



The Plant as a Habitat for Entomophagous Insects

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Abstract

Populations of herbivorous insects are naturally consumed by other predacious or predatory insect species. These entomophagous insects are thus plant-dwelling organisms that use the plant for several vital functions and are affected by plant traits at the evolutionary, organism and population levels. Many entomophagous species are used for the biological control of insect pests worldwide. The aim of this chapter is to provide an exhaustive review of mechanisms underlying the interactions between plants and entomophagous insects, including those governing life history traits at the individual level, as well as those acting on population and community structure and dynamics. We detail how properties of host-infested plants determine parasitism behaviour, development (in the case of parasitoids) and nectar consumption by adult entomophagous insects. We detail how plants respond to and benefit from natural enemies attacking insect herbivores. We also illustrate how plant architecture, the vegetation communities and their climatic correlates can influence predator and parasitoid behaviour and populations. This chapter considers the biology and ecology of the interactions and mentions some implications for the biological control of plant pests.



1. INTRODUCTION

Herbivorous insects are consumed by predatory and parasitic ('entomophagous' or 'carnivorous') arthropods. These entomophagous arthropods, mainly insects, spiders and mites, visit plants not only to find hosts or prey, but they may also mate, feed and develop on plants. Various plant traits can affect entomophagous arthropods (Bottrell, Barbosa, & Gould, 1998; Kaiser, Couty, & Cortesero, 2013). The importance of the plant in the evolution and diversification of entomophagous species is evident in their searching and oviposition behaviours, which are adapted to the vegetational structure inhabited, and often created or transformed by their hosts. There are thus spectacular adaptations of the third trophic level to the first. For instance, ichneumonid wasps of the genus *Megarhyssa* that attack wood-boring larvae possess an ovipositor equipped with a hydraulic pressure system and a saw-like terminal part to drill through the wood and sting the host within (Gauld & Bolton, 1988; Quicke, 2015). Different strategies have evolved in response to similar constraints exerted by the host habitat. For instance, parasitoids of grain borers that are adapted to locate their host within seeds have different ways to reach the host. *Dinarmus basalis* (Rondani, 1877) (Chalcidoidea: Pteromalidae) pierces the seed coat with its ovipositor, just above the cavity inhabited by the host, whereas *Eupelmus vuilleti* (Crawford, 1913) (Chalcidoidea: Eupelmidae) inserts its ovipositor

inside the tiny tunnel bored by the host larva (Jaloux, 2004). Similarly, stem borer Lepidoptera larvae can be attacked through the stem by *Iphiaulax* spp., which are relatively large wasps equipped with long ovipositors (Quicke, 1988, 2015) (Fig. 1), or by much smaller species like *Cotesia sesamiae* (Cameron, 1906) which enters the tunnel and walks up to the host larva (Kimani-Njogu & Overholt, 1997). Beyond these obvious adaptations, the reader of this chapter will discover that entomophagous insects can respond behaviourally and physiologically to a wide array of plant traits often modified by the herbivorous host to insure their reproductive success.

The plant is also a direct resource, providing water and nectar, especially to adult entomophagous arthropods. Besides these trophic interactions, the plant also offers a physical refuge (e.g., trichomes, domatia and shelter) from unfavourable weather conditions and higher level predators.

Most studies of multitrophic interactions involve chemically mediated effects of plants on higher trophic levels; e.g., the emission and perception of plant volatiles by entomophagous insects, and the physiological response of entomophagous insects to plant compounds that mediate resistance to phytophagous insects. These interactions have been particularly well studied in the case of insect parasitoids that lay eggs in or on an insect host which later dies, following the larval development of the parasite. This intimate connection between life histories of host and parasitoid, presumably driven by reciprocal selection between host immune defences and virulence of the parasitoids, often leads to extremely specialized host–parasite interactions. It is within Hymenoptera that the largest number of parasitoid species (parasitic wasps) is found. To a lesser extent, multitrophic interactions have also been documented in the case of parasitoid flies (especially the tachinids), predatory insects (e.g., hoverflies, lacewings, ladybugs and hemipteran bugs) and predatory mites. Much literature has been published on responses of the third trophic level to plant resistance mechanisms since 1990 (Agrawal, 2000a, 2000b; Ode, 2006; Turlings & Wäckers, 2004). More recently, plant-mediated multitrophic interactions, i.e., involving several herbivores, pathogens, primary and hyper parasitoids, have been the focus of several studies (Gish, De Moraes, & Mescher, 2015; Hare, 2011; Mooney & Singer, 2012; Poelman & Dicke, 2014). Several books have been dedicated to the biology and evolution of insect parasitoids (Godfray, 1994; Quicke, 1997, 2015; Wajnberg, Bernstein, & Van Alphen, 2007).

The aim of this chapter is to provide an exhaustive review of the mechanisms underlying the interactions between plants and entomophagous insects, those governing adult and larval life history traits at the individual

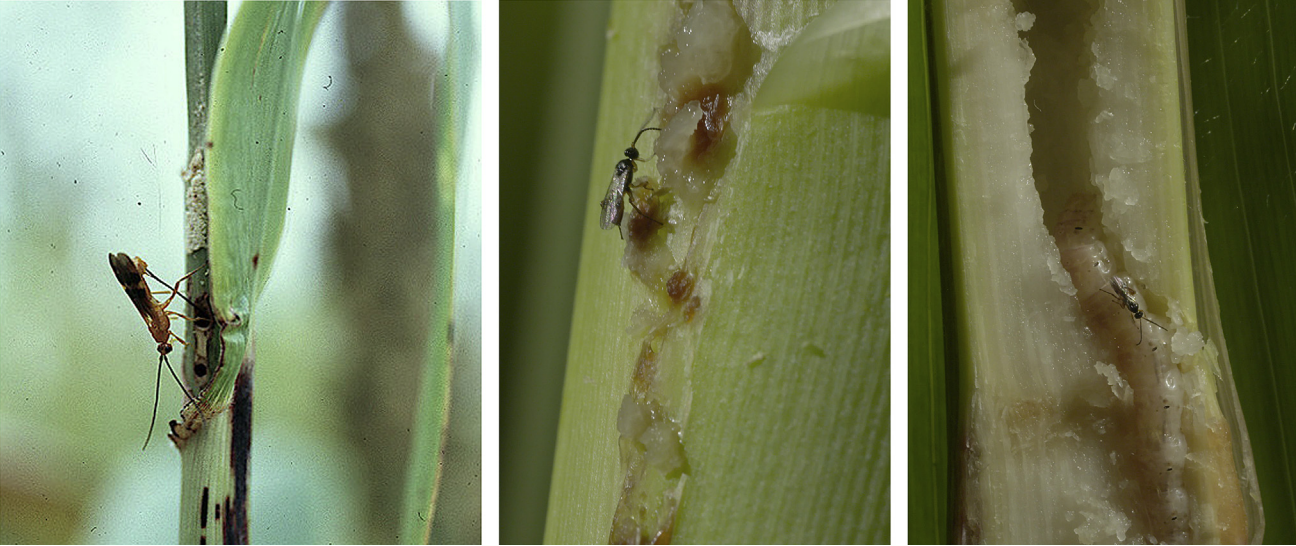


Figure 1 Left: *Iphiaulax* species are relatively large Hymenoptera that can either insert their long ovipositor in the host larval tunnel, as seen here on a sorghum stem bored by *Chilo partellus* (Lepidoptera: Crambidae), or drill through the stem to oviposit on the host larva. Middle: on a maize stalk, tiny *Cotesia sesamiae* examines faeces of its stem borer host left at the entrance of the larval tunnel. Right: once in the tunnel, *C. sesamiae* oviposits in the larval body, here *Sesamia nonagrioides* Lefebvre (Lepidoptera Noctuidae). Courtesy of *Iphiaulax*: J. van der Berg; *C. sesamiae*: © 2016 « Les nouveaux guerriers des champs » un film de Claude-Julie Parisot pour Galaxie Presse & Arte France.

level and those acting on population and community structure and dynamics. We detail how properties of host-infested plants determine parasitism behaviour, larval development (in the case of parasitoids) and nectar consumption by adult entomophagous insects. We detail how plants respond to and benefit from natural enemies attacking insect herbivores. We also illustrate how plant architecture, the vegetation communities and their climatic correlates can influence predator and parasitoid behaviour and populations. This chapter considers the biology and ecology of the interactions; it mentions some implications for the biological control of plant pests, which are topics further developed in other books and reviews (e.g., [Van Driesche, Hoddle, & Center, 2008](#)).



2. THE PLANT: PLACE OF PREDATION AND PARASITISM

The plant is the most frequent place of predation and parasitism of herbivorous insects, with the exception of predation and parasitism of hosts that are no longer on or in the plant, such as parasitism of host pupae that undergo metamorphosis in the soil. How carnivorous insects select herbivorous host insects has been mainly studied in insect parasitoids, because host selection behaviour directly determines the developmental success of these species. Host selection typically involves the following sequence of behaviours ([Godfray, 1994](#); [Nordlund, Jones, & Lewis, 1981](#)): searching for the appropriate host habitat (often, the plant), usually by remote-oriented flight; searching on the plant for the host by an exploration accompanied by antennal examinations of leaf area and faeces of the host; examination of the host; and finally, egg-laying.

