

# Interactions between parasitoids and higher order natural enemies: intraguild predation and hyperparasitoids

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Parasitoids kill and live at the expense of their hosts, but they also serve as food for intraguild predators and hyperparasitoids. Natural enemy diversity can thus challenge herbivore suppression by parasitoids, but this depends on the ecological niches of the species involved and their functional diversity. The spatial context is another important layer of complexity, particularly in areas with reduced habitat complexity and increased fragmentation. Parasitoids have evolved strategies to locate their host, but this can be affected by risk of intraguild predation or hyperparasitism. To better understand these interactions we need more long-term experiments and trophic-web studies. This will provide fundamental knowledge, improve pest control, and allow ecologists to better predict the impact of human activities on species extinctions.

## Addresses

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## Introduction

Parasitoids kill and live at the expense of their hosts, but they can also serve as food for other organisms like intraguild predators or hyperparasitoids. Intraguild predation occurs when competing natural enemies prey on each other, and when they occur between parasitoids and predators, the parasitoid is always the subordinate species (i.e. the intraguild prey) as their larvae can be eaten by the intraguild predator [1,2]. Hyperparasitism involves parasitoids that attack other parasitoid species [3]. In plant-based ecosystems, these interactions have been extensively studied because they have major consequences for the

control of pest species, primary productivity and nutrient cycling [4–6]. Intraguild predation and hyperparasitism are ubiquitous in natural trophic webs [3,7–10], which contrasts with theoretical work that suggests restricted scenarios for species coexistence [6,11,12]. During the past few decades, both theoretical and experimental research has tried to explain this discrepancy. Parasitoids of herbivorous insects have played a relevant role in these developments because many population dynamics models have been inspired by host–parasitoid systems, and because parasitoids have been used to test their predictions (e.g. [13]).

There is an intense debate about whether herbivore suppression is enhanced at larger natural enemy diversity. The main reason is that although herbivore suppression often correlates positively with natural enemy diversity, natural enemies may engage in antagonistic interactions like intraguild predation or hyperparasitism [4]. In this review, I show that although natural enemy diversity might challenge herbivore suppression by parasitoids, this depends on the ecological niches of the species involved. I also discuss the importance of long-term, multi-generational experiments, and of trophic web studies in this context. The spatial context is another layer of complexity that affects intraguild predation and hyperparasitism, especially due to human impacts that reduce habitat complexity and increase fragmentation. I also hypothesise that in complex communities, host location has driven selection on parasitoid behaviour, but these strategies also include avoiding antagonistic interactions. Finally I discuss future avenues for research and their applied implications in view of the global changes imposed by human activities (Figure 1).

## Diversity impacts on herbivore suppression

Many studies exploring intraguild predation in parasitoids have been restricted to a single insect generation, and have studied simple webs composed of three species [1,7,8]. These studies have been useful to understand the behavioural strategies underlying species interactions, but they have limited ability to predict long-term community dynamics. For example, over multiple generations, parasitoids and intraguild predators can exploit their hosts at different moments of the host life cycle, or parasitoids can develop when intraguild predators are less active [13]. Studies with complex communities in natural ecosystems have also revealed emergent impacts of diverse predatory guilds on herbivore suppression, which are difficult to

predict from pairwise interactions [14<sup>\*\*</sup>,15,16]. These studies, and work with other animal taxa, have revealed that niche complementarity is an important characteristic to consider [17,18]. Functionally diverse predatory guilds might partition the prey resource leading to increased herbivore suppression [19,20]. Given their different life histories, complementarity is thought to be particularly strong between parasitoids and intraguild predators [19]. For instance, in an experiment with the aphid *Eriosoma lanigerum*, consistent aphid suppression was only achieved when the parasitoid *Aphelinus mali* was paired with a diverse guild of generalist predators [14<sup>\*\*</sup>]. Even within parasitoid guilds, niche complementarity may depend on parasitoid host range [20], facultative hyperparasitism [21,22], and potentially on phylogenetic diversity [23<sup>\*\*</sup>].

