



Behaviorally plastic host-plant use by larval Lepidoptera in tri-trophic food webs

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Plant–insect interactions research emphasizes adaptive plasticity of plants and carnivores, such as parasitoids, implying a relatively passive role of herbivores. Current work is addressing this deficit, with exciting studies of behavioral plasticity of larval Lepidoptera (caterpillars). Here I use select examples to illustrate the diversity of behaviorally plastic host-plant use by caterpillars, including anti-predator tactics, self-medication, and evasion of dynamic plant defenses, as proof of the agency of caterpillar behavior in plant–insect interactions. I emphasize the significance of adaptive behavioral plasticity of caterpillars in the context of tri-trophic interactions. Recent research on trait-mediated indirect interactions places adaptive behavioral plasticity of herbivores at the center of community and food web dynamics, with far-reaching consequences of issues such as community stability.

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Introduction

Behaviorally plastic host-plant use by herbivores demonstrates the active role of herbivores in their interactions with plants. Some have argued that herbivore behavior has been a blindspot in the plant defense literature [1], and I add here that behavioral plasticity has been especially ignored. Much more attention has been given to defensive plasticity of plants [1,2] and plastic responses of carnivores to induced plant defenses [3,4] (Figure 1). Recently, however, studies of herbivore feeding plasticity have begun to link behavioral and physiological mechanisms to theory in evolutionary, community, and ecosystem ecology [5•]. This increased attention to mechanisms of herbivore behavior in the context of adaptive plasticity theory is informing many issues old and new, such as tri-trophic

interactions, nutritional ecology, and ecological immunology. Because these studies were framed in disparate ways by their original authors, one goal here is to link them under the conceptual umbrella of adaptive plasticity theory, which rests on the notion of fitness trade-offs of alternative phenotypes or behaviors under detectably different ecological circumstances. My focus here is behavioral plasticity of host-plant use by larval Lepidoptera (caterpillars), one of the most species-rich and ecologically important groups of herbivores in terrestrial ecosystems [6•]. Importantly, new evidence of adaptively plastic behavior of caterpillars shows their agency in a variety of tri-trophic interactions, and offers promise for furthering understanding of tri-trophic dynamics at the community and food web levels.

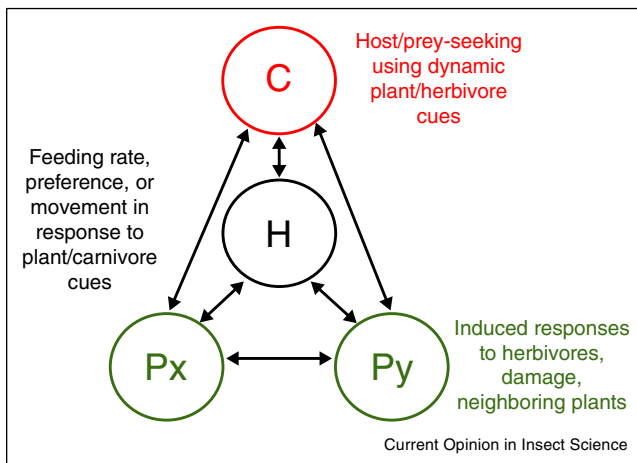
Caterpillar behavior: agency and diversity

In the following sections, I describe several key examples of the active role of caterpillars in the dynamics of plant–herbivore interactions as well as the diversity of caterpillar behaviors involved (i.e. feeding and non-feeding activity) (Figure 1). These descriptive examples provide observations needed to inform theory on the ecological dynamics of tri-trophic interactions [7]. The small set of examples here, intended to be representative but not comprehensive, reveal some patterns consistent with existing theory as well as behavioral diversity that raises questions with the potential to offer new theoretical insight. For example, how do mechanisms and ecological consequences of behavioral plasticity differ across the distribution of dietary specialization recently described for caterpillars and other insect herbivores [6•]?