Although the use of plant visual cues such as shape and colour has been demonstrated in some parasitoids ([Wäckers & Lewis, 1999](#)), most species rely on chemical cues during host searching and acceptance.

2.1 In-flight Search for Host and Prey

Insect parasitoids and predators can use various chemical cues as a reliable source of information about the presence of host or prey, which are often small and inconspicuous ([Wajnberg & Colazza, 2013](#)). Among all possible chemical cues, the volatile organic compounds (VOCs) emitted by plants in response to herbivory have long been recognized as playing an important role for the in-flight searching by natural enemies ([Dicke, 2016](#); [Erb, Robert, Hibbard, & Turlings, 2011](#); [Heil, 2008](#)). This indirect defence

mechanism was documented for the first time in the 1990s by two pioneering and independent studies: one conducted on the parasitoid *Cotesia marginiventris* (Cresson, 1865) (Hymenoptera: Braconidae), which parasitizes a maize pest caterpillar (Turlings, Tumlinson, & Lewis, 1990); the other on the mite *Phytoseiulus persimilis* Athias-Henrio 1957 (Acarina: Phytoseiidae), which is a predator of apple pest mites (Dicke, Sabelis, & De Jong, 1988). Since then, several comprehensive reviews have been published on the attraction of parasitoids and predators towards VOCs, showing that it is a widespread ecological phenomenon recorded for at least 50 plant species belonging to about 30 different families, including both monocots and dicots (Mumm & Dicke, 2010). In several cases, insect parasitoids and predators can recognize specific plant volatile blends induced by their herbivore hosts (Dicke & Baldwin, 2010; Heil & Karban, 2010). This indicates that plants have specific responses to herbivory, depending on the identity of the herbivore (Dicke, 2016). A growing body of literature has documented the dynamic and specific nature of odours produced as well as their biosynthetic pathways (Ode, 2013; Schuman & Baldwin, 2016), and it is now recognized that plant VOCs can be induced either by feeding (named herbivore-induced plant volatiles (HIPVs)) or by egg-laying (named oviposition-induced plant volatiles (OIPVs)). The role of HIPVs has been extensively documented in larval parasitoids (Hare, 2011). For example, in a tritrophic system comprising maize, the Lepidoptera *Spodoptera* spp. and several larval endoparasitoids, damage induced by *Spodoptera* larvae stimulates the release of green leaf volatiles and the accumulation of two plant hormones, jasmonic acid (JA) and ethylene (Carroll, Schmelz, Meagher, & Teal, 2006). These plant hormones are responsible for the emission of indole, terpenoids and other compounds, which attract larval parasitoids, and this attraction can increase the fitness of the attacked plants. Volatile emission is not limited to the part of the plant attacked. The emission spreads throughout the plant, including roots, through the release of internal plant hormones, such as JA, salicylic acid (SA) and their volatile derivatives, methyl jasmonate and methyl salicylate. This spreading extends even to neighbouring plants, through air- or soil-transmitted chemicals. The reaction of plant defence can be induced by salivary enzymes of the herbivores. In particular, chewing insects (e.g., caterpillars) tend to induce the JA-signalling pathway, while phloem feeders (e.g., aphids) can induce both JA and -SA pathways, depending on insect species (Hare, 2011).

Many endoparasitoids of herbivorous insects do not immediately kill their hosts (termed 'koinobiotic parasitoids'), so plants continue to be

injured even after successful parasitism (De Rijk, Dicke, & Poelman, 2013). The emission of OIPVs upon herbivore egg-laying can be an effective indirect defence strategy that attracts egg parasitoids, which prevent the pest from hatching (Pashalidou et al., 2015). Furthermore, OIPVs are highly reliable and detectable for egg parasitoids (Colazza et al., 2004; Hilker & Fatouros, 2015). Evidence of this ‘early herbivore alert’ was provided in a pioneering study by Meiners and Hilker (2000). They showed that oviposition by elm leaf beetles *Xanthogaleruca luteola* (Müller, 1766) (Coleoptera: Chrysomellidae) on elm *Ulmus minor*, caused wounding of the plant tissue, which induced OIPVs that attracted the specialist egg parasitoid *Oomyzus gallerucae* (Fonscolombe, 1832) (Hymenoptera: Eulophidae).

Recent studies indicate that plant volatiles can mediate community interactions between parasitized and unparasitized herbivores (Poelman, Zheng, Zhang, Heemskerk, & Cortesero, 2011), and even at the fourth trophic level (parasitoids of parasitoids). For example, Poelman et al. (2012) showed that *Lysibia nana* (Gravenhorst, 1829) (Hymenoptera: Ichneumonidae), a solitary hyperparasitoid that attacks pupae of braconid wasps, is able to locate its host using HIPVs from cabbage plants attacked by *Pieris rapae* (L.) (Lepidoptera: Pieridae) that were parasitized by *Cotesia glomerata* (Linnaeus, 1758) (Hymenoptera: Braconidae).

In a complex natural environment, in-flight search by parasitoids for their hosts may be impeded by the presence of different herbivores on different food plants, or by herbivores in different feeding guilds that induce different VOC blends in the same plant (Cusumano, Weldegergis, Colazza, Dicke, & Fatouros, 2015). For example, the attraction of the egg parasitoid, *Trissolcus basalus* (Wollaston, 1858) (Hymenoptera: Scelionidae) towards *Nezara viridula* (Linnaeus, 1758)-egg induced volatiles produced by the fava bean *Vicia faba* is disrupted by the nonhost beetle, *Sitona lineatus* (Linnaeus, 1758) (Coleoptera: Curculionidae) feeding on the roots or leaves (Moujahed et al., 2014). VOC emission can also be induced by plant pathogen development, and its effects on insect parasitoids have received recent and growing interest, especially because the identification of biochemical defence pathways induced by pathogens and herbivores is making rapid progress (Appel et al., 2014; Pieterse, Van der Does, Zamioudis, Leon-Reyes, & Van Wees, 2012). Depending on the plant as well as the pathogen and herbivore species, the blend and timing of volatile emission vary and may interfere with responses of predators and parasitoids, which may decrease (Desurmont, Xu, & Turlings, 2016), remain unchanged or increase (Ponzio, Gols, Weldegergis, & Dicke, 2014). Similar to the interaction

between herbivores in different feeding guilds, such interference can be interpreted as the outcome of crosstalk between the pathways induced by each plant enemy (Appel et al., 2014).

Because HIPVs and OIPVs are central to the ability of natural enemies to find hosts, their use in the manipulation of parasitoid host searching behaviour in biological controls is promising (Meiners & Peri, 2013). However, whether their use can improve the effective biological control of plant pests, it is still an open question, which requires more study taking into account crop-specific aspects and landscape context (Gish et al., 2015; Kaplan, 2012a; Trapero, Wilson, Stiller, & Wilson, 2016).

2.2 Searching for Hosts While on Plants and Host Acceptance

Host acceptance behaviour by parasitoids depends on the perception of several host criteria, including species identity, growth stage, health status and size, among many others. The abundant studies on host searching and acceptance mechanisms allow us to establish a general trend; the importance of direct plant signals (e.g., VOCs emitted by infested plants) for parasitoids decreases when approaching the host, whereas the host-specific contact sensory cues become increasingly important (e.g., chemical, visual, vibrational) (Godfray, 1994). Although parasitoids may use nonchemical information sources (e.g., physical cues) to locate their target host, they are differentially attracted mostly on the basis of specificity of host-derived kairomones (semiochemicals that benefit the receiver to the detriment of the emitter; Nordlund & Lewis, 1976; Dicke & Sabelis, 1988). These chemicals constitute reliable cues for the foraging parasitoid, especially in the final stages of host location, recognition and acceptance (Godfray, 1994; Afsheen, Wang, Li, Zhu, & Lou, 2008). Parasitoids exploit both volatile and nonvolatile contact kairomones to differentiate host and nonhost species as well as host developmental stage. These kairomones are emitted by a specific herbivore stage (egg, larva, pupa or adult) or by-product (e.g., frass, exuvia, mandibular gland secretion or defensive secretion) of its specific host (see Afsheen et al. (2008) for review) (Table 1).

The kairomones identified so far include various chemical groups but are predominately hydrocarbons such as aldehydes, esters and terpenoids (Table 1). Rani, Kumari, Sriramakrishna, and Sudhakar (2007) proposed that compounds that have a high number of carbon atoms might act as contact stimulants, whereas the chemicals with less than 10 carbon atoms are more likely to be volatile and might attract parasitoids to the vicinity of the host.

