

# Host Plants as Mediators of Caterpillar-Natural Enemy Interactions



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Aposematic, sequestering catalpa sphinx *Ceratomia catalpae* caterpillar with parasitoid cocoons.  
Photo: John T. Lill

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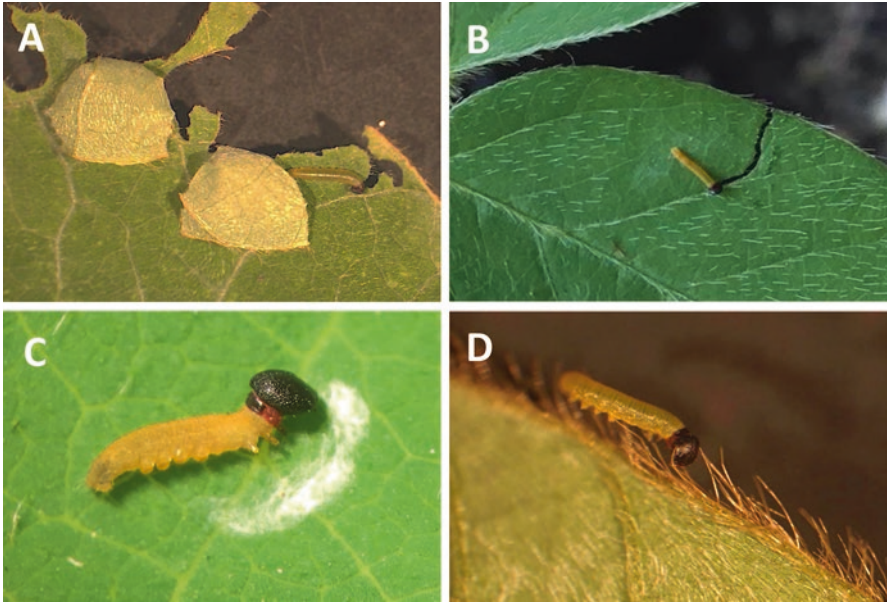
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## Introduction

The preceding chapters in this book have summarized the large and growing body of work focusing on adjacent trophic level interactions (e.g., those between plants and caterpillars and between caterpillars and their various natural enemies). The chapters in this section consider some of the complex ways that three (or more) trophic levels can interact to shape caterpillar ecology and evolution. Beginning in the early 1980s, as Price et al. (1980) and Bernays and Graham (1988) began the initially contentious task of integrating across multiple trophic levels, and as evidence of terrestrial trophic cascades involving plants, herbivores, and natural enemies began to accumulate (Marquis and Whelan 1994; Schmitz et al. 2000; Mooney et al. 2010; Mooney and Singer 2012; Abdala-Roberts and Mooney 2013), we gained new insights into the myriad ways that members of these three trophic levels could interact with one another, both directly and indirectly (Abdala-Roberts et al. 2019). Additionally, the evolutionary implications of these tritrophic interactions began to become increasingly apparent. Singer and Stireman (2005) pushed these ideas forward with a new conceptual framework, outlining how tritrophic niches are both formed and occupied, and empirical studies from a variety of systems are now validating these ideas (e.g., Condon et al. 2014).

While it is now widely recognized that both bottom-up and top-down forces often interact to shape the phenology, morphology, behavior, physiology, and fitness of caterpillars (Hunter and Price 1992; Kaplan et al. 2016), in this chapter we focus on describing the accumulated evidence supporting and/or refuting proposed mechanisms for host plant mediation of interactions between caterpillars and their natural enemies. The evidence that genetically based intraspecific trait variation mediates herbivore-natural enemy interactions has been reviewed elsewhere (e.g., Hare 1992) and is beyond the scope of this chapter. We instead focus here on the much wider trait variation that can be found among host plant species utilized by oligophagous or polyphagous caterpillars (e.g., *Epargyreus clarus*; Plate 1). Interspecific variation in plant traits can alter the risk of mortality from natural enemies directly or can function indirectly, via effects on caterpillar behavioral and/or physiological responses to their host plants, which in turn affect larval risk of mortality from natural enemies (Agrawal 2000). Because many traits can influence both the 2nd and the 3rd trophic levels simultaneously, we have organized our discussion around the major themes of plant traits implicated in tritrophic interactions (rather than by interaction pathway) and indicate the relevant interaction pathway(s) within each section (Plate 2).

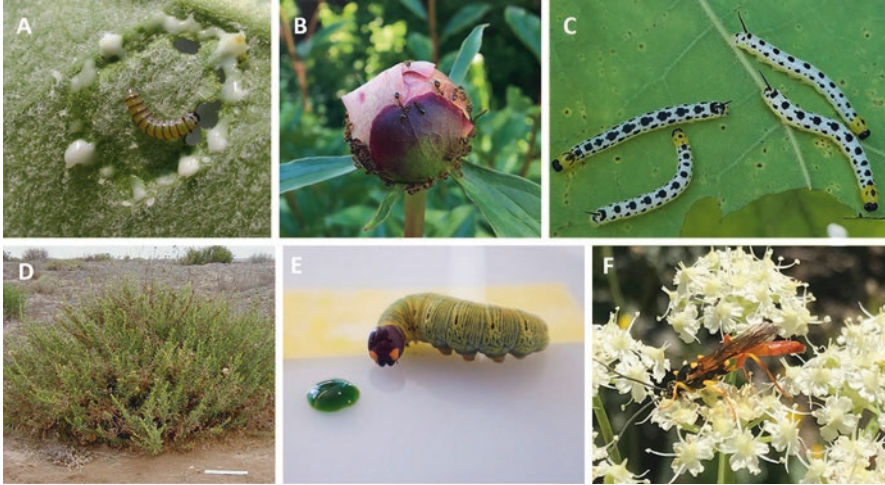
While many of these traits and their hypothesized effects on herbivore-natural enemy interactions were initially described in Price et al. (1980), a considerable amount of empirical evidence has accumulated in the ensuing 40 years, and additional interaction pathways have emerged that require further exploration. For example, there is now widespread appreciation for the rapid and sometimes incredibly specific ways in which plant damage by caterpillars can elicit the release of herbivore-induced plant volatiles (HIPVs; Turlings and Erb 2018) that have



