**Evolutionary ecology:** **Plant volatile profile changes after escaping specialist insects**

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**SUMMARY**

There has been considerable debate about the role of plant volatiles in plant defence against insects. A new study by Turlings and colleagues provides evidence for evolutionary changes in an invasive plant that supports the defensive role of plant volatiles.

**MAIN TEXT**

Coevolution between insects and plants has been theorised as a major factor driving plant chemistry with plants evolving chemicals to deter herbivores that are subsequently adapted to by specialist insects. A classic paper by Ehrlich and Raven1 drew attention to how certain butterfly phylogenies are associated with particular plant phylogenies and suggested that plant chemistry could explain this as specialist insects were adapted to the chemistry of their host plants. Furthermore, the existence of a plant “cry for help” signal when attacked by herbivores to call in natural enemy “bodyguards” for protection has been suggested for over 30 years 2–5. While there are many examples of natural enemies responding to herbivore induced plant volatiles (HIPVs)6, there has been considerable debate as to whether HIPVs are actually coevolved tritrophic signals or merely foraging cues 7,8. A key question relates to whether plant fitness is improved by releasing HIPVs to attract natural enemies 8.

In this issue of *Current Biology*, Turlings, Lin and colleagues 9 provide evidence using the tritrophic study system of common ragwort, *Jacobaea vulgaris* as a host plant model, the specialist herbivore *Tyria jacobaeae* (cinnabar moth) and its specialist parasitoid *Cotesia popularis*;as well as the generalist herbivore *Mamestra brassicae.* They 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 populations. The invaded plants, from all three locations, had changed. The authors discovered clear differences in volatile emission between native and invasive plant 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 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 if HIPVs are signals or cues 7. 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 which 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 individual 15. For HIPV emission to be considered to function as a co-evolved “signal” both the emitting plant and the receiving insect should benefit whereas if it only benefits the receiver it should be considered a “cue” 7. Although the current paper 9 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 used in interactions with insects because when the insect community changes it is selected against. It is possible that other factors could have changed volatile emission 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 genotypes than in invasive ones in a field experiment.

Differences in constitutive volatile emission were found with higher emission from invasive plants 9. Bioassays with herbivores 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 supress 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. Ragwort produces toxic pyrrolizidine alkaloids which make it unsuitable for generalist herbivores and volatiles associated with this may be avoided. It is possible that invasive ragwort could have evolved enhanced volatile emission to repel generalist herbivores.

The paper 9 provides critical evidence that the exclusion from a specialized 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 signal used in tritrophic interactions with insects because their production is selected against when specialist parasitoids are absent. This complements other studies which have shown fitness benefits from HIPV production. For example, Schuman et al 16 found that HIPV silenced *Nicotiana attenuata* 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 were more susceptible to insect feeding damage in an outdoor experiment with potted plants and in a field plot trial.

The paper by Lin and colleagues 9 provides insight into how plant volatiles may evolve in the absence of specialised insects and could be an example of evolution in action. It is hypothesised that the observed changes in ragwort volatile emission are driven by escape from the specialised herbivore *T. jacobaeae*, commonly known as the cinnabar moth*.* Ragwort is a noxious weed because the alkaloids it produces are toxic to grazing cattle. In attempts at biological control, cinnabar moth has been introduced into Australia 18 New Zealand 19, and North America 20 as a biological control agent for invasive ragwort. Although there have been challenges in establishing cinnabar moth populations in Australia it is considered a success in western North America 20. If 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 cinnabar moth caterpillar damage, there will be selection pressure for plants to reduce constitutive volatile emission to make themselves less apparent to the specialist herbivore. Furthermore, if the specialist parasitoid also arrives there will be selection pressure to increase HIPV emission to call in these parasitoids when attacked by the herbivore. If sufficient levels of cinnabar moth become established, it will be interesting to see if ragwort volatile emission changes again and reverts back to the profiles of native plants and, if it does, how long this coevolutionary process will take.

**REFERENCES**

1. Ehrlich, P.R., and Raven, P.H. (1964). Butterflies and plants: A study in coevolution. Evolution *18*, 586–608.

2. Dicke, M., and Baldwin, I.T. (2010). The evolutionary context for herbivore-induced plant volatiles: beyond the “cry for help.” Trends Plant Sci. *15*, 167–175.

3. Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N., and Weis, A.E. (1980). Interactions among three trophic levels: Influence of plant on interactions between insect herbivores and natural enemies. Annu. Rev. Ecol. Syst. *11*, 41–65.

4. Dicke, M., and Sabelis, M.W. (1988). How plants obtain predatory mites as bodyguards. Netherlands J. Zool. *38*, 148–165.

5. Turlings, T.C.J., Tumlinson, J.H., and Lewis, W.J. (1990). Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. Science *250*, 1251–1253.

6. Turlings, T.C.J., and Erb, M. (2018). Tritrophic interactions mediated by herbivore-induced plant volatiles: Mechanisms, ecological relevance, and application potential. Annu. Rev. Entomol. *63*, 433–452.

7. Allison, J.D., and Hare, J.D. (2009). Learned and naïve natural enemy responses and the interpretation of volatile organic compounds as cues or signals. New Phytol. *184*, 768–782.

8. Heil, M. (2014). Herbivore-induced plant volatiles : targets , perception and unanswered questions. New Phytol. *204*, 297–306.

9. Lin, T., Vrieling, K., Laplanche, D., Klinkhamer, P.G.L., Lou, Y., Bekooy, L., Degen, T., Bustos-Segura, C., Turlings, T.C.J., and Desurmont, G. Evolutionary changes in an invasive plant support the defensive role of plant volatiles. Curr. Biol., 1–36.

10. Kessler, A., and Baldwin, I.T. (2001). Defensive function of herbivore-induced plant volatile emissions in nature. Science *291*, 2141–2144.

11. de Lange, E.S., Farnier, K., Degen, T., Gaudillat, B., Aguilar-Romero, R., Bahena-Juárez, F., Oyama, K., and Turlings, T.C.J. (2018). Parasitic wasps can reduce mortality of teosinte plants infested with fall armyworm: Support for a defensive function of herbivore-induced plant volatiles. Front. Ecol. Evol. *6*, 55.

12. Rodriguez-Saona, C.R., and Frost, C.J. (2010). New evidence for a multi-functional role of herbivore-induced plant volatiles in defense against herbivores. Plant Signal. Behav. *5*, 58–60.

13. Greendfield, M.. (2002). Signalers and receiver: Mechanisms and evolution of arthropod communication M. . Greendfield, ed. (Oxford University Press Inc.,).

14. Searcy, W.A., and Nowicki, S. (2005). The evolution of animal communication: Reliability and deception in signaling systems. In The Evolution of Animal Communication (Princeton University Press), pp. 1–23.

15. Diggle, S.P., Griffin, A.S., Campbell, G.S., and West, S.A. (2007). Cooperation and conflict in quorum-sensing bacterial populations. Nature *450*, 411–414.

16. Schuman, M.C., Barthel, K., and Baldwin, I.T. (2012). Herbivory-induced volatiles function as defenses increasing fitness of the native plant *Nicotiana attenuata* in nature. elife *1*, e00007.

17. Christensen, S.A., Nemchenko, A., Borrego, E., Murray, I., Sobhy, I.S., Bosak, L., Deblasio, S., Erb, M., Robert, C.A.M., Vaughn, K.A., et al. (2013). The maize lipoxygenase, ZmLOX10, mediates green leaf volatile, jasmonate and herbivore-induced plant volatile production for defense against insect attack. Plant J. *74*, 59–73.

18. Bornemissza, G.F. (1966). An attempt to control ragwort in Australia with the cinnabar moth, *Callimorpha jacobaeae* (L.) (Arctiidae : Lepidoptera). Aust. J. Zool. *14*, 201–243.

19. Syrett, P. (1983). Biological control of sapstain in New Zealand: a review. Aust. Weeds *2*, 96–101.

20. Markin, G.P., and Littlefield, J.L. (2008). Biological control of tansy ragwort (*Senecio jacobaeae*, L.) by the cinnabar moth, *Tyria jacobaeae* (CL) (Lepidoptera: Arctiidae), in the northern Rocky Mountains. In Proceedings of the XII International Symposium on Biological Control of Weeds (CAB International), pp. 583–588.

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**DECLARATION OF INTERESTS**

The authors declare no competing interests

**FIGURE LEGEND**

**Figure 1. Evolutionary changes of plant volatiles upon invasion**

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