Table 1 Diversity of Kairomones Involved in Host Recognition and Acceptance by Parasitoids and Their Sources

References	Compound	Source	Category	Parasitoid Species	Host Species
Ananthakrishnan, et al. (1991). <i>Journal of Biosciences</i> , 16, 111–119.	Hexatriacontane, pentacosane, docosane 2,6,10-dodecatrienal- 3,7,11-trimethyl	Moth scale	Egg	<i>Trichogramma chilonis</i>	<i>Heliothis armigera</i>
Arakaki, et al. (2011). <i>Applied Entomology and Zoology</i> , 46, 195–200.	(6Z, 9Z, 11S, 12S)-11, 12-epoxyhenicosa-6,9-diene	Sex pheromone	Egg	<i>Telenomus euproctidis</i>	<i>Orgyia postica</i>
Bénédet, et al. (1999). <i>Journal of Insect Physiology</i> , 45, 375–384.	Four glycopolypeptides	Silk cocoon	Pupal	<i>Diadromus pulchellus</i>	<i>Acrolepiopsis assectella</i>
Burks, & Nettles (1978). <i>Environmental Entomology</i> , 7, 897–900.	Cuticular extracts	Cuticle of the larvae	Larval	<i>Eucelatoria</i>	<i>Heliothis virescens</i>
Boo, & Yang (2000). <i>Journal of Chemical Ecology</i> , 26, 359–375.	Z11-16:Ac E12-14:Ac	Sex pheromone Sex pheromone	Egg Egg	<i>T. chilonis</i> <i>T. chilonis</i>	<i>Helicoverpa assulta</i> <i>Ostrinia funacalis</i>
Calatayud, et al. (2001). <i>Journal of Chemical Ecology</i> , 27, 2203–2217.	O-caffeoylserine	Host cover	Larval	<i>Acerophagus coccois</i> , <i>Aenasius vexans</i>	<i>Phenacoccus herreni</i>
Colazza, et al. (2007). <i>Journal of Chemical Ecology</i> , 33, 1405–1420.	<i>n</i> -nonadecane	Adult tarsi and scutella	Egg	<i>Trissolcus basalis</i>	<i>Nezara viridula</i>

(Continued)

Table 1 Diversity of Kairomones Involved in Host Recognition and Acceptance by Parasitoids and Their Sources—cont'd

References	Compound	Source	Category	Parasitoid Species	Host Species
DeLury, et al. (1999). <i>Journal of Chemical Ecology</i> , 25, 2419–2431.	Heptanal, octanal, nonanal, decanal undecan-2-one, dodecanal, pentadecan-2-one, (<i>Z</i>)-6-pentadecen-2-one, (<i>Z</i>)-9-hexadecenal, (<i>Z</i>)-6-heptadecen-2-one, 3,7,11-trimethyl-2E,6E, 10-dodecatrien-1-ol acetate	Scales	Egg	<i>Ascogaster quadridentata</i>	<i>Cydia pomonella</i>
Fatouros, et al. (2005). <i>Journal of Insect Behavior</i> , 20, 53–65.	Benzyl cyanide	Antiaphrodisiac	Egg	<i>Trichogramma brassicae</i>	<i>Pieris brassicae</i>
Gauthier, et al. (2004). <i>Journal of Insect Physiology</i> , 50, 1065–1074.	Polypeptides	Silk cocoon	Pupal	<i>D. pulchellus</i>	<i>A. assectella</i>
Millar, & Hare (1993). <i>Journal of Chemical Ecology</i> , 19, 1721–1736.	O-caffeoyltyrosine	Host cover	Larval	<i>Aphytis melinus</i>	<i>Aonidiella aurantii</i>
Hilker, et al. (2000). <i>Journal of Chemical Ecology</i> , 26, 2591–2601.	Acetate and propionate of (2S,3R,7R)-3,7-dimethyl- 2-tridecanol (2S,3S,7S)-3,7-dimethyl-2-pentadecyl acetate	Sex pheromone	Egg	<i>Chrysonotomyia ruforum</i>	<i>Diprion pini</i>
Jones, et al. (1971). <i>Science</i> , 17, 842–843.	13-Methylhentriacontane	Frass, larvae	Larval	<i>Microplitis croceipes</i>	<i>Heliothis zea</i>

Jones, et al. (1973). <i>Environmental Entomology</i> , 2, 593–596.	Docosane, tricosane	Wing scales	Egg	<i>Trichogramma evanescens</i>	<i>H. zea</i>
Kuwahara, et al. (1983). <i>Agricultural and Biological Chemistry</i> , 47, 1929–1931.	2-Palmitoyl- and 2-oleoyl-cyclohexane-1, 3-dione	Frass		<i>Venturia canescens</i>	<i>Plodia interpunctella</i>
Lewis, et al. (1982). <i>Journal of Chemical Ecology</i> , 8, 1323–1331.	(Z)-9-Hexadecenal	Sex pheromone	Egg	<i>Trichogramma pretiosum</i>	<i>H. zea</i>
Lou, et al. (1999). In J. Du (Ed) <i>Proceedings of first Asia–Pacific conference on chemical ecology</i> , Shanghai, China. November 1–4, 1999.	Palm oil	Adult, nymph	Egg	<i>Anagrus nilaparvatae</i>	<i>Nilaparvata lugens</i>
Lou, & Cheng (2001). <i>Entomologia Experimentalis et Applicata</i> , 101, 59–67.	Palm oil	Adult, nymph	Egg	<i>A. nilaparvatae</i>	<i>Sogatella furcifera</i>
Mattiacci, et al. (1993). <i>Journal of Chemical Ecology</i> , 19, 1167–1181.	α^{β} – unsaturated aldehyde, (E)-2-decenal	Defensive metathoracic gland	Egg	<i>T. basalis</i>	<i>Nezara viridula</i>
Mizutani (2006). <i>Japanese Journal of Applied Entomology and Zoology</i> , 50, 87–99.	(E)-2-hexenyl (Z)-3-hexenoate (E2HZ3H)	Aggregation pheromone	Egg	<i>Ooencyrtus nezarae</i>	<i>Riptortus clavatus</i>

(Continued)

Table 1 Diversity of Kairomones Involved in Host Recognition and Acceptance by Parasitoids and Their Sources—cont'd

References	Compound	Source	Category	Parasitoid Species	Host Species
Ma, et al. (1992). <i>Annals of the Entomological Society of America</i> , 85, 72–79.	11 free amino acids including serine and glutamic acid	Frass, oral secretion	Larval	<i>Eriborus terebrans</i>	<i>Ostrinia nubilalis</i>
Mudd, & Corbet (1982). <i>Journal of Chemical Ecology</i> , 8, 843–850.	2-Acylcyclohexane-1-3-diones	Mandibular glands	Larval	<i>Nemeritis canescens</i>	<i>Ephestia kuehniella</i>
Mudd, et al. (1984). <i>Journal of Chemical Ecology</i> , 10, 1597–1601.					
Nemoto, et al. (1987). <i>Agriculture and Biological Chemistry</i> , 51, 1805–1810.	2-Palmitoyl- 2-stearoylcyclohexane-1,3-dione	Frass	Larval	<i>V. canescens</i>	<i>Cadra cautella</i> <i>Plodia interpunctella</i>
Nettles, & Burks (1975). <i>Journal of Insect Physiology</i> , 21, 965–978.	Protein (30 kD)	Frass, haemolymph	Entire larvae, pupae, emerged adults	<i>Archytas marmoratus</i>	<i>H. virescens</i>
Nordlund, & Lewis (1985). <i>Entomologia Experimentalis et Applicata</i> , 38, 109–112.	13-Methylhentriacontane	Larval frass	Larval	<i>Microplitis demolitor</i>	<i>H. zea</i>
Obonyo, et al. (2010). <i>Biological Control</i> , 54, 270–275.	Protein (enzyme?)	Larval body extract Larval frass regurgitants	Larval	<i>Cotesia flavipes</i> <i>Cotesia sesamiae</i>	<i>Chilo partellus</i> <i>Busseola fusca</i>
Ramachandran, et al. (1991). <i>Journal of Agricultural Food Chemistry</i> , 39, 2310–2317.	3-Octanone and guaiacol	Larval frass	Larval	<i>M. demolitor</i>	<i>Pseudoplusia includens</i>

Rani, et al. (2007). <i>Journal of Chemical Ecology</i> , 33, 59–73.	Long chain alkanes and alkenes like docosane, tetracosane, pentacosane, and eicosane	Adult extracts	Egg	<i>Trichogramma japonicum</i>	<i>Scripophaga incertulas</i>
Reddy, et al. (2002). <i>Journal of Chemical Ecology</i> , 28, 131–143.	Z11-16:Ald, Z11-16:Ac, and Z11-16:OH in a 1: 1: 0.01 ratio	Sex pheromone	Egg	<i>T. chilonis</i>	<i>Plutella xylostella</i>
	Z11-16:Ac alone, 1:1 blend of Z11-16:Ac and Z11-16:Ald allyl isothiocyanate	Larval frass	Egg	<i>T. chilonis</i>	<i>Plutella xylostella</i>
Renou, et al. (1992). <i>Entomologia Experimentalis et Applicata</i> , 63, 291–303.	(Heneicosane, tricosane) pentacosane, heptacosane and nonacosane), ethyl and palmitic acid palmitate	Egg extract	Egg	<i>T. brassicae</i>	<i>O. nubilalis</i> <i>Mamestra brassicae</i>
Roux, et al. (2007). <i>Chemoecology</i> , 17, 13–18.	Lipids	Larval cuticle	Larval	<i>Cotesia plutellae</i>	<i>Plutella xylostella</i>
Shu, et al. (1990). <i>Journal of Chemical Ecology</i> , 16, 521–529.	Mixture of 11,15-, 13,17- and 15,19-dimethylnonatriacontanes	Moth scale	Egg	<i>Trichogramma nubilale</i>	<i>O. nubilalis</i>
Silva, et al. (2006). <i>Pesquisa Agropecuaria Brasileira</i> , 41, 1093–1098.	Methyl 2,6,10-trimethyltridecanoate	Male sexual pheromone	Egg	<i>Telenomus podisi</i>	<i>Euschistus heros</i>
Steidle, & Ruther (2000). <i>Journal of Chemical Ecology</i> , 26, 2665–2675.	Alpha-tocopherol, beta-tocopherol beta-tocotrienol, cholesterol, ergosterol, and beta-sitosterol	Feces	Larval	<i>Lariophagus distinguendus</i>	<i>Sitophilus granaries</i>