Feeding

Here I draw on select examples to show recent evidence for individual variation and adaptive plasticity in feeding behavior by caterpillars. Consistent with evidence from other herbivores, research on caterpillars shows that cues of carnivores (predators, parasites, pathogens) often cause reductions in herbivore feeding rate or dietary quality, which increases herbivore survival at the expense of growth or reproduction [8,9,10•]. For example, dietary specialist *Manduca sexta* caterpillars reduced their feeding rates in response to the presence of predators, accompanied by compensatory post-ingestive physiological changes [9]. Because the act of feeding and defecating can greatly increase a caterpillar's risk of predation [11,12], the reduction in feeding rate is likely to be adaptive for the caterpillar. However, the signature trade-off of adaptive plasticity was apparent: growth costs

Figure 1



Tri-trophic network of plasticity, with circles representing adaptively plastic traits of two plant phenotypes or species (green, Px, Py), herbivores (black, H), and carnivores (red, C). Arrows represent possible interactions inducing or induced by trait plasticity. Behavioral plasticity of herbivores, the subject of this article, has received less attention than plasticity of plants and carnivores.

of these behavioral and physiological adjustments appeared later in development [9,13*].

Another potentially widespread phenomenon is adaptive plasticity in diet choice by herbivores to gain resistance against parasites. As in the case described above, the adaptive change in diet in response to parasites entails other fitness costs. Recent studies in nutritional ecology show that caterpillars can change their nutrient preferences in response to microparasites. For example, the grass-specialist *Spodoptera exempta* caterpillars not only reduced their total feeding rate, but also dynamically adjusted the ratio of macronutrient intake over the course of viral infection [14**]. Reduced carbohydrate intake, resulting in a high protein-to-carbohydrate ratio, increased the survival rate of infected caterpillars. This therapeutic nutrient intake pattern departs sharply from self-selected diets and optimal growth of uninfected caterpillars [15], indicating the foraging trade-off between growth and defense.

With respect to plant secondary metabolites, caterpillars show adaptive plasticity in pharmacophagy. The polyphagous grazer, *Grammia incurrupta*, increases its gustatory response to and ingestion of pyrrolizidine alkaloids (PA) when infected with tachinid parasitoids [16–18]. While PA consumption confers anti-parasitoid resistance, it also entails costs in survival [17] and growth efficiency [19]. Therefore, this therapeutic medication response is adaptive for caterpillars battling parasitoid infections, but not for unparasitized individuals. More work is needed here to understand how medication behavior plays out in field settings [20*].

Movement

Movement behavior by caterpillars reinforces the notion of their active role in insect–plant interactions, which has not always been accounted for in plant defense theory. Many caterpillars move about extensively on the plant (e.g. [21,22,23*]) or among different plants (e.g. [24,25]), and such movements can help caterpillars feed selectively and adaptively. The focus here is plasticity in movement behavior. As a counterploit to induced plant defenses, caterpillars can avoid dynamic chemical resistance traits of plants (e.g. [26,27]), which tend to be heterogeneously distributed even when systemically induced (e.g. [28,29]). One of the functional hypotheses for induced chemical resistance in plants (moving target model [30]) proposes that heterogeneity and unpredictability of induced defenses would be especially challenging for herbivores to overcome. However, a recent study demonstrates that caterpillars can move adaptively in response to cues of a plant's incipient increase in chemical resistance [31**]. These researchers mapped in real time both induced changes in *Arabidopsis thaliana* resistance expression and preemptive avoidance behavior by polyphagous *Helicoverpa armigera* caterpillars. Interestingly, this study found no such avoidance response by *Plutella xylostella* caterpillars, which are dietary specialists adapted physiologically to mustard oil defenses of *A. thaliana* and related Brassicaceae [32].

By moving within host plants, between host plants, or off host plants altogether, caterpillars might avoid mortality or non-consumptive fitness costs from invertebrate carnivores that cue in to feeding damage, byproducts, or areas of induced plant response (e.g. [11,12,33]). Careful and extensive study of two polyphagous species of slug caterpillars (Limacodidae) revealed a general pattern of plastic movement patterns that depended on host-plant species, light environment, and predator density [23*]. Interestingly, the slug caterpillars moved (and fed) more frequently in shady versus sunny microsites, the latter associated with increased attack risk from parasitoids [34*]. Functional consequences of diverse caterpillar movement patterns are not well understood.

Other behaviors

Caterpillars employ a multitude of plastic behavioral defenses against their enemies [35]. Here I will illustrate this with an example that clearly qualifies as ‘host-plant use’ while excluding others, such as facultative myrmecophily and plasticity in shelter-building (e.g. [36]), due to space limitations. Regurgitation is one of most widely observed behavioral responses by caterpillars and other insects to physical attack, such as prodding, grasping, or biting by a predator [35]. It has also been observed as a response to parasitoids, such as tachinid flies (e.g. [37]). The regurgitant is a combination of ingested plant material and caterpillar secretions. Because this behavioral response presumably uses plant material to provide defense against

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