100–160 years ago and, until a few decades ago, no specialist herbivores or parasitoids were present in invasive ragwort populations. The new study reveals that the invasive plants, from all three locations, had changed. The authors discovered clear differences in volatile emission between native and invasive ragwort populations and hypothesise that this is due to evolution in response to the lack of specialised herbivores and parasitoids in the areas where plants have invaded. HIPV emission was much reduced in plants from the invasive populations, but constitutive volatile emissions were higher. The changes in constitutive volatile emission made invasive plants less attractive to the generalist herbivore but more attractive to the specialist herbivore, while changes in HIPV emission meant that invasive plants were less attractive to the specialist parasitoid (Figure 1). This supports the idea that the evolution of foliar volatile emissions is driven by their defensive role against insects. Although the defensive function of HIPVs has been proposed previously^{10–12}, this study shows for the first time that reverse evolution can occur in areas where specialised parasitoids are absent and the HIPV emission trait is reduced.

It has been questioned whether HIPVs are signals or cues⁷. Are they coevolved signals emitted by the plant for the purpose of attracting natural enemies? Or are they merely foraging cues that natural enemies benefit from? A 'signal' is a stimulus that is emitted to elicit certain responses in a specific intended receiver that feed back to the emitter^{13,14}. By contrast, a 'cue' represents a product of a primarily endogenous process that carries reliable information on the identity, localisation or physiological condition of an individual and, thus, can be used for decision making by another individual¹⁵. For HIPV emission to be considered to function as a

coevolved signal, both the emitting plant and the receiving insect should benefit, whereas if HIPV emission only benefits the receiver it should be considered a cue⁷. Although the current paper⁹ does not provide hard evidence that plant fitness is improved, it does show that, when specialised parasitoids are absent, the HIPV emission trait is reduced. This suggests that HIPVs are indeed produced as signals that are used in interactions with insects because, when the insect community changes, HIPV emission is selected against. It is possible that other factors could have changed volatile emissions, but this seems highly unlikely because the same effects were found in invasive ragwort plants from Australia, New Zealand and North America. When given a choice between the HIPVs from native and invasive ragwort plants, specialised *C. popularis* parasitoids clearly preferred the odours of the native plants, which emitted more HIPVs. This can explain why a higher parasitism rate was found in native ragwort populations than in invasive ones in a field experiment.

Differences in constitutive volatile emissions were also found, with higher emissions from invasive plants⁹. Bioassays, with herbivores, of egg laying preference, revealed that the specialist *T. jacobaeae* was more attracted to the odours of invasive ragwort plants and laid more eggs on these plants. This is because it is a specialist and is attracted to the odour of its host plant. Conversely, the generalist *M. brassicae* preferred the odours of native plants, which emitted fewer volatiles. This suggests that ragwort plants in the native range suppress volatile emission to avoid making themselves apparent to the specialist *T. jacobaeae*. When ragwort plants 'escape' from the specialist, they then are selected to increase volatile emission because generalists such as *M. brassicae* may avoid these volatile emissions. Ragworts produce toxic pyrrolizidine alkaloids, which make it unsuitable for generalist herbivores, and volatiles associated with these alkaloids might be avoided by generalists. It is possible that invasive ragwort could have evolved enhanced volatile emission to repel generalist herbivores.

The new work⁹ provides critical evidence that the exclusion from a specialised key herbivore and its main parasitoid has led to repeated and convergent changes in both constitutive and herbivore-induced volatile emissions in ragwort. The study supports the idea

that HIPVs are produced as a signal used in tritrophic interactions with insects because their production is selected against when specialist parasitoids are absent. This complements other studies showing fitness benefits from HIPV production. For example, Schuman *et al.*¹⁶ found that HIPV-silenced *Nicotiana attenuata* (coyote tobacco) plants had higher herbivory and lower fitness in a two-year field study, thus providing experimental evidence from the field that HIPV emission can improve plant fitness. Christensen *et al.*¹⁷ similarly found that HIPV-deficient mutant maize plants (*Zea mays*) were more susceptible to insect-feeding damage in an outdoor experiment with potted plants and in a field plot trial.