(Continued)

Table 1 Diversity of Kairomones Involved in Host Recognition and Acceptance by Parasitoids and Their Sources—cont'd

References	Compound	Source	Category	Parasitoid Species	Host Species
Strand, et al. (1989). <i>Journal of Chemical Ecology</i> , 15, 1491–1500.	2-Acylcyclohexane-1-3-diones	Mandibular glands	Larval	<i>Bracon hebetor</i>	<i>E. kuehniella</i>
Takabayashi, & Takahashi (1989). <i>Entomologia Experimentalis et Applicata</i> , 52, 221–227.	2, 5-dialkyltetrahydrofuran	Frass	Larval	<i>Apanteles kariyai</i>	<i>Pseudaletia separata</i>
Thompson, et al. (1983). <i>Environmental Entomology</i> , 12, 1312–1314.	Phenols, alcohols	Frass	Larval	<i>Lixophaga diatraeae</i>	<i>Diatraea saccharalis</i>
Vinson, et al. (1975). <i>Entomologia Experimentalis et Applicata</i> , 18, 443–450.	Mixture of three long chain hydrocarbons (11-methyl-hentriacontane, 16-methyl-dotriacontane and 13-methyl-hentriacontane)	Mandibular glands	Pupal	<i>Cardiochiles nigriceps</i>	<i>H. virescens</i>
Weseloh (1977). <i>Journal of Chemical Ecology</i> , 3, 723–735.	Sericin or fibrinogen likeprotein	Silk producing glands	Larval	<i>Apanteles melanoscelus</i>	<i>Limantria dispar</i>

Updated table of Afsheen, S., Wang, X., Li, R., Zhu, C.-S., & Lou, Y.-G. (2008). Differential attraction of parasitoids in relation to specificity of kairomones from herbivores and their by-products. *Insect Science*, 15, 381–397.

Most of the identified kairomones have been associated with egg or larval parasitoids (Table 1). In the case of egg parasitoids, kairomones come from the insects' host itself (i.e., sex pheromones, adult host products such as scales or egg coating), whereas in the case of larval parasitoids, the kairomones are coming from the host feeding activities (i.e., frass, oral secretions). In the latter, kairomones may have plant origin or be derived from plant products and may thus be also classified as synomones. In addition, the wax layer of the host plants where the herbivores are located can also play an important role in the detection of host's kairomones for both egg (e.g., Colazza, Salemo, & Wajnberg, 1999; Conti, Salemo, Bin, Williams, & Vinson, 2003) and larval parasitoids (e.g., Rostas, Ruf, Zabka, & Hildebrandt, 2008). Parasitoids are sensitive to chemical footprints left by herbivores as they walk over the substrate. Furthermore, the chemical composition of the plant wax layer modulates the detectability of these footprints. However, the chemistry of both wax layer and footprints remains to be elucidated.

2.3 Learning and Memory Involved in Host Searching

Odour learning has been mostly studied in parasitic wasps. As detailed above, plants damaged by herbivore feeding often produce particular VOCs, which are attractive to parasitoid insects (Kaplan, 2012a; McCormick, Unsicker, & Gershenson, 2012; Vet & Dicke, 1992). While some species show innate plant odour preferences (Kaplan, 2012b), others rely on experience, having to learn the host-associated VOCs (e.g., Canale, Geri, & Benelli, 2014; Simpson et al., 2011; Steidle & Schöller, 1997; Vet & Van Opzeeland, 1984). Even in species with innate preferences, their response can be strengthened by rewarding odour experiences, as has been recently reviewed by Giunti et al. (2015). From the plant's perspective, producing odours that attract the enemies of its herbivores has often been considered advantageous (Hare, 2011; Turlings et al., 1995). In general, plant-produced odours, such as those that are attractive from relatively large distances (Braasch & Kaplan, 2012; De Boer & Dicke, 2006; Geervliet, Ariens, Dicke, & Vet, 1998) are more easily detectable for foraging wasps than odours directly emitted by a potential host, which have evolved to be cryptic. Plant-derived odours are, on the other hand, less reliable and, as hosts may feed from more than one plant species, more variable than cues produced directly by the host. The ability to recognize reliable odours through learning from previous experience therefore has a great potential to increase a wasps' foraging success and most species studied in this regard are able to learn a plant odour

in association with successful oviposition experience (Steidle & Van Loon, 2003; Turlings, Wäckers, Vet, Lewis, & Tumlinson, 1993).

Once a parasitoid can respond to the odour of a rewarding plant species, future host location is greatly facilitated. So how do unexperienced wasps locate their first host? Some studies have shown that naive wasps acquire the ability to orient to their developmental plant odour, either as immature (Barron, 2001; Gandolfi, Mattiacci, & Dorn, 2003), or at adult eclosion, during antennal exploration of plant tissues or host remains, a process termed ‘early adult learning’ (e.g., Van Emden, Sponagl, Baker, Ganguly, & Douloumpaka, 1996; Kester & Barbosa, 1991) (Fig. 2). Studies have also shown that preferences can be reversed when wasps have rewarding experiences with initially nonpreferred odours (e.g., Kester & Barbosa, 1991), or unrewarding experiences (Fig. 2) with initially preferred or neutral odours (Papaj, Snellen, Swaans, & Vet, 1994), rendering the odours attractive and repellent, respectively. In addition, odours that a wasp will not encounter in a natural habitat, e.g., vanilla or banana, can become highly attractive

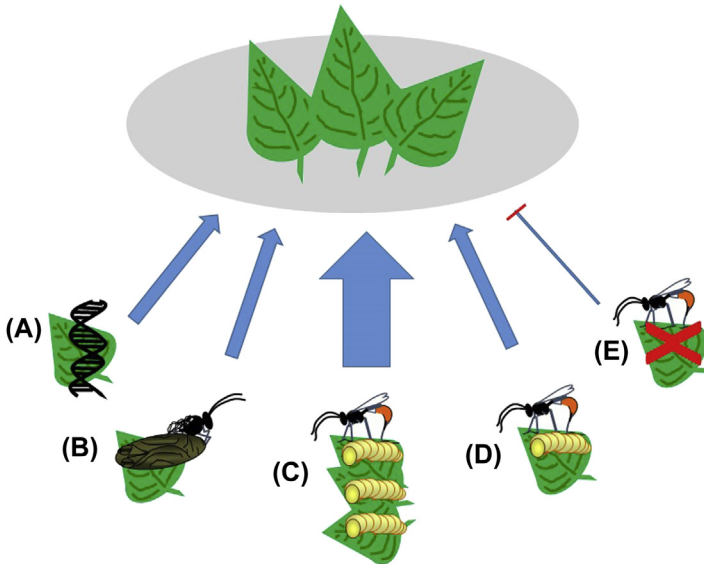


Figure 2 A parasitic wasps responsiveness towards specific plant volatiles can be genetically fixed (A). Very often however, relevant plant odours are learned early in life, e.g., during eclosion (B) or during experience with a suitable host (D). Existing preferences might then be strengthened by further rewarding experiences (C) or weakened by unrewarding experiences (E), allowing the wasp to develop a chemosensory search-pattern that matches the current host availability.

once a host has been encountered together with such an odour plume (e.g., Kaiser, Perez-Maluf, Sandoz, & Pham-Delegue, 2003; Takasu & Lewis, 2003). However, some wasp species restricted to plant-specialized host don't have this ability (e.g., Geervliet, Vreugdenhil, Dicke, & Vet, 1998).

Interestingly, laboratory experiments have revealed striking differences in learning speed and memory retention within (Koppik, Hoffmeister, Brunkhorst, Kiess, & Thiel, 2015; Thiel, Schlake, & Kosior, 2013) and between (Patt, Hamilton, & Lashomb, 1999; Tamo, Ricard, Held, Davison, & Turlings, 2006) parasitoid wasp species, and gene expression accounting for such differentiation is being explored (Van Vugt et al., 2015). Cognitive ability and the 'preparedness to learn' are most likely related to the specific environmental settings experienced by individual species, and the cost of learning and memory formation (Mery, 2013; Smid & Vet, 2016). Learning and memory dynamics is also plastic. The nature of the reward experienced during learning trials might also influence the strength of the learned association: with more valuable rewards, fewer repetitions are necessary until the information is memorized and/or until it enters long-term memory (Koppik et al., 2015; Kruidhof et al., 2012; Luo, Michaud, Li, Liu, & Zhang, 2013). Plasticity may be also linked to symbionts, as recently demonstrated with the tiny egg-parasitoid *Trichogramma brassicae* Bezdenko 1968, which has lower memory retention when infected with *Wolbachia* bacteria, possibly due to the costs of carrying *Wolbachia* (Farahani et al., 2016).