**Plate 1** Silver-spotted skipper (*Epargyreus clarus*, Hesperiiidae) caterpillars interact with their leguminous host plants in several ways that may influence their vulnerability to predators and parasitoids: all silver-spotted skipper caterpillars cut and silk their host leaves to produce shelters, a time-consuming activity that increases their exposure to natural enemies (a); caterpillars often must spend time removing trichomes (i.e., “mowing the lawn”) on densely pubescent leaves prior to initiating shelter-building (b); sharp trichomes, like those on the surface of *Desmodium* leaves, can impale a young caterpillar, making it vulnerable to enemies and/or desiccation and impeding its forward motion, resulting in a thick white crescent of silk on leaves with impaled caterpillars (c); and dense trichomes found on the edges and surfaces of young kudzu leaves slow the forward progress of an early instar larva (d) (all photos by M. Weiss)

important impacts on herbivore mortality. The myriad ways in which plants directly or indirectly provision a broad set of natural enemies that engage in mutualistic relationships with plants have also become increasingly apparent (Bronstein 1998; Stapley 1998; Wäckers et al. 2005). Recent research has also highlighted the importance of plant architecture and foliar pubescence as two important drivers of caterpillar and natural enemy foraging and patch use. Finally, because plant traits and their influence on both herbivores and natural enemies have been shown to change over ontogeny (Boege and Marquis 2005; Boege et al. 2019), this axis of variation must be explicitly considered in designing experimental tests to examine the direct and indirect effects of these traits.

We have worked for many years on the ecology and behavior of the silver-spotted skipper, *Epargyreus clarus* (Hesperiiidae), a widespread oligophagous butterfly, the biology of which provides useful insights into the many ways in which plant traits can influence the outcomes of herbivore-natural enemy interactions. We highlight some of our most recent findings in pertinent sections below.



**Plate 2** Examples of ways in which plant traits can mediate caterpillar-natural enemy interactions. Caterpillars like this monarch larva feeding on lactiferous plants often spend considerable time trenching prior to feeding, which can increase exposure to natural enemies (**a**; photo by A. Agrawal); host plant variation in provisioning, including the extrafloral nectaries of peonies that strongly recruit ants, can pose differential threats to caterpillars (**b**; photo by M. Weiss); host plant variation in concentrations of plant secondary chemicals like catalpol in *Catalpa* spp. can influence levels of sequestration by specialist herbivores like these catalpa sphinx caterpillars, which in turn can impact larval defenses against parasitoids and predators (**c**; photo by J. Lill); plant architectural traits like the growth form and branching pattern of Menzie’s goldenbush have been shown to influence access to these plants by insectivorous birds, which in turn impacts the strength of trophic cascades in the California chaparral (**d**; Nell and Mooney 2019; photo by D. Valov); foliar water content of alternative host plants can influence caterpillar defensive behaviors, as in this silver-spotted skipper caterpillar (**e**; photo by C. Block); and the chemical composition of floral nectar can influence parasitoid foraging, potentially increasing encounters with host caterpillars (**f**; photo by A. Zemenick)

## Chemical Defenses

We begin by briefly discussing plant chemical defenses, which can indirectly affect natural enemies by altering caterpillar behavioral and physiological responses. While we follow the traditional division of plant secondary metabolites into lethal vs. sublethal “defensive” compounds, we note that this narrative has been recently challenged (Smilanich et al. 2016). As such, we encourage future researchers to assess multitrophic interactions without presumption and focus on elucidating the specific modes of action of these compounds within their natural ecological contexts.

**Lethal Compounds** Host plants that defend their tissues with toxins (e.g., furanocoumarins, cardenolides, glucosinolates, pyrrolizidine alkaloids, cyanogenic and iridoid glycosides, and aristolochic acids) are typically attacked by highly specialized caterpillar taxa that have evolved physiological and/or behavioral detoxification mechanisms that enable larval feeding (Berenbaum 1983; Boppré 1990;

Nishida 2002; Wittstock et al. 2004; Dobler et al. 2011; Agrawal et al. 2012). Because these toxins often deter or kill most herbivores that attempt to feed on them, their role in modulating caterpillar-natural enemy interactions is somewhat limited, as noted by Price et al. (1980). However, the various host plant species imbued with these chemicals can vary considerably in both toxin concentration and composition (e.g., Agrawal et al. 2015). For caterpillars that have evolved to subvert, tolerate, or detoxify these compounds (rather than sequester them), the interspecific variation in plant chemical defenses encountered on alternative hosts can theoretically translate into variation in caterpillar susceptibility to natural enemies. However, beyond demonstrating host plant variation in caterpillar performance measures on alternative toxin-containing plants (e.g., non-sequestering milkweed-feeding caterpillars assayed in Petschenka and Agrawal 2015), we are unaware of any studies that clearly link the toxin concentrations of alternative host plants and differential natural enemy attack for non-sequestering specialist caterpillars.