The paper by Lin, Vrieling *et al.*⁹ provides insight into how plant volatiles may evolve in the absence of specialised insects and could be an example of evolution in action. These authors hypothesise that the observed changes in ragwort volatile emission are driven by escape from the specialised herbivore *T. jacobaeae*. Ragwort is a noxious weed because the alkaloids it produces are toxic to grazing cattle. In attempts at biological control of invasive ragwort, the cinnabar moth has been introduced into Australia¹⁸, New Zealand¹⁹ and North America²⁰. Although there have been challenges in establishing cinnabar moth populations in Australia, their introduction has been considered a success in western North America²⁰. If the cinnabar moth is established in invasive ragwort populations, then the selection pressure for differences in volatile emission will be reversed. Artificial releases could mean that the 'escape period' for the invasive plants is ending. Once faced again with damage from cinnabar moth caterpillars, selection pressure will drive plants to reduce constitutive volatile emission to make themselves less apparent to the specialist herbivore. Furthermore, if the specialist parasitoid also becomes established in the invasive populations, there will be selection pressure on the plants to increase HIPV emission to attract these parasitoids when attacked by the herbivore. If sufficient levels of cinnabar moth become established, it will be interesting to see whether ragwort volatile emissions change again and revert back to the profiles of native plants and, if they do, how long this coevolutionary process will take.

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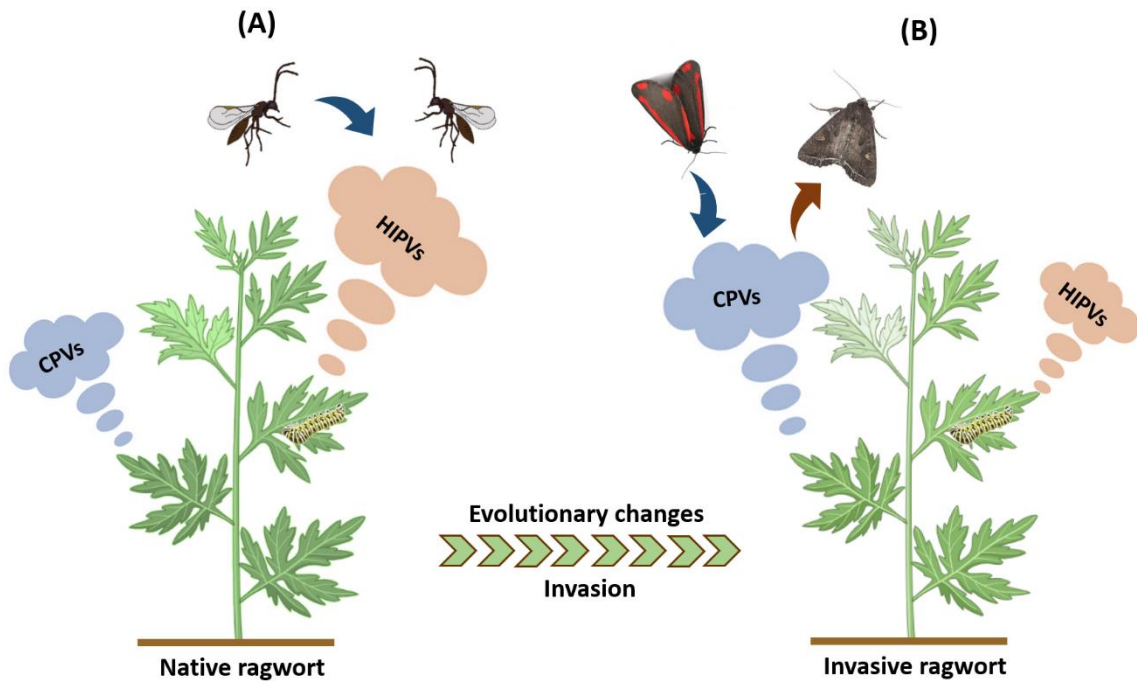


Figure 1. Evolutionary changes of plant volatiles upon invasion.

The figure illustrates the changes in the emission of constitutive plant volatiles (CPVs) and herbivore-induced plant volatiles (HIPVs) between native and invasive ragwort plants. The specialist parasitoid (*Cotesia popularis*) is strongly attracted to caterpillar-damaged native ragwort HIPVs but less responsive to invasive ragwort HIPVs. Invasive ragwort releases higher levels of CPVs and lower amounts of HIPVs compared with native plants, which renders the invasive plants more attractive to the specialist herbivore (*Tyria jacobaeae*) and less attractive to the generalist herbivore (*Mamestra brassicae*).