Experiments in field cages or under open field conditions have shown that wasps that had the opportunity to associate one of the plant odours present with the presence of hosts had a significantly higher probability of finding their hosts in semi-natural conditions as well as finding it faster (Kruidhof et al., 2015; Papaj & Vet, 1990). It has recently been suggested that training mass-reared wasps before releasing them for biocontrol purposes should be considered as a means of increasing wasp efficacy (Giunti et al., 2015; Kruidhof, Smid, Thiel, Hoffmeister, & Vet, 2014).

While olfactory orientation by female parasitoids towards host-related cues is probably the best studied learning response in parasitic wasps, these insects are also able to associate odours with food (nectar or honeydew) rewards (e.g., Canale et al., 2014; Ngumbi, Jordan, & Fadamiro, 2012; Patt et al., 1999; Takasu & Lewis, 1996). This ability has been studied in male wasps as well (Takasu, Rains, & Lewis, 2007). Finally, foraging parasitoids can learn to associate cues other than chemicals, such as colours or shapes with hosts, food or mates (e.g., Baeder & King, 2004; Benelli & Canale, 2012; Lucchetta, Bernstein, Thery, Lazzari, & Desouhant, 2008;

Oliai & King, 2000; Wäckers & Lewis, 1999). In some species, resources (prospective mates within the host's pupa or host egg masses for oviposition) are present in the wasp's environment for longer periods, but are suitable for exploitation only at a very specific time (i.e., at eclosion of the female or perfect age of the host egg). In these cases, wasps regularly revisit the resources, using learned landmark cues for orientation (Danci, Hrabar, Ikoma, Schaefer, & Gries, 2013; Van Nouhuys & Kaartinen, 2008).



3. THE PLANT, PLACE OF DEVELOPMENT

Physical and chemical plant traits can have both direct and indirect effects on entomophagous insects (Bottrell et al., 1998; Hare, 2002). Indirect effects are those that alter some aspect of herbivore abundance or quality, which in turn influences development/survivorship of insect natural enemies. Indirect effects can be further divided into 'density-mediated effects' that influence herbivore density (and ultimately natural enemy abundance) and 'trait-mediated indirect effects' that influence natural enemies through altering herbivore quality as a prey or host resource (Mooney & Singer, 2012). In general, but by no means exclusively, most studies have explored either the direct effects of plant physical and chemical traits on the foraging success of entomophagous insects or the indirect effects of plant chemical traits on the developmental success and survivorship of entomophagous insects.

3.1 Effects of Plant Physical Traits on Entomophagous Insect Development

While plant physical characteristics are well known to influence the foraging behaviour of both predators and parasitoids (Bottrell et al., 1998; Casas & Djemai, 2002; Price et al., 1980), far fewer studies have examined the effects of plant physical traits on the development of immature insect predators and parasitoids. In part, this is likely because relatively few studies have carefully distinguished between plant trait effects on oviposition decisions and trait effects on the development success and survivorship of immature entomophagous insects. Plant physical traits such as waxiness, trichomes and leaf thickness are expected to influence predators more than parasitoids, as most predators directly interact with the surface of the plant as they forage for prey. Several studies have demonstrated that predatory coccinellid beetle larvae develop more quickly and have lower mortality when developing on certain plant species or cultivars (e.g., Al-Zyoud, Tort, & Sengonca, 2005; Inbar & Gerling, 2008); however, in many studies, it is difficult to determine

whether a physical aspect of the plant influences predator performance or if these effects are due to differences in defensive chemistry in the host plant. Yet, some plant physical characters, notably leaf domatia — small chambers produced by the plant that house predatory insects and mites, clearly have positive effects on some predators (Agrawal, Karban, & Colfer, 2000; O’Dowd & Willson, 1991). Such domatia appear to be important in reducing parasitism and predation of the predators’ eggs and nymphs, which in turn results in higher predation of herbivores (Agrawal et al., 2000; Romero & Benson, 2005).

While most studies of the impact of plant physical traits on entomophagous insect development have focused on predators, a few studies suggest that plant physical traits can also influence parasitoid development. A study of *Encarsia pergandiella* Howard 1907, a parasitoid of the silverleaf whitefly *Bemisia argentifolii* Bellows & Perring, found that the number of parasitoids that successfully develop was substantially greater on a glossy (low-wax) variety of collard (*Brassica oleracea* L.) compared to a normal wax variety, even though the two varieties differ by only one gene for waxiness (McAuslane, Simmons, & Jackson, 2000). The difference between glossy versus normal wax plants could have been due to differential oviposition by adult females, differential mortality of developing parasitoids or a combination. In a study of two cultivars of poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch) that differed by 15% in trichome density, successful development of several species of *Encarsia* on *B. argentifolii* was greater on the cultivar with higher trichome densities, despite the fact that parasitism rates were greater on the poinsettia cultivar with lower trichome densities (Heinz & Parrella, 1994). This difference in the correlation between trichome density and attack rate versus trichome density and parasitoid emergence (survivorship) is suggestive of an effect of trichomes on parasitoid development.

3.2 Effects of Plant Defensive Chemistry on Entomophagous Insect Development

The effects of plant chemistry on parasitoids and predators have been well studied (Dicke & Baldwin, 2010; Harvey, 2005; Hunter, 2003; Ode, 2006, 2013; Price et al., 1980). Plant antiherbivore toxins can negatively affect the development and survivorship of natural enemies of herbivores. Studies of plant toxin effects on the third trophic level have taken a variety of approaches including (1) comparisons of plant populations or cultivars (which differ in their secondary plant chemistry profiles) in terms of their effects on herbivores and their natural enemies (e.g., Gols, Van Dam,

Raaijmakers, Dicke, & Harvey, 2009; Harvey & Gols, 2011; Ode, Berenbaum, Zangerl, & Hardy, 2004; Ode, Harvey, Reichelt, Gershenzon, & Gols, 2016), (2) artificial diet studies where known quantities of specific plant toxins are added to a herbivore's diet (e.g., Barbosa, Gross, & Kemper, 1991; Barbosa et al., 1986; Campbell & Duffey, 1979; Lampert, Zangerl, Berenbaum, & Ode, 2008, 2011) and (3) manipulation of the JA signalling pathway to alter the production of plant toxins through the use of exogenous applications of JA mimics (e.g., Thaler, 1999). The use of transformed lines, where genes in the JA pathway have been silenced, has been used in wild tobacco where it has been shown alter susceptibility to herbivores and attractiveness to natural enemies (e.g., Kessler, Halitschke, & Baldwin, 2004); however, we are unaware of application of this technique to explore how parasitoids and predators are affected by plant toxins.

Plant defensive chemistry can influence the development and survivorship of an entomophagous insect by either reducing the quality of its host/prey (e.g., smaller size, reduced nutritive quality) or by direct exposure to plant toxins that it encounters in the body of its host/prey (either unmetabolized or metabolic byproducts of ingested plant toxins) (Kaplan, Carrillo, Garvey, & Ode, 2016). Yet, relatively few studies have attempted to distinguish between these two possibilities. One approach has been to determine whether plant toxins pass unmetabolized into the haemolymph of a herbivore where it would be directly encountered by developing parasitoids. This has been demonstrated in several systems including the parasitoid *Hyposoter exiguae* (Viereck, 1912), which encounters the glycoalkaloid α -tomatine in its host *Heliothis zea* (Boddie, 1850) feeding on tomato (Campbell & Duffey, 1979), *Cotesia congregata* (Say, 1836) exposed to nicotine in its host *Manduca sexta* feeding on tobacco (Barbosa et al., 1986) and *Copidosoma sosares* Walker, 1837 encountering unmetabolized xanthotoxin in its host *Depressaria pastinacella* (Duponchel, 1838) when feeding on wild parsnip (Lampert et al., 2008, 2011; McGovern, Zangerl, Ode, & Berenbaum, 2006). In each of these cases, parasitoids experienced decreased survivorship, decreased body sizes and sometimes morphological deformities apart from any effects of reduced host quality. Whether parasitoids are able to metabolize plant toxins that they encounter in their hosts is largely unknown. In the case of *C. sosares*, neither larvae nor embryos show any capacity to metabolize the furanocoumarin xanthotoxin (Lampert et al., 2008, 2011; McGovern et al., 2006). At least in the cases of parasitoids of specialist herbivores, efficient metabolism and/or excretion of plant toxins by these herbivores may reduce significant exposure to plant toxins.