For the subset of specialist caterpillars that has evolved the ability not only to tolerate, but to *sequester* plant toxins (e.g., monarchs, queens, pipevine swallow-tails, buckeyes, catalpa sphinx, and woolly bears (discussed in detail in Bowers, Chapter “Sequestered Caterpillar Chemical Defenses: From “Disgusting Morsels” to Model Systems”), reduced caterpillar palatability and/or rates of mortality by a variety of natural enemies often result (Järvi et al. 1981; Bowers and Farley 1990; Dyer and Floyd 1993; Dyer 1995; Theodoratus and Bowers 1999; Sime 2002). A diverse set of caterpillar taxa sequestering different secondary compounds has also been found to deposit these compounds in their integuments (reviewed in Sime 2002), presumably as an honest signal of their unpalatability that may prevent lethal injury by naive predators. In systems where sequestration levels reflect dietary toxin concentrations, alternative host plant associations could result in differential attack and consumption of these variably defended caterpillars by natural enemies (Dyer and Bowers 1996; Camara 1997; Theodoratus and Bowers 1999). The natural enemies themselves could respond either positively (e.g., some specialist parasitoids; Richards et al. 2012) or negatively (e.g., many generalist predators) to sequestered toxin concentrations of their hosts and prey, respectively. In their study involving specialist caterpillars feeding on two different toxin-containing host plants, Richards et al. (2012) found that iridoid glycoside (IG) sequestration levels of buckeye caterpillars (*Junonia coenia*, Nymphalidae) were positively correlated with growth but negatively correlated with host immune responses to parasitism, suggesting possible ecological trade-offs in how these toxins may affect different measures of caterpillar fitness.

For predators that use olfaction as the proximate cue in assessing caterpillar prey quality/palatability (e.g., many ant species, most small mammals), there may be a greater potential for host plant-determined levels of sequestration to modulate prey selection behaviors. Moreover, for specialist parasitoids that often use host plant-produced volatile organic compounds (VOCs) as coarse-grained host location cues (Godfray 1994), such non-toxin cues could be honest signals of potential host sequestration levels that result in differential parasitism. As a hypothetical example,

parasitoids of catalpa sphinx (*Ceratomia catalpae*) caterpillars feeding on species of *Catalpa* differing in levels of IGs may prefer VOC signals of the tree species hosting caterpillars with the highest IG sequestration levels, which consequently have the lowest immune responses (following from Richards et al. 2012, cited above). We propose that additional research on the tritrophic consequences of a wider array of specialist caterpillars reared on alternative host plants in natural settings or common gardens could potentially shed light on how different natural enemy complexes may be shaping local patterns of host plant preference and use.

**Sublethal Compounds** A second major category of plant traits hypothesized to influence caterpillar-natural enemy interactions includes sublethal plant secondary chemicals, which while not typically toxic to most caterpillars have been shown to have significant impacts on a variety of caterpillar performance measures. Historically referred to as “quantitative” defenses (Feeny 1976), these include a wide array of mostly higher molecular weight, nonvolatile secondary compounds such as phenolics, lectins, some terpenoids, and proteinase inhibitors as well as structural compounds such as lignins, cellulose, etc. (Rosenthal and Berenbaum 1991). While these “dose-dependent” compounds can theoretically defend plants by directly impeding caterpillar feeding and biomass gain (reviewed in Ayres et al. 1997), the primary mode of action is thought to be indirect; by slowing down caterpillar growth, particularly during highly vulnerable early instars, these plant compounds could potentially increase natural enemy-mediated mortality and decrease plant damage (Benrey and Denno 1997). This slow-growth high-mortality hypothesis (hereafter abbreviated as SG-HM hypothesis; Clancy and Price 1987) highlights the importance of the third trophic level as a critical component of the arsenal of plant defenses. Historically, an additional appeal of the SG-HM hypothesis has been that it neatly resolves a paradox of sublethal plant defenses: in the absence of natural enemies, compounds that reduce the ability of herbivores to assimilate nutrients from plant food (i.e., that reduce digestibility or limit access to limiting nutrients) increase herbivore consumption and plant damage (Moran and Hamilton 1980; Price et al. 1980; but see Neuvonen and Haukioja 1984). For example, when oxidized, some phenolic compounds found in the foliage of many broad-leaved trees produce quinones, which bind to leaf proteins, inhibiting their digestion in caterpillar guts (Taranto et al. 2017). Presumably, caterpillars feeding on plants containing these compounds would grow more slowly, thus exposing them to increased risk of predation and parasitism.

