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# Indirect plant–parasitoid interactions mediated by changes in herbivore physiology

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In occupying an intermediate trophic position, herbivorous insects serve a vital link between plants at the base of the food chain and parasitoids at the top. Although these herbivore-mediated indirect plant–parasitoid interactions are well-documented, new studies have uncovered previously undescribed mechanisms that are fundamentally changing how we view tri-trophic relationships. In this review we highlight recent advances in this field focusing on both plant-driven and parasitoid-driven outcomes that flow up and down the trophic web, respectively. From the bottom-up, plant metabolites can impact parasitoid success by altering host immune function; however, few have considered the potential effects of other plant defense strategies such as tolerance on parasitoid ecology and behavior. From the top-down, parasitoids have long been considered plant bodyguards, but in reality the consequences of parasitism for herbivory rates and induction of plant defensive chemistry are far more complicated with cascading effects on community-level interactions.

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## Introduction

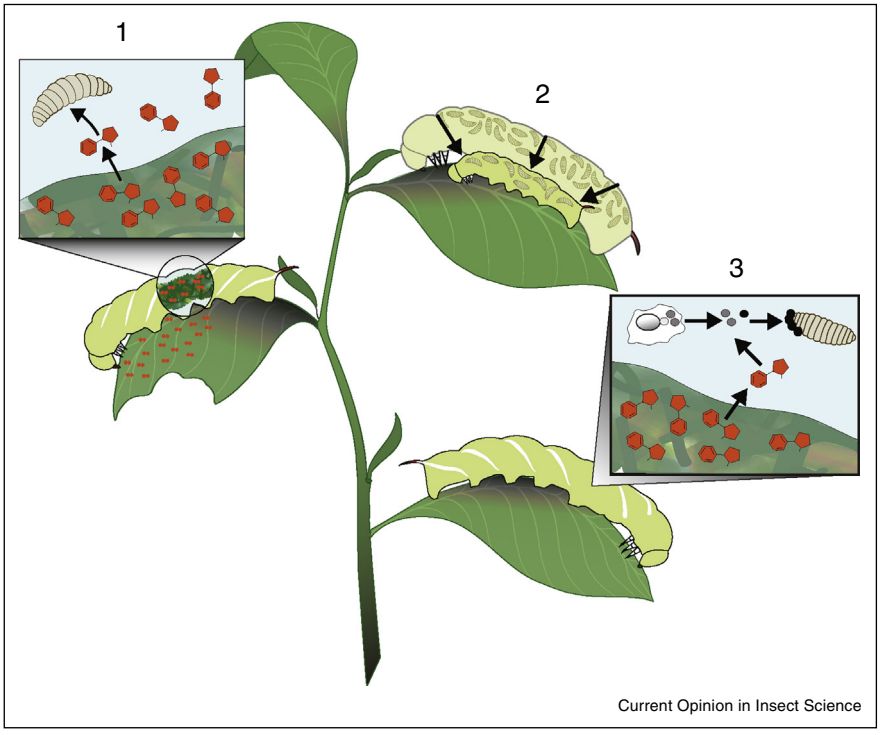
Plants often experience an ecological conflict between two effective, and seemingly independent, defensive strategies: poisoning consumers and conserving bodyguards. Although plants often synthesize large quantities of highly toxic chemicals that deter herbivory, those same toxins can also kill or impair parasites developing inside of herbivorous hosts. This trade-off has led many to question the optimal level of defense that exploits both strategies to minimize herbivore damage. Indeed, the inhibitory role of toxic plants in establishing robust parasitoid populations was recognized in some of the earliest published research on tri-trophic interactions [1]. Although much of the impetus surrounding this topic derives from its relevance to biocontrol–crop resistance relationships for pest management, more recent work has emphasized its importance in structuring food webs in natural ecosystems [2,3•,4].