Some of the more spectacular examples of how plant toxins can negatively affect parasitoids are found in herbivores that sequester plant chemicals as defence against their natural enemies. Sequestration — the selective uptake, transport and storage of plant toxins — can result in ‘enemy-free space’ for herbivores, a process well documented for predators (Dyer, 1995; Nishida, 2002) and to a lesser extent for parasitoids (Gauld, Gaston, & Janzen, 1992). Sequestration is a widespread phenomenon, documented in over 250 insect species feeding on plants from over 40 families (Opitz & Müller, 2009). Although it is well established that specialist herbivores are more efficient than generalist ones at metabolizing and/or excreting plant toxins (Lampert et al., 2011; Ratzka, Vogel, Kliebenstein, Mitchell-Olds, & Kroymann, 2002; Wittstock et al., 2004), recent evidence suggests that there are also specialist herbivores among sequestering herbivores, and their efficiency at sequestering plant toxins thereby confers greater protection against parasitoids (Lampert, Dyer, & Bowers, 2014; Züst & Agrawal, 2016). The question of whether narrow host plant range leads to an ability to sequester or, if parasitism/predation pressure selects for this ability are best approached using phylogenetic studies and by gaining a better understanding of the physiological mechanisms of sequestration (Erb & Robert, 2016; Petschenka & Agrawal, 2016). Despite years of study of the ecological significance of sequestration, little is known about how insect herbivores transport, store and release bioactive plant origin defensive compounds (Erb & Robert, 2016).

A few studies have examined the role of sequestration of plant toxins on immune defence against parasitoids (e.g., Lampert, Dyer, & Bowers, 2010; Sime, 2002; Singer, Mace, & Bernays, 2009). For instance, the effects of sequestered chemicals have been assessed by measuring the encapsulation rates (host immune response) of inert silica beads, which have been widely used as proxies for parasitoid eggs. While such studies have provided valuable insight into how plant chemistry is related to herbivore’s immune system (e.g., Quintero, Lampert, & Bowers, 2014; Smilanich, Dyer, Chambers, & Bowers, 2009; Vogelweith, Moreau, Thiéry, & Moret, 2015), parasitoids are much more than inert glass beads (Kaplan et al., 2016). Most parasitoids inject venoms along with their eggs during oviposition, and braconid and ichneumonid parasitoids also inject polydnviruses — both of which are involved in the suppression of host immune responses (Drezen, Chevignon, & Huguet, 2014; Poirié, Colinet, & Gatti, 2014). Therefore, it is important to realize that parasitoids can be expected to evolve in response to changing selective pressures from host plant chemistry and host immune responses.



4. EFFECTS OF NATURAL ENEMIES ON PLANT DEFENCE TRAITS

The preceding sections of this chapter demonstrate the diversity of ways that plant traits, especially those involving antiherbivore chemistry, can influence the fitness of entomophagous insects. Such strong effects of plant traits on parasitoids, in particular, are expected as parasitoids are wholly dependent on their herbivorous hosts, which in turn generally feed on a single host plant. The vast majority of research involving multitrophic interactions has been from a ‘bottom-up’ perspective, focusing on the impact of plant traits on behavioural (e.g., foraging and acceptance decisions) and physiological (e.g., digestion, development) adaptations of carnivorous insects. Far fewer studies have considered top-down influences of entomophagous insects on plant traits. Therefore, the question of whether the presence of natural enemies of insect herbivores enhances plant fitness remains largely unanswered. Hare (2002) put forth several criteria necessary to demonstrate evolution of plant traits in response to entomophagous insects, including the presence of additive genetic variance for a plant trait that increases natural enemy success as well as enhances plant fitness.

Evidence for the potential selective impact of parasitoids on plant fitness remains scarce. On the one hand, the existence of many successful biological control programs against insect herbivores suggests that plant biomass and fruit/seed production is higher in the presence of natural enemies (DeBach & Rosen, 1991; Van den Bosch, 1971; Van Driesche et al., 2008; Williams, Arrendondo-Bernal, & Rodríguez-del-Bosque, 2013). However, it is important to realize that the effects of parasitoids and predators on individual plant fitness are rarely, if ever, measured in biological control, preventing an assessment of whether natural enemies can select for plant traits in such situations (Van der Meijden & Klinkhamer, 2000). A handful of field studies using exclusion cages to prevent parasitism have experimentally demonstrated that the presence of parasitoids can reduce rates of herbivory and increase plant fitness (Gómez & Zamora, 1994; Stiling & Moon, 2005). Similarly, a greenhouse study of *Arabidopsis thaliana* (L.) showed that herbivory by unparasitized *Pieris rapae* (Linnaeus) resulted in decreased lifetime seed production compared to plants attacked by *P. rapae* parasitized by the solitary *Cotesia rubecula* (Marshall, 1885) (Van Loon, De Boer, & Dicke, 2000).

In general, parasitism by solitary parasitoids (a single parasitoid offspring developing in or on a host) results in reduced feeding damage to an individual plant by the herbivore (e.g., Van Loon et al., 2000). However, parasitism

by gregarious parasitoids (multiple parasitoid offspring per host) can result in either decreased or increased herbivory and seed production. This is because in some cases large broods of gregarious parasitoids increase the amount the herbivore eats (Karowe & Schoonhoven, 1992; Smallegange, Van Loon, Blatt, Harvey, & Dicke, 2008). In the case of polyembryonic parasitoids, where brood sizes can exceed 1000 clone mates, feeding damage by parasitized herbivores can be dramatically higher than that by unparasitized herbivores. For example, *Trichoplusia ni* (Hübner, 1803) parasitized by the polyembryonic *Copidosoma floridanum* (Ashmead, 1900) feeds approximately 50% more than unparasitized *T. ni* and induces higher production of the indole glucosinolates when the herbivores feed on wild cabbage *Brassica oleracea* (L.) (Ode et al., 2016). While the effects on plant fitness were not measured by Ode et al. (2016), it is likely that plants attacked by parasitized herbivores suffered decreased fitness as seen in Smallegange et al. (2008). While parasitoids that induce increased consumption by herbivores may, in the short term, harm plant fitness, it is possible that in the long-term plants in populations whose herbivores experience chronic parasitism pressure may benefit. Such an argument has been made in another system involving a polyembryonic species, *C. sosares*, which attacks the parsnip webworm — a specialist herbivore of the wild parsnip *Pastinaca sativa* L. Webworms parasitized by *C. sosares* feed 55% more than unparasitized larvae (McGovern et al., 2006). Nevertheless, parsnip plants in western Europe (where this system is native) experience reduced levels of chronic herbivory and, consequently, invest less in costly furanocoumarin defences compared to plants in eastern North America where herbivory is higher and the parasitoid is absent (Ode et al., 2004).



5. THE PLANT AS FOOD SOURCE

Many members of the third trophic level are not exclusively carnivorous but also consume plant products such as pollen, nectar or honeydew and plant tissue. Use of these plant-produced or plant-derived food sources can be mandatory or optional and occur occasionally during certain phases of insect development, or regularly throughout their life. Among the optional consumers are, for example, species of predatory mites, spiders, bugs or ants and a number of parasitoid species that feed primarily on their hosts (host feeding). Among the mandatory consumers are hoverflies and many species of parasitoids that do not feed on hosts as adult and thus

solely depend on food resources from plants. Plants provide essential food for their survival and ability to forage as well as their ability to mature eggs (see [Jervis & Kidd, 1996](#); or [Wäckers, van Rijn, & Bruin, 2005](#) for reviews). Flowers' visual and olfactory signals can be used by entomophagous insects. Thus, unfed females of the parasitoid *C. rubecula* are particularly attracted to yellow, the most common flower colour ([Weevers, 1952](#)); they are also able to recognize the smell of the flowers ([Wäckers & Lewis, 1999](#)). The different sources of food derived from plants have characteristics that determine their use by entomophagous insects.

5.1 Characteristics and Use of Pollen

Pollen is mainly composed of proteins and free amino acids, but also contains some sterols, lipids and starch ([Wäckers, 2001](#)). Some predators such as ladybirds, adult hoverflies, predatory bugs and mites supplement their diet by consuming pollen ([Wäckers et al., 2005](#)). Although this consumption is less prevalent among parasitoids, some species like *Edovum puttleri* Grissel 1981 and *Pediobius foveolatus* (Crawford, 1912) (Hymenoptera, Eulophidae), parasitoids of beetles, also feed on pollen ([Patt, Hamilton, & Lashomb, 1997](#)). The relative proportion of these elements and their nature differ according to the species, and they influence the development and reproduction of entomophagous insects consuming pollen ([Wäckers et al., 2005](#)). As pollen is produced by insect-pollinated or wind-pollinated plant species, its availability and accessibility varies. In the case of insect-pollinated plants, which actively recruit pollinators, pollen is signalled by the colour or odour of the flower. The pollen itself can also emit odours, which are attractive at short distances ([Dobson & Bergström, 2000](#)).

5.2 Characteristics and Use of Floral Nectar

The nectar produced by flowers, usually in order to attract pollinators, can also be consumed by predators and parasitoids. Like pollen of entomophilous plants, nectar is easily detectable by entomophagous insects. Nectar is a major source of carbohydrates and can also contain amino acids, proteins, lipids and even vitamins. Nectar carbohydrates are mainly fructose, glucose and sucrose. Its consumption has been shown to increase longevity and fecundity of parasitoids ([Araj & Wratten, 2015](#)) and predators ([Robinson, Jonsson, Wratten, Wade, & Buckley, 2008](#)), but some sugars such as raffinose, galactose, mannose or xylose, present even in small quantities, can have negative effects on different life history traits of entomophagous insects ([Wäckers, 2001](#)). Depending on the floral

architecture, accessibility of nectaries often limits the use of this resource, because the mouthparts of many entomophagous insects are short or their head is relatively large. Thus, the parasitoids *E. puttleri* and *P. foveolatu* differ in their ability to use the nectar: the first can only access exposed nectaries, while the second can also access nectaries hidden under petals and stamens (Patt et al., 1997). Their slight difference in size (1.5–2.5 mm vs 2–3.5 mm long, respectively) is sufficient to result in these contrasted abilities. Neither species can, however, access nectaries located at the bottom of tubular flowers.