While the basic tenets of the SG-HM hypothesis – that caterpillars exhibit differential growth rates and/or “windows of vulnerability” when reared on host plants differing in nutritional quality – have been demonstrated in multiple laboratory/greenhouse studies (e.g., Isenhour et al. 1989; Benrey and Denno 1997; Medina et al. 2005; Coley et al. 2006; Kursar et al. 2006; Shikano et al. 2018), evidence from field studies has mostly failed to find empirical support for the SG-HM hypothesis in caterpillars (Lill and Marquis 2001; Murphy 2004; Cornelissen and Stiling 2006; Kursar et al. 2006) or has demonstrated the opposite, i.e., that natural enemy pressure was *greater* for faster-growing caterpillars on higher-quality plants

(Damman 1987; Leather and Walsh 1993; Idris and Grafius 1996; Benrey and Denno 1997; Medina et al. 2005; Singer et al. 2012). It is worth noting that the only manipulative field experiments involving caterpillars that have supported the predictions of the SG-HM hypothesis have altered caterpillar growth using intraspecific “treatments” (as noted in Farkas and Singer 2013). These have included adding fertilizer to produce plants with different levels of foliar nitrogen (Loader and Damman 1991), rearing caterpillars on plants with different leaf ages (Parry et al. 1998), or contrasting caterpillar performance on resistant vs. susceptible cultivars (Johnson and Gould 1992). In contrast, we are not aware of any field experiments in which caterpillar growth was manipulated by rearing them on alternative host plant species that have supported the hypothesis.

Two reviews of the SG-HM hypothesis (Williams 1999; Chen and Chen 2018) have pointed out the need for rigorous experiments that track herbivore development and survival under natural field conditions where they are exposed to the full complement of potential natural enemies, for the duration of larval development. In our recent work on the evolutionary ecology of host use in the silver-spotted skipper (*E. clarus*), we tracked the individual fates of hundreds of bagged and exposed caterpillars from egg hatch to the end of larval development on six different leguminous host plants which varied markedly in nutritional content. Despite strong and consistent differences in development time on these alternative host plants, we found little to no support for the SG-HM hypothesis across 3 years and eight generations of *E. clarus* caterpillars, in what we believe is the most comprehensive field-based test of the hypothesis to date (Weiss, Lill & Lind, in preparation). Four decades after it was first proposed to explain the functioning of sublethal plant chemical defenses, the SG-HM hypothesis has been little supported in tritrophic systems involving caterpillars.

## Physical Defenses

Physical features of the plant, including trichomes, surface waxes, and leaf toughness, can directly affect the movements and behaviors of herbivores (Kaur et al. Chapter “Surface Warfare: How Plant Structural Defenses Battle Caterpillars”) and can also impact those of natural enemies both directly and indirectly (Kennedy 2003; Cortesero et al. 2000; Peterson et al. 2016). Plant physical defenses are often integrated into biological control strategies, but the dynamics can be complicated, as plant surface traits that impede herbivores may also help or hinder the abilities of natural enemies to attack targeted pests (Eigenbrode et al. 1995; Cortesero et al. 2000; Peterson et al. 2016).

Trichomes, both nonglandular and glandular, can directly affect caterpillar behaviors in ways that impact natural enemies. For example, trichomes can impede feeding, movement, and other larval “establishment” activities (shelter-building, burrowing into a leaf to produce a mine), slowing them down and thereby increasing visibility, exposure time, and/or vulnerability to natural enemies. These impacts can

be particularly consequential for first instar larvae, which suffer very high mortality, the specific causes of which are difficult to untangle (Zaluki et al. 2002).

In a field investigation of the success of first instar silver-spotted skipper (*Epargyreus clarus*) hatchlings at establishment on six different leguminous host plants, Weiss et al. (in preparation) found a consistent sixfold range in larval failure to construct a leaf shelter within 24 h, depending on plant species. We note that all *E. clarus* larvae obligately construct leaf shelters on their host plants, starting soon after hatching, and making four or five different shelters across their larval lifespan (Weiss et al. 2003); first instar larvae that cannot make a shelter do not survive. Trichome densities on the plants ranged from smooth to densely hairy, but this factor alone was not predictive of hatchling establishment; the host plant with the highest trichome density had the lowest hatchling failure rate, and the plant with the lowest trichome density had the highest failure rate. The plants also differed in leaf toughness and chemistry, traits that are likely to contribute to success at establishment. Although trichome density in the field did not correlate with failure to construct a shelter, follow-up laboratory studies demonstrated that *time* to complete a shelter was in fact correlated with trichome density and that larval behavior varied consistently across the three host plants with the densest trichome coverage, adding another layer of complexity to the plant-herbivore interface (Weiss et al., in prep). As Bernays (2003) demonstrated in her oft-cited paper, “Feeding by lepidopteran larvae is dangerous,” caterpillars may face as much a 100-fold higher risk of predation when feeding than when resting, presumably because head movements (and perhaps chewing sounds) attract the attention of predators. Shelter-building by *E. clarus* is even more visually apparent than feeding, and so it is likely that an extended shelter-building time exposes larvae to increased predation risk.

Consistent with predictions by Boege and Marquis (2005), plant ontogeny can affect the course of plant-herbivore interactions, as can the age or ontogenetic stage of the herbivore. On kudzu (*Pueraria montana*), first instar *E. clarus* larvae were unable to initiate shelter construction on densely haired young leaves and were able to do so only after the leaf had expanded to the point that the larvae were able to contact the leaf surface. Third and fourth instar larvae, however, were able to initiate feeding on younger leaves (Weiss et al., in prep.). Kariyat et al. (2018) reported, similarly, that first and second instar *Manduca sexta* (Sphingidae) larvae were effectively deterred from initiating feeding by the presence of nonglandular trichomes on a number of different solanaceous species, while third instar larvae were not similarly inhibited.