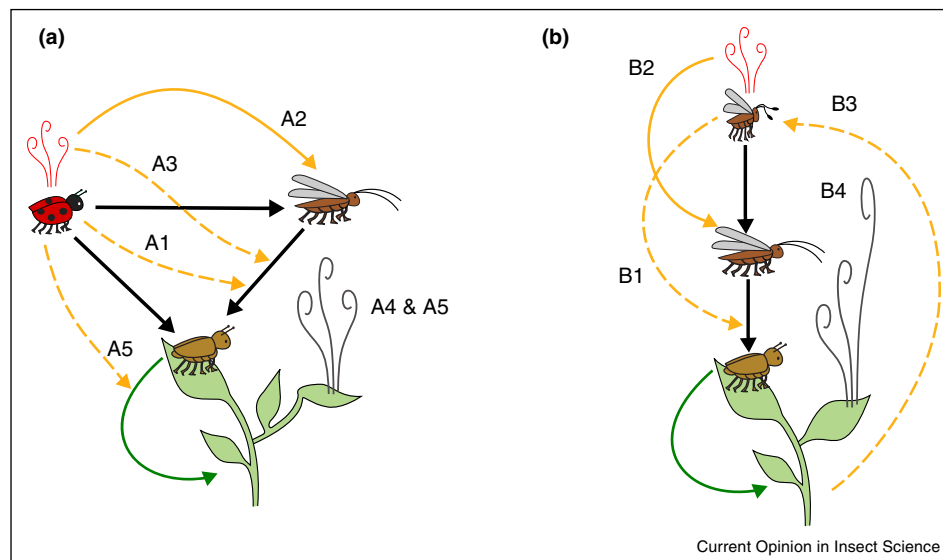
Hyperparasitoids have the potential to release herbivorous insects from their primary parasitoids [3,9]. Theoretical models and field data, however, suggest that in the long-term hyperparasitoids can sometimes promote herbivore population suppression by stabilising insect–parasitoid dynamics [3,11]. As with intraguild predation, exploring

complex scenarios and long-term dynamics is needed to understand hyperparasitoid ecology. In a long-term field study, *Cotesia vestalis* was the main parasitoid of the diamondback moth, *Plutella xylostella*. When hyperparasitism levels were high, however, other primary parasitoids were the dominant ones [24]. Quantitative trophic webs have also provided detailed information on how hyperparasitoid networks regulate primary parasitoid populations (e.g. [10,25]). Parasitoids of bigger aphid species, for instance, might represent stronger links in trophic webs because they host a larger number of hyperparasitoids, with female biased sex-ratios [26,27]. At the evolutionary level, another aphid study has revealed that trophic webs are phylogenetically constrained, from the plant to the hyperparasitoid level [28]. These examples reveal that although trophic web studies usually consider species identities, interactions can be importantly modulated by species traits and their evolutionary history.

### The role of spatial complexity

Intraguild prey usually suffer less predation in structured habitats, potentially due to reduced encounter rates with

Figure 1



Parasitoids often engage in antagonistic interactions with higher order natural enemies like (a) intraguild predators and (b) hyperparasitoids. Direct trophic effects involve a consumer–resource interaction (black solid lines), whereas direct trait-mediated effects involve changes in the behaviour or morphology of the interacting species (yellow solid lines). Interactions among species can be indirect if they are mediated by at least a third species (yellow dashed lines). Herbivory has a direct effect on plant traits or defensive state (solid green lines), and also an indirect effect on parasitoid foraging through herbivore-induced plant volatiles (grey vapour lines). (a) Intraguild predators (represented by a ladybird) can reduce herbivore suppression by parasitoids by preying on parasitoid larvae (A1). Herbivore suppression, however, is influenced by the functional niche of the intraguild predator, and by the diversity of the community of natural enemies, at both the species and the phylogenetic level. Parasitoids detect and avoid chemical cues from intraguild predators (A2), and these responses can have consequences for host–parasitoid dynamics (A3). Risk of intraguild predation can alter parasitoid attraction to herbivore-induced plant volatiles (A4). Risk of predation can also affect the way herbivores feed on plants and hence plant volatile induction, with consequences for parasitoid foraging (A5). (b) Hyperparasitoids (top trophic level) attack primary parasitoids and can affect herbivore–parasitoid dynamics (B1). This effect, however, depends on the trophic web of herbivores, primary parasitoids and hyperparasitoids, and on the traits and evolutionary history of the species involved. Primary parasitoids detect and avoid chemical cues from hyperparasitoids (B2). Herbivory can affect plant traits or defensive state, and these changes can cascade up to the hyperparasitoid level (B3). Hyperparasitoids can use herbivore-induced plant volatiles to locate their hosts (B4). For both intraguild predation and hyperparasitism, these interactions are influenced by spatial complexity, at both the plant and the landscape level.

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