The availability of floral nectar varies greatly in time and space. It depends particularly on the plant community composition, the phenology of species in these communities and climatic conditions (Brandenburg, Dell’Olivo, Bshary, & Kuhlemeier, 2009). Visiting flowers, whether to search for pollen or nectar, is not without risk. Flowers are indeed hunting sites for other entomophagous arthropods such as crab spiders (Thomisidae).

5.4 Characteristics and Use of Extrafloral Nectar

Flowers are not the only plant organs to carry nectaries; extrafloral nectaries can be found on the leaves, stalks, bracts and fruits of some plants. These nectaries are usually visited by predators and parasitoids, but not by pollinators. Predators using these food resources include ants, mites, lacewings, wasps, beetles and even some species of spiders (Heil, 2015; Wäckers et al., 2005). Extrafloral nectar has several advantages over the floral nectar: it is easy to access (nectaries are apparent and are found on the surface of plant organs that carry them), it is abundant (often much more than floral nectar) and it is available for a very large part of the vegetative growth of plants and not only at the time of flowering. The discovery of extrafloral nectar is however more difficult because nectaries are generally not associated with obvious visual or olfactory cues like in flowers (Belz, Kölliker, & Balmer, 2013). Some nectaries nevertheless emit odours detected at a short distance by parasitoids (Stapel, Cortesero, De Moraes, Tumlinson, & Lewis, 1997) or have special coloration that could help locate them on the plant. The composition of the floral nectar and that of extrafloral nectar is fairly similar: the latter contains sugars (mainly fructose, glucose and sucrose, and sometimes raffinose, galactose, arabinose or xylose), amino acids, lipids and vitamins. Thanks to these nutrients, the oophagous parasitoid *Gryon pennsylvanicum* (Ashmead, 1893) (Hymenoptera, Scelionidae) can live more than 17 days if it consumes the extrafloral nectar of zucchini (*Cucurbita pepo* L. (Cucurbitaceae)), whereas it survives on average 3 days

without food (Olson & Nechols, 1995). Furthermore, parasitoids feeding on zucchini nectar produced three times the eggs as parasitoids that did not feed on nectar. Despite these interesting nutrients, extrafloral nectar does not contain all the elements essential to the diet of entomophagous insects. The low content of essential amino acids can be seen as an adaptation of the plants with extrafloral nectaries, since it encourages predators to seek other sources of protein including herbivorous prey (Wäckers et al., 2005). For example, the production of extrafloral nectar greatly increases levels of predation and parasitism of phytophagous arthropods (Jamont, Crépeillère, & Jaloux, 2013; Rezende, Venzon, Perez, Cardoso, & Janssen, 2014) and is considered as an indirect defence strategy, as well as the emission of volatile compounds attracting entomophagous insects. Moreover, like these volatile compounds, nectar production can be seen as an induced defence, because the attack of the plant by a herbivore increases the secretion of nectar (Fig. 3) (Mathur et al., 2013).

5.5 Characteristics and Use of Honeydew

Even if it is not produced directly by plants, honeydew excreted by the Sternorrhyncha hemipterans, such as aphids, can play an important role in supplying entomophagous insects with sugars produced by plants and normally circulating in the phloem. This diet can be particularly useful outside the flowering periods. In a study on the parasitoids *C. glomerata* and *Microplitis mediator* (Haliday, 1834) (Hymenoptera, Braconidae), 80% and 50% (respectively) of individuals caught in cabbage fields had fed on honeydew (Wäckers & Steppuhn, 2003). The main constraint to feeding on honeydew is its detectability, because producers are generally less visible and fragrant than flowers (Wäckers et al., 2005). In addition, the nutritional quality of this resource seems generally lower than that of nectar (Wäckers, Van Rijn, & Heimpel, 2008). The composition and relative proportions of the various sugars can be modified by the sap-sucking insect. Some honeydews, for example, do not contain any glucose or sucrose (Wäckers, 2001). Honeydew also contains generally more amino acids than does nectar, but they are often nonessential amino acids, essential ones being assimilated by the sap-sucking insects. These differences in nutritional quality can have a significant impact on life history traits of entomophagous insects. For example, the parasitoid *Diadegma insulare* (Cresson, 1865) (Hymenoptera, Ichneumonidae) lives only 6–7 days if fed exclusively honeydew from *Aphis* (*Aphis glycyines* Matsumura, 1917 (Hemiptera, Aphididae) against more than

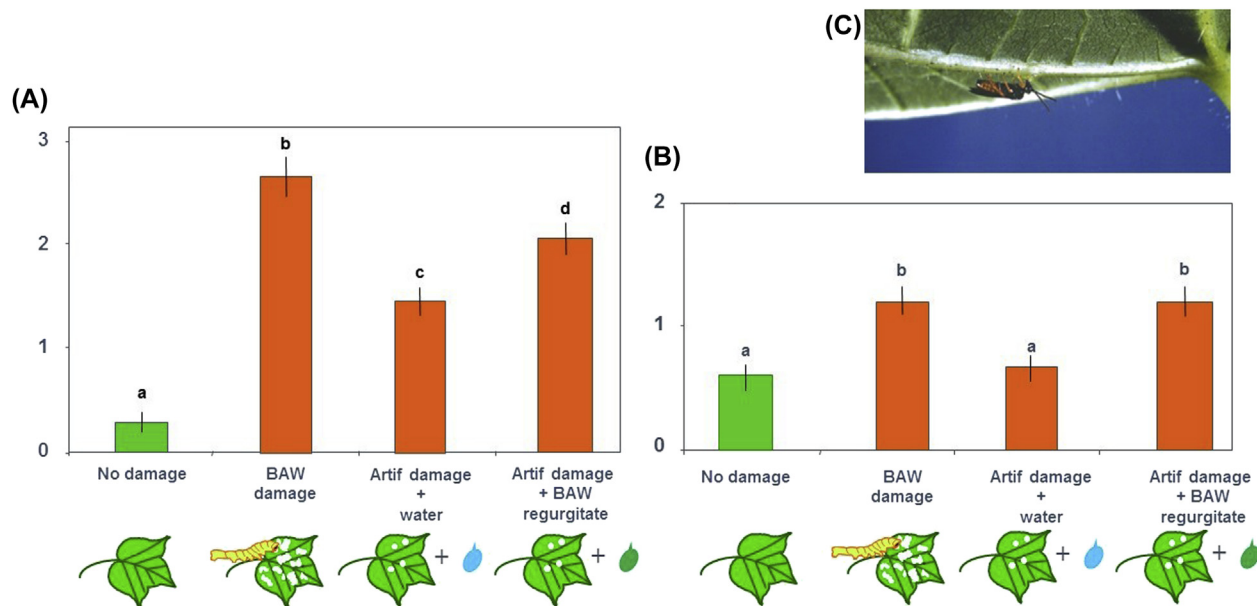


Figure 3 Average amount of extrafloral nectar per plant (+ESM) collected from damaged leaves (A) and undamaged leaves (B) of cotton plants that received *Spodoptera exigua* (BAW) damage, artificial damage + BAW regurgitate, artificial damage + water, and no damage for 7 days. Different letters in bars indicate significant difference in nectar production between treatments (Tukey's Multiple Comparison Test, $P < .05$). (C) The parasitic wasp *Microplitis demolitor* feeding on extrafloral nectar located under a cotton leaf. (A and B) Unpublished data from A.M. Cortesero, J.O. Stapel, F.L. Wäckers, & W.J. Lewis. (C) Photo: A.M. Cortesero.

15 days if fed buckwheat floral nectar (*Fagopyrum esculentum* Moench (Polygonaceae)) (Lee, Heimpel, & Leibe, 2004).



6. THE ROLES OF LOCAL PLANT COMPOSITION AND LANDSCAPE COMPLEXITY ON DIVERSITY, ABUNDANCE AND THERMOTOLERANCE OF ENTOMOPHAGOUS INSECTS

Beyond the influence of characteristics of plant individuals on the third trophic level, entomophagous insect behaviour as well as population and community dynamics is also influenced by the composition of the plant community. At a large scale, plant biomes (such as tropical forest, savanna or boreal forest) harbour different insect communities. Within a biome, the distribution of plants and habitat patches across a landscape is important. Finally, at the smallest scale is the heterogeneity of the foraging environment experienced by an individual foraging insect (Van Nouhuys & Hanski, 2002).