In addition to directly impacting feeding, movement, and establishment by caterpillars, leaf surface characteristics can indirectly affect herbivores by impeding or, rarely, facilitating movement by predators or parasitoids. In many cases, trichome coverage causes more harm than good to natural enemies (Riddick and Simmons 2014). The interaction between trichomes and the third trophic level has been particularly well studied in tomatoes and their relatives (*Solanum* and *Lycopersicon* spp.), the leaves of which bear many types of glandular and nonglandular trichomes (Kennedy 2003, and refs therein). It has been demonstrated, for example, that on *Lycopersicon* spp., nonglandular trichomes can hamper searching behavior of



predators and parasitoids, glandular trichomes can entrap small hymenopterous parasitoids in sticky exudates and reduce predator mobility, and exudates of glandular trichomes can be directly toxic to natural enemies of pests. Similarly, on tobacco leaves, tiny *Trichogramma minutum* wasps get trapped in the sticky exudate of glandular trichomes and are unable to parasitize *Manduca sexta* eggs, though the wasps readily parasitize the eggs on other substrates (Keller 1987). Lacewings, predatory beetles, parasitoids, and true bugs can die when they get stuck in exudates from glandular trichomes or are impaled on sharp nonglandular trichomes, though a consequent negative impact on plant fitness has not been demonstrated (Riddick and Simmons 2014). Conversely, some “sticky plants” enjoy higher densities of predators that are attracted by the accumulated insect carrion found on plants bearing glandular trichomes. This easily accessible prey can be particularly important during the juvenile stages of these predaceous insects, which in later developmental stages shift from feeding on immobile carrion to mobile prey, including caterpillars (Krimmel and Pearse 2013). In an interesting twist on the defensive role of trichomes, Weinhold and Baldwin (2011) reported that consumption of glandular trichomes of *Nicotiana attenuata* by neonate *Manduca sexta* larvae imparts a distinctive volatile profile to both their body and frass and that ground-foraging *Pogonomyrmex rugosus* ants use these distinctive odors to locate their larval prey.

Plant exudates, including latex and resins, are another widespread category of defense, with both physical and chemical components. These sticky exudates can gum up the mouthparts of chewing herbivores and can also dose them with a range of toxic chemicals (Doussord 2017 and refs therein). Caterpillars in many families have evolved behavioral counteradaptations to these defenses, including vein cutting, trenching, girdling, and leaf clipping, which drain the latex or resin and allow the caterpillar to safely feed distal to the cut (Doussord and Eisner 1987; Doussord 2017). While the exudates themselves are a direct plant defense against herbivory, the caterpillars’ time-consuming and visible pre-feeding behaviors, like the shelter-building behaviors described above for *E. clarus*, are likely to increase caterpillar exposure to natural enemies (Bergelson and Lawton 1988; Greeney et al. 2012) and thus could constitute an indirect defense, the effectiveness of which may vary among host plants.

Epicuticular waxes, another common leaf surface feature, can positively or negatively affect the movement of herbivores and their enemies, such that the net effect of three-dimensional waxy blooms on herbivory will vary from system to system (Eigenbrode 2004). Commonly, on surfaces covered with dense 3D waxes, insects are able to attach only weakly, and are manifold less able to hold on, relative to non-waxy surfaces (Gorb and Gorb 2017 and refs. therein). Eigenbrode and Espelie (1995) reported that three different generalist predators were more effective at capturing *Plutella xylostella* larvae on wax-deficient glossy-leaved than on normal-wax cabbage plants, due to the improved mobility of the walking predators on glossy leaf surfaces. They also reported reduced mining by *P. xylostella* on glossy leaves, potentially increasing larval exposure to predation.

The protective nature of leaf toughness is generally considered in a bitrophic context, with recent work exploring the role of various leaf structural traits in

defense against different kinds of herbivores and with attention to ontogenetic changes in both insect feeding behavior and plant structural defenses (Hanley et al. 2007; Malishev and Sanson 2015; Caldwell et al. 2016). Such ontogenetic changes in both plant and insect may interact in ways that are affected by the third trophic level. For example, Damman (1987) described an interesting situation in which *Omphalocera munroei* (Pyrilidae) larvae collectively built leaf ties on older, tougher leaves, which, though nutritionally inferior to tender young leaves, were more resistant to predator attack. The toughness of the older leaves necessitated that larvae feed in groups of at least 20 individuals, which together were able to manipulate the relatively inflexible leaf. Given the ubiquity of shelter-building and use by lepidopteran larvae (Marquis et al. Chapter “[The Impact of Construct-Building by Caterpillars on Arthropod Colonists in a World of Climate Change](#)”), additional studies relating leaf toughness to the defensive properties of their shelters against natural enemies, particularly for caterpillars that feed on multiple host plant taxa, are needed.