In this review we briefly highlight several research directions for the field of plant–herbivore–parasitoid interactions that are either gaining popularity in the published literature or show promise for future development. Thus, our intention is purely to showcase select topics that are both new and potentially transformative, not provide a comprehensive overview of the field (such reviews already exist: [5,6]). In the sections that follow we first outline a mechanism by which parasitoids are affected by plant defense via its influence on host immune function. We then broaden our perspective on plant defense strategies to include not only resistance but also tolerance, which we argue circumvents the trade-off inherent to toxin–parasitoid interactions. We end by discussing the role that parasitoids play in shaping plant chemistry. These research areas have largely followed a unidirectional framework (plant → parasitoid) and mostly neglected the possibility of a reciprocal effect (plant ← parasitoid). Emerging data now clearly show that this is a bidirectional relationship with parasitized hosts exerting a strong impact on plants, with the potential for strong eco-evolutionary dynamics; however, these reciprocal, herbivore-mediated effects remain understudied.

## Bottom-up effects of plant defense on host–parasitoid interactions

The vast majority of published research on how plant traits affect parasitoids assumes that the insect host is incapable of defense, leading to two potential mechanistic pathways: first, plant toxins interfere with the development of parasitoid larvae via direct exposure inside the host (Figure 1(1)); or second, plant toxins indirectly reduce parasitoid performance by reducing host size and thus resource availability (Figure 1(2)) (see also [7] for related mechanisms at a population-level). Under these scenarios, the herbivore essentially functions as a non-interactive conduit linking the effects of plant metabolites to parasitoids, disregarding the sophisticated immune responses mounted by insects to foreign invaders. Relaxing this assumption leads to a third possible mechanism whereby plant defenses mediate parasitoid success by modulating host immune function

**Figure 1**




Plant defensive metabolites are thought to impact parasitoids via several mechanistic routes. (1) Developing parasitoid larvae are directly exposed when toxins infiltrate the host's hemocoel, resulting in reduced growth and survival, for example [21]. (2) Defenses reduce herbivore developmental rate, resulting in smaller hosts with correspondingly fewer adult parasitoids emerging. (3) Defensive chemistry affects the nature and/or magnitude of host immune responses to immature parasitoids. These mechanisms are restricted to toxic compounds ingested by hosts and does not include volatiles used in adult foraging decisions
Illustration by Rebecca Clark.

(Figure 1(3)), for example, increasing or decreasing the likelihood for encapsulation. It is rather surprising that this perspective has only recently gained momentum in the tri-trophic interaction literature because the insect immune system has long been recognized as a central component to host–parasitoid relationships, at least in a bi-trophic framework [8,9]. Recent interest in this topic dovetails the newly established field of eco-immunology, which seeks to disentangle the causal factors driving immune variation in wild animal populations. Indeed, consumption of plant products, including secondary plant compounds, by a variety of insect pollinators (e.g., [10,11]) and herbivores (e.g., [12–14]) are known to enhance immunity against an array of microbes including protozoan, viral, and bacterial pathogens. Such findings stress the importance of incorporating the effects of plant chemistry (as opposed to simply rearing insects on artificial diet in the laboratory) when studying host immune responses against parasites and parasitoids.

## Plant resistance-mediated immunity

Because the magnitude of an herbivore's immune defense tends to tightly correlate with its vigor [15,16], plant traits that retard herbivore growth may indirectly impact parasitism by suppressing immune function in what has been termed the 'immunocompromised host hypothesis' [17] or 'vulnerable host hypothesis' [18••]. Both hypotheses predict increased parasitism on chemically well-defended plants. In general, the existing empirical literature seems to support the concept of weaker immune responses for herbivorous insects developing on highly defended or poor quality plants (e.g., plants with low levels of primary metabolites such as growth-limiting amino acids) [19•]. Interestingly, these hypotheses contradict the large body of literature documenting lower parasitoid survival on hosts reared from toxic plants, for example [20–22], including those demonstrating that parasitized hosts actively seek out toxic plants in their diet, seemingly to rid themselves of their parasites, a.k.a. self-medication or pharmacophagy [23]. These broad findings suggest that, at least in many trophic systems, the effects of host immunity against parasitism is weak relative to the direct (Figure 1(1)) and indirect (Figure 1(2)) effects of plant defense compounds on parasitoids. Given these discrepancies, it would be helpful for future studies to invest more effort in identifying factors that predict when toxins are beneficial versus detrimental to parasitoid development. Herbivore diet