

FE SPOTLIGHT

Co-infections and the third trophic level

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The proverb ‘the enemy of my enemy is my friend’ is axiomatic in community ecology and the study of tri-trophic interactions. This is particularly relevant for studies of plant–herbivore–parasitoid interactions. Parasitoid wasps eavesdrop on plant volatiles emitted after plants are attacked by herbivores (De Moraes *et al.* 1998). This facilitates host finding by parasitoids, attack by parasitoids reduces population size of herbivore hosts (Rosenheim 1998), and the plants and parasitoids each benefit by the interaction (van Loon *et al.* 2000). One takes for granted the observation that most plant secondary compounds likely evolved as plant defences against natural enemies, but this was formally proposed as a mechanism only 52 years ago (Frankel 1959). Similarly, plant–insect herbivore–parasitoid interactions are key to understanding plant population dynamics and community ecology, although the conceptual framework for this is also relatively new (Karban *et al.* 1999). A closer look at life in the tangled bank reveals highly complex ecological interactions and evolutionary outcomes among plants, insect herbivores and the third trophic level. Taking just the case of plant–insect–parasitoid interactions, one finds that most plants are attacked by many herbivore species (co-infections), which are in turn attacked by many parasitoid species, which are attacked by hyperparasitoids, and so on. When examined in detail, such interactions can be driven by complex, unimaginable mechanisms—for example, a phage virus toxin encoded in the genomes of bacterial symbionts of aphids renders hosts resistant to parasitoid wasps (Oliver *et al.* 2009).

Such a complex (and wonderful) ecological and evolutionary milieu might be viewed as an intellectually intractable morass. For example, two herbivorous insect species using a common host plant may compete with or facilitate one another, or may not affect the other’s fitness at all—and—the direction and strength of such interactions are likely to be highly context-dependent. Can we build a robust framework for predicting the direction and strength of plant–herbivore–parasitoid interactions in real ecological communities? Advances in network theory and competition theory are likely to be helpful in understanding how such systems work from an ecological perspective, and potentially how they evolve (Chesson & Kuang 2008; Guimarães *et al.* 2011). But are there more fundamental traits of plants that can be leveraged to gain insight into the direction and strength of

ecological interactions within these complex communities? In this issue of *Functional Ecology*, Soler *et al.* (2012) provide fresh insight into how co-infections robustly modulate plant defence signalling, and then tests whether this influences tri-trophic interactions in a natural ecological community.

Widespread signalling cross talk, primarily via the three plant hormones jasmonic acid (JA), salicylic acid (SA) and ethylene (ET), allows plants to coordinate and fine-tune their defences against the diversity of potential natural enemies. Plants deploy distinct, but often overlapping defence strategies against biotrophic microbes, phloem-feeding insects and leaf-chewing herbivores (Stout *et al.* 2006). Numerous studies have examined the physiological and molecular genetic basis of plant signalling and cross talk, mostly in model plant species (*Arabidopsis thaliana*, tomato and tobacco). Herbivores and many fungi typically induce the JA pathway and many bacterial and some fungal pathogens the SA pathway, and ET seems to be modulator of cross talk between the two pathways. While extremely insightful, these studies have led to some typological thinking—that herbivores induce the JA pathway and that bacteria induce the SA pathway. This hazard is apparent when one considers that the causative agent of bacteria speck disease (the Gram-negative bacterium *Pseudomonas syringae*) in plant leaves will induce either the JA pathway or the SA depending on the presence or absence of single avirulence or virulence genes (Cui *et al.* 2005). This indicates that it may well be difficult to make predictions about how particular natural enemies induce plant defences, and whether this scales up the trophic cascade to predators. Nonetheless, there are widespread, repeatable and ecologically relevant cross-talk phenotypes present across host plant taxa. For example, the SA pathway and JA pathway are largely mutually antagonistic in plants. How such antagonism affects the their trophic level, as well as interactions among co-infecting natural enemies is relatively unknown, but clearly likely to be extremely important ecologically and evolutionarily (Thaler 1999).

Only a handful of elegant studies (e.g. (Rodríguez-Saona *et al.* 2005)) have examined how plant defence hormone signalling is affected by attack from multiple herbivore species, and how this translates into effects on the herbivores and their parasitoids in the third trophic level. Soler *et al.* (2012) provide an important step forward by studying co-infection of *Brassica oleracea* plants by a leaf-chewing herbivore and a phloem-feeding herbivore. The authors cast the effects of

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each herbivore in terms of how their influences on plant hormone defence signalling affect two specialized parasitoid species. The principle hypotheses tested are that previous or simultaneous infection of plants with one species, from one feeding guild, influences susceptibility (performance) towards species from other feeding guilds, and that this difference in performance translates up to predators in the next trophic level. The main ecological idea is that there is fine-tuning, trade-offs and constraints faced by plants when attacked by very different natural enemies. Clever experiments allowed ecological dissection of the strength and direction of ecological interactions between each player, across two feeding guilds and to the third trophic level, through the channel of plant defence signalling. Two ecologically distinct mustard-specialist herbivore species, the caterpillar *Pieris brassicae* and nymphs and adults of the aphid *Brevicoryne brassicae* were forced to either singly, doubly or sequentially attacked a single host individual. Plant defence signalling metabolic and gene expression readouts, as well as herbivore performance and parasitoids performance data, were collected and analysed in an integrative framework. Results showed, interestingly, a susceptibility phenotype in both directions during sequential and simultaneous co-infections—which the authors interpreted as ecological facilitation. Aphids were stronger inducers of susceptibility to caterpillars than caterpillars were to aphids. This was not likely to be mediated by SA–JA antagonism, because SA levels remained relatively constant throughout the experiment. An unknown mechanism is repressing JA-levels, which were significantly lower in aphid-infested plants, and likely to be causing the increase in *P. brassicae* performance. The nature of the elicitor or effector causing JA suppression is unknown. The performance of both parasitoids increased during co-infections, but perhaps the most intriguing finding was that although caterpillars only affected aphid development early in their life cycle, this subtle effect translated into a positive effect on aphid parasitoid performance, which was subtle at the herbivore level. This suggests that effects from herbivore co-infection on the third trophic level may be cryptic more generally.

As Soler *et al.* (2012) rightly point out, this is the first step in dissecting how co-infections influence ecological interactions in this model ecological system. Because the host plant is closely related to the plant genetic model *A. thaliana*, there is promise that functional genetic studies on plant defence mechanisms mediating the phenotypes can be identified. This

manuscript also provides an excellent context for re-examining assumptions and typological paradigms in this field. For example, while competition is viewed as the most common type of ecological interaction between herbivores, this study shows that for interguild interactions, co-infections are likely to lead to facilitation. The authors also show that although co-infections may directly benefit individuals from each herbivore guild, they are a boon for parasitoids. Host plants are probably getting the last laugh after all, because bigger parasitoids likely translate into higher parasitoid fitness and with it, plant fitness. Perhaps the enemy of my enemy is a plant's friend, but what about the enemy of its enemy's enemy?

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