## Plant Architecture

It is now widely recognized that plant architecture, which is also referred to as plant structural complexity (McCoy and Bell 1991), is an important plant trait that can mediate predator-prey dynamics broadly (Grof-Tisza et al. 2017) and herbivore-natural enemy interactions specifically (reviewed in Marquis and Whelan 1996). Here we treat plant architecture as a trait that acts directly on the third trophic level, by facilitating or impeding natural enemy foraging activities and/or access to caterpillar prey. While several studies have found that leaf shape, size, arrangement, and surface features can influence arthropod predator and parasitoid foraging success (e.g., Kauffman and Kennedy 1989; Grevstad and Kleptetka 1992; Clark and Messina 1998; Reynolds and Cuddington 2012), most of these studies have not involved caterpillars. There is some evidence that plant architecture can influence the dynamics of caterpillar-vespid wasp (e.g., Geizenauer and Bernays 1996) and caterpillar-parasitoid (e.g., Pimentel 1961) interactions, but the overwhelming majority of studies involving caterpillars have focused on caterpillar-insectivorous bird interactions on woody plants with variable architectures. The physical size, arrangement, and density of structural elements (leaves and stems) on woody plants have been shown to affect multiple aspects of avian foraging, including host plant preference, searching time, and energy expenditures (Holmes and Robinson 1981; Robinson and Homes 1984; Whelan 1989, 2001), with resulting impacts on caterpillar densities, folivory, and plant biomass (e.g., Marquis and Whelan 1994; Van Bael et al. 2008; Whelan et al. 2008; Mäntylä et al. 2011). More recent work has focused on how woody plant architecture, specifically the density and heterogeneity of structural elements, can serve as a size-selective filter that could limit the access to potential predators (Grof-Tisza et al. 2017). A recent study found a strong negative relationship between the structural complexity of shrubs in the California

coastal sage scrub ecosystem and the ability of resident birds to reduce insect herbivore abundance on those plants (Nell and Mooney 2019); plants with more open, less dense branching patterns offered birds greater access to the interior of these shrubs, thus enhancing their ability to glean herbivores from their foliage. Moreover, because avian-mediated indirect defenses traded off with direct, anti-herbivore plant defenses in this set of co-occurring shrubs, the earlier suggestion by Marquis and Whelan (1996) that natural enemies can exert selective pressures on plant architectural traits was strongly supported (Nell and Mooney 2019). We expect that advances in three-dimensional imaging technologies may facilitate the speedy and precise quantification of plant architectural traits (e.g., the fractal index and plant complexity index described in Halley et al. 2004 and Grof-Tisza et al. 2017, respectively), spurring additional research in this fruitful area.

## Resources

We briefly discuss two categories of plant resources that are used by the third trophic level: plant provisioning of tangible resources (e.g., food and shelter) and plant provisioning of information (i.e., volatiles that can indicate location and in some cases identity of the caterpillar).

**Tangible Resources** In a botanical illustration of the adage, “the enemy of my enemy is my friend,” plants from a broad taxonomic range provide physical resources, including food, water, and shelter, to natural enemies of their herbivores, potentially resulting in a reduction of herbivore damage (Koptur et al. 2015; Heil 2015; Wackers et al. 2005). Such relationships can be obligate or facultative.

The most common category of obligate relationship occurs between ants and their partner “ant plants,” or myrmecophytes. These relationships, which are often very specialized, involve tropical angiosperms in at least 20 families (Davidson and McKey 1993) and ants in 5 subfamilies of Formicidae (Davidson 1997; Bronstein et al. 2006). The plants commonly provide nourishment to the ants in the form of carbohydrate from extrafloral nectaries and protein from specialized food bodies (pearl bodies, Beltian bodies, etc.), as well as specialized structures in which the ants can make a nest. The ants, for their part, patrol the plant and chase off or kill potential herbivores (e.g., Rico-Gray and Oliveira 2007). Exclusion of ants from myrmecophytes results in increased levels of herbivory (Heil and McKey 2003; Heil 2008). Several relatively recent reviews document these fascinating relationships (Bronstein et al. 2006; Rico-Gray and Oliveira 2007; Heil 2015).

More taxonomically and geographically widespread than obligate ant-plant relationships, many plants have facultative relationships in which they provide food resources to natural enemies, including ants as well as mites, spiders, parasitic hymenopterans, and predatory hymenopterans, hemipterans, and beetles (Wäckers et al. 2005; Koptur et al. 2015). Plants in over 108 plant families (Weber and Keeler 2013) secrete extrafloral nectar (EFN) from specialized secretory cells that can be

located on many different plant tissues (e.g., leaf bases and blades, flower buds, petioles, and developing fruits). The number, distribution, and nectar production rate of EFNs can be induced by herbivory, either directly or through exposure of undamaged plants to herbivore-induced volatiles (Heil 2015 and references therein, Yamawo and Suzuki 2018).

In a number of experimental trials in which ants were excluded from EFNs, herbivory levels on the test plants were increased over those on unmanipulated controls; some studies explicitly note attacks on or removal of lepidopteran herbivores (Koptur et al. 2015; Yamawo et al. 2012; Yamawo and Suzuki 2018). Hymenopteran parasitoids were reported to remain longer and attack more larvae of *Helicoverpa zea*, in the presence of extrafloral nectar (Stapel et al. 1997). Patrolling ants may or may not reduce oviposition by butterflies (Koptur et al. 2015), and their effectiveness varies depending on the growing conditions of the plant with nectaries (Jones et al. 2017). Rudgers and Strauss (2004), in one of the few studies that integrates trait expression, plant fitness, and genetic variation, demonstrated that reduction of nectar production by EFNs on wild cotton resulted in reduced ant recruitment, increased herbivory, and decreased plant fitness.

While EFNs provide resources for predators and parasitoids, and flowers often provide nectar for pollinators, natural enemies can also benefit from access to floral nectar (Heimpel and Jervis 2005; Zemenick et al. 2019; Patt et al. 1997; Tooker et al. 2006). A range of hymenopteran and dipteran predators and parasitoids (including syrphids, tachinids, and eulophids) have been recorded nectaring on a diversity of flowering plants, particularly on flowers with either exposed or partially exposed nectaries, such as many plants in the Apiaceae (Patt et al. 1997). As with extrafloral nectar, acquisition of carbohydrates from floral nectar can contribute to the longevity, fecundity, and, potentially, prey encounter rate of natural enemies (Russell 2015 and references therein).

Guttation droplets are also a potentially important plant resource that may play a role in multi-trophic interactions. Though droplets released from the margins of leaves through guttation have long been considered a water source for insects, Urbaneja-Bernat et al. (2020) recently reported that the liquid in fact contains proteins and carbohydrates and is a reliable source of nutrients for herbivores, parasitoids, and predators throughout the growing season. Insects fed on guttation droplets had higher fecundity and longevity relative to insects fed on water, and furthermore, in field trials, the presence of guttation droplets increased the number of predators and parasitic wasps visiting the plants. Further studies should investigate the generality of this finding and the potential impacts of guttation droplets on multi-trophic plant-insect interactions.

Leaves of many plants bear domatia, very small invaginations in the leaf epidermis, or dense tufts of hair at vein junctions that provide refuge for small predatory arthropods, most commonly predatory or fungivorous mites (Walter and O'Dowd 1992; Norton et al. 2001; Romero and Benson 2005) but also predatory minute pirate bugs (Agrawal et al. 2000). This mutualistic association between arthropods and plants, which is particularly common in temperate deciduous forest trees (as well as a range of agricultural crops), has been shown to decrease herbivore damage

to leaves, particularly through reduction of herbivorous mites by predatory mites (Romero and Benson 2005). Although predatory mites rarely attack caterpillars, small predaceous arthropods such as the minute pirate bug do, so it is likely that the presence of leaf domatia may indirectly impact lepidopteran herbivores.

**Information Resources** Over the last several decades an explosion of research in the field of chemical ecology has revolutionized our understanding of how the complex blends of herbivore-induced plant volatiles (HIPVs) produced by plants in response to herbivore interactions with plants convey information to at least four trophic levels: plants, caterpillars (and adult moths and butterflies), a variety of natural enemies, and even hyperparasitoids (Kessler and Heil 2011; Peterson et al. 2016; Turlings and Erb 2018; Cusumano et al. 2019). The HIPVs of a wide array of plants, including some well-studied model systems (e.g., *Arabidopsis thaliana*, *Nicotiana tabacum*, *Zea mays*, *Solanum lycopersicum*, various *Brassica* spp.), have been characterized using gas chromatography/mass spectroscopy (GC/MS) approaches. By capturing and analyzing the headspace around plants exposed to lepidopterans, researchers have detected HIPV-based responses to caterpillar feeding (Karban and Baldwin 1997; Howe and Jander 2008; Body et al. 2019), oviposition (e.g., Cusumano et al. 2015; Hilker and Fatouros 2015), and even arthropod movement on leaf surfaces (e.g., Hilker and Meiners 2010; Tooker et al. 2010). Three major types of HIPVs that respond to caterpillar activities, green leaf volatiles (GLVs), terpenoids, and the sulfur- and nitrogen-containing volatiles associated with the myrosinase/glucosinolate defenses of brassicaceous plants (Wittstock et al. 2003; Muller and Wittstock 2005; Mumm and Dicke 2010; Turlings and Erb 2018) have each been shown to be the most responsive to actual caterpillar feeding, with caterpillar oral secretions playing a pivotal role (Alborn et al. 1997). In addition, both GLV and terpenoid blends have been shown to convey specific information about the species of caterpillar causing the induced response (Allmann and Baldwin 2010), likely due to differences in the elicitors found in caterpillar oral secretions (Turlings and Erb 2018). Moreover, the HIPV signature for a given plant species can vary with the amount and type of damage (Delphia et al. 2007; Peterson et al. 2016), ontogenetic stage (Takabayashi et al. 1995), and even parasitization status (e.g., Poelman et al. 2011; Zhu et al. 2015; Cusumano et al. 2019) of the lepidopteran, providing a wealth of ecological and taxonomic information to “receivers” from any of the four trophic levels mentioned above.

While initial studies of caterpillar-based HIPVs considered parasitoid wasps to be the primary receivers of this chemically communicated information (Turlings and Erb 2018), the taxonomic makeup of documented receivers (and responders) has broadened considerably (Mumm and Dicke 2010) to include social wasps (Vespidae; McPherson and Mills 2012; Saraiva et al. 2017), ladybird beetles (James 2005), predatory bugs (e.g., *Geocoris* sp. and *Orius tristicolor*; James 2005; Allmann and Baldwin 2010), entomopathogenic nematodes (Ali et al. 2012), multiple fly families (Tachinidae, Chloropidae, Sarcophagidae, Syrphidae, and Agromyzidae; James 2005), and even insectivorous birds (Amo et al. 2013; Mäntylä et al. 2008; Mrazova and Sam 2017, 2019). Both innate and learned responses to

HIPVs have been documented in a variety of predators and parasitoids (Vet et al. 1995; Steidle and van Loon 2003; De Boer and Dicke 2006; Glinwood et al. 2011), and natural enemy abilities to detect subtle differences in HIPV blends appear to exceed that of available instrumentation (Mumm and Dicke 2010).

Acknowledging that the use of chemical information by the natural enemies of caterpillars is now well established, its functioning as a “defense trait” in plants is much less certain (Peñuelas and Llusía 2004; Kessler and Heil 2011). Plant *de novo* synthesis of novel volatiles in response to herbivory appears likely to have evolved primarily as a means of rapid intraplant communication and/or a means of deterring additional herbivores, raising the possibility that most natural enemy responses to HIPVs can be attributed to “eavesdropping” rather than plant-derived “SOS” signals (Dicke 2009; Dicke and Baldwin 2010). Because the koinobiont strategy used by many caterpillar parasitoids (Godfray 1994) allows their hosts to continue feeding and developing, functional responses of parasitoids to this information (i.e., increased parasitism rates) are unlikely to decrease plant damage in the short term (but see van Loon et al. 2000); however, for long-lived plants, numerical declines in herbivore populations resulting from increased parasitism may hold greater promise for reducing damage. By contrast, when plant signaling attracts generalist predators that effectively remove caterpillars, thus preventing further damage, these signaling traits have a greater likelihood of serving as indirect plant defenses. Agricultural field tests with lures containing synthetic HIPVs to augment biocontrol efforts of lepidopteran pests are likely to provide valuable insights into this debate, although there are a number of mitigating factors that may limit its effectiveness (reviewed in Kaplan 2012).

## Future Directions

Complementing the well-studied mechanisms detailed above, additional types of plant trait-mediated caterpillar-natural enemy interactions warrant further study based on some intriguing initial findings. These include investigations of how host plant affiliations affect the expression and/or effectiveness of antipredator behaviors such as regurgitation (a common caterpillar response to natural enemy attack) and caterpillar dropping behaviors (reviewed in Greeney et al. 2012). Because the foliage of alternative host plant species can differ in water content and allelochemical composition, both the amount of regurgitant produced (Peiffer and Felton 2009; Block et al. *in review*) and the effectiveness of the regurgitant in deterring predators (Theodoratus and Bowers 1999) may vary among host plants. Additional experiments testing the expression and effectiveness of regurgitation as an antipredator behavior in a wider range of oligophagous and polyphagous caterpillar taxa, and against a wider range of natural enemies (both arthropod predators and parasitoids), are needed. A second common caterpillar antipredator behavior that is likely to be impacted by host plant identity is their dropping/escape behavior. A variety of caterpillars respond to perceived predation threats by vigorously wriggling and/or

simply dropping off of their host plant (Gross 1993; Greeney et al. 2012) to avoid predation. When these behaviors are elicited by substrate-borne vibrations produced by natural enemies, as was demonstrated for the geometrid *Macaria aemulataria* (Castellanos and Barbosa 2006), physical and structural features of their host plant (e.g., wood density, leaf stiffness) could facilitate or impede signal transmission (McNett and Cocroft 2008; Hill 2009), potentially altering the effectiveness of these escape strategies.

Lastly, because some important natural enemies of caterpillars are themselves spatially restricted (e.g., many ant species), traits that determine a plant's microhabitat preferences (e.g., physiological tolerances for light, moisture, and various edaphic features) are likely to affect the abundance and/or community composition of natural enemies patrolling particular host plant species. In one of the most convincing demonstrations to date of how host plant shifts can be promoted and/or maintained by enemy-free space, Murphy (2004) found that the novel host plants (Asteraceae) used by the Alaskan swallowtail butterfly (*Papilio machaon alaska*) grew at higher elevations than their ancestral host plants (Apiaceae); as a consequence, caterpillars feeding on the novel host plants were not exposed to their most important predator (*Formica podzolica*), which co-occurs only with the ancestral host plant. Plant species restricted to serpentine soils, many of which also hyperaccumulate metals that can be toxic to a variety of herbivores (Brady et al. 2005), might also expose their caterpillars to different natural enemy pressures than their close relatives growing on non-serpentine soils (Robinson 2017). In short, by expanding the suite of "plant traits" hypothesized to influence caterpillar-natural enemy interactions to include interspecific differences in plant physiological tolerances for environmental variables, we can begin to assess their hypothesized role in environmental filtering (e.g., Bazzaz 1991; Swenson et al. 2012). Alternative host plants may also differ in their biotic associations (e.g., mycorrhizal fungi, nitrogen-fixing bacteria, and foliar endophytes), all of which have been shown to affect the expression of antiherbivore chemical defenses in their plant hosts (Kempel et al. 2009; Saikkonen et al. 2010; Jung et al. 2012), which in turn can modulate caterpillar-natural enemy interactions by any of the mechanisms described above. By extending the concept of plant phenotypes to include both their microhabitat associations and their many symbionts, a greater array of ecologically relevant modes of interaction can be investigated.

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