6.1 Insect Communities and Biomes

As for other species, the diversity of natural enemies has been found to be greatest in the tropics. Though the explanation for the latitudinal gradient in species diversity is still unresolved (Brown, 2014), it has been especially well illustrated over the last decade by large-scale barcoding projects revealing the great diversity parasitoids in tropical forests (Smith et al., 2008). These contrast strongly with what is being found in the much less structured high arctic insect community (Wirta et al., 2015). Within a latitudinal zone, there is also variation of natural enemy diversity associated with vegetation type. Hawkins (1994) conducted an extensive literature review to identify the determinants of species diversity and abundance of parasitoids. He found that while herbivore—host feeding niche (e.g., leaf eaters, leaf miners, gall-making insects) was very important, the type of plant (herbs, shrubs, trees) was not. However, larger plants, such as trees, have greater diversity than smaller plants simply because of their size and because their physical architecture provides a variety of habitats for a diversity of herbivores, and consequently a diversity of natural enemies.

6.2 Landscape-Scale Habitat Complexity and Fragmentation

The effects of plants on entomophagous insects on a landscape scale have been primarily approached in two ways: through the roles of landscape

complexity and through the connectivity of suitable habitats in the landscape. These aspects will be more developed in chapter: Plant-Insect Interactions in a Changing World by [Pincebourde et al. \(2016\)](#). The study of how landscape complexity affects entomophagous insects had mostly been driven by the interest in controlling insect pests of agricultural crops ([Tscharntke et al., 2008](#)). A series of studies in which habitat complexity is quantified as the percentage of land devoted to agriculture in a landscape have demonstrated that abundance of herbivorous pests of agricultural crops is generally independent of landscape complexity or increase of landscape simplification (a larger fraction of the land that is agricultural) (reviewed in [Bianchi, Booij, & Tscharntke, 2006](#); [Chaplin-Kramer, O'Rourke, Blitzer, & Kremen, 2011](#)). Entomophagous insects, on the other hand, tend to increase in abundance or diversity ([Gardiner et al., 2009](#)) or rate of parasitism (e.g., [Marino & Landis, 1996](#); [Thies, Steffan-Dewenter, & Tscharntke, 2003](#)) with increasing habitat complexity (a smaller fraction of the land agricultural). This association is stronger for generalist natural enemies than for natural enemies with narrow host ranges ([Chaplin-Kramer et al., 2011](#)). In some cases, the increase in natural enemy diversity with habitat complexity is associated with subsequent increased pest control ([Rusch et al., 2016](#)). The simplest explanation for the overall pattern is that the crop provides a large resource for growth of the herbivore population ([Rand, Waters, Blodgett, Knodel, & Harris, 2014](#)), but that the entomophagous insects benefit from alternate food (both alternate host or prey species and nectar for adult parasitoids) and shelter, so they thrive in a more diverse landscape. There are other more subtle aspects of this pattern that have been explored (see [Marino, Landis, & Hawkins, 2006](#); [Tscharntke et al., 2012](#)).

The role of habitat connectivity in determining the community structure and population dynamics of entomophagous insects has mostly been explored in the context of conservation and habitat degradation due to fragmentation. As suitable habitat becomes fragmented, there is less of it, it becomes inaccessible to species that don't disperse easily between fragments, and the habitat quality tends to decrease as the amount of edge increases. All of these things lead to decreased abundance of individual species and thus decreased species diversity ([Fahrig, 2003](#); [Hanski, 2015](#)). Entomophagous insects experience a more fragmented landscape than do their hosts because the hosts are present in only a fraction of the available habitat. Thus we expect that, like other higher trophic level species, they suffer more from habitat fragmentation than do species at

lower trophic levels (Holt, Lawton, Polis, & Martinez, 1999; Komonen, Penttila, Lindgren, & Hanski, 2000). This has proven to be the case for some parasitoids (Cronin & Reeve, 2005) and predators (Langellotto & Denno, 2004), but it is not universal because generalist natural enemies may use more than one habitat type (Van Nouhuys, 2005). Furthermore, some specialized natural enemies are well adapted to using a host that is spread out in the landscape (reviewed, for parasitoids, in Nair & Van Nouhuys, 2016).

6.3 Local-Scale Plant Heterogeneity

Most entomophagous insects forage at a scale larger than an individual plant, especially if we consider both their juvenile and adult movements. Thus, they must locate prey or hosts on a plant, but they also have to narrow their search to that plant. Heterogeneity at the scale of a patch of plants has generally been found to reduce foraging efficiency of predators (Kareiva, 1987) and parasitoids (Gols et al., 2005; Kruidhof et al., 2015). This can be explained by olfactory cues and associative learning being obscured by surrounding plants and the nonhost herbivores on those plants. Alternatively, the high potential resource concentration of a homogeneous environment may attract entomophagous insects and cause them to stay in the area rather than leaving (Hambäck & Englund, 2005).

Nonetheless, local plant heterogeneity can also be advantageous to entomophagous insects that use more than one type of plant, or type of vegetation. For instance, parasitoids benefit from plants that provide nectar even if no hosts are present (Bianchi & Wäckers, 2008). Both predators and parasitoids might prey on insects that live on a variety of plants, at different times, so a heterogeneous environment may be a more stable resource than a homogeneous one (Tylianakis, Tscharntke, & Klein, 2006). Finally, predators and some parasitoids need an overwintering environment that might be different than their feeding environment. This has been demonstrated in agricultural setting where hedgerows provide overwintering sites for predators (e.g., Gareau, Letourneau, & Shennan, 2013).

6.4 Plant-Made Microclimate and Consequences on the Third Trophic Level

Climate changes such as variations of precipitation and temperature patterns, variation of CO₂, O₃, methane in the atmosphere, can affect the third trophic level by their impact on plant quality, which in turn affect herbivores

and their parasitoids. For example, Yarnes and Boecklen (2006) showed that in warmer, dryer sites, trees exhibit greater seasonal variation in foliar nitrogen which was found to be positively correlated to the parasitism rate on the leaf miners *Phyllonorycter* spp. Calatayud, Polonia, Seligmann, and Bellotti (2002) showed that reducing water supply to cassava plants favoured the growth and development of the mealybug *Phenacoccus herreni* Cox & Williams, 1981 (Sternorrhyncha, Pseudococcidae) and impaired the development of its parasitoids (increased host immune resistance, reduction in the size of the adult parasitoids). The emission of plant volatiles is influenced by air pollution and it can modify their attractiveness for the third trophic level (Blande, Holopainen, & Niinemets, 2014).

In addition to the effects of climate on plant quality and consequences on herbivore parasitism or predation, plants themselves create a microclimate at the local habitat level or at the landscape level, which conditions thermal responses of insects. Air temperature can be several Celsius degrees lower than temperature measured on the leaf surface and inside structures like leaf miner gallery, due to gas exchanges (Pincebourde & Casas, 2006) and light reflection/absorption balance. The temperature pattern on the plant also depends on the interaction with herbivorous insect development, as shown for the Lepidoptera *M. sexta* (Linnaeus, 1763) which increases leaf temperature relative to air depending on larval instars (Woods, 2013). Vegetation cover offers a microclimate which can buffer atmospheric variations depending on plant height, density, architecture and colour, and benefits the plant dwelling insects, whatever their trophic level (Suh, Orr, Van Duyn, & Borchert, 2002; see Pumarino et al., 2015 for a review in agroforestry). Thermal refuges created by plants could play a growing role in increasing the resilience of the ecosystem to climate changes (increase of extreme climatic events such as heat or cold waves, Easterling et al., 2000, 1997; IPCC, 2013; Karl, Knight, & Baker, 2000, Walther et al., 2002), and allowing some individuals to escape thermal stresses.

The structure of the vegetation can create microclimates at the landscape scale that can affect the thermotolerance of phytophagous insects and their natural enemies (Tougeron, Van Baaren, Burel, & Alford, 2016). This latter case is detailed below.

Several studies have shown that vegetation structure can affect microclimates at the landscape level. For example, the role of hedges as windbreaks and in reducing freezing has been widely confirmed in agricultural landscapes. There is also evidence that the mean temperature and extreme temperatures in wooded and open areas differ over both daily

and season scales (Argent, 1992; Chen et al., 1999; Quénot & Beltrando, 2006). Few studies have investigated the effects of landscape structure on thermal tolerance of ectotherms such as entomophagous insects, which are highly dependent on the external temperature to ensure their biological functions. Their maintenance in the environment and their resistance to unfavourable temperatures are ensured by their physiological capacity of thermal tolerance. In an agricultural environment in Britain, Tougeron et al. (2016) investigated the effects of the landscape structure and composition on thermal tolerance of three groups of insects: aphids, their natural enemies (braconid parasitic wasps) and carabid beetles. Individuals were sampled along a gradient of landscape complexity and their physiological thermotolerance was measured according to the experimental design of Powell and Bale (2006). For the collected braconids, insects originating from open landscapes were more thermotolerant than those collected in woody landscapes, regardless of their species (Fig. 4). This landscape effect was however not found in aphids or carabids, for which the behavioural thermoregulation was invoked: carabids can indeed buffer the effects of thermal stress using their mobility to find shelters in different parts of their habitats, and aphids can resist to cold temperatures thanks to their ability to stay on their host plant (Alford, Andrade, Georges, Burel, & Van Baaren, 2014). These studies showed that landscape structure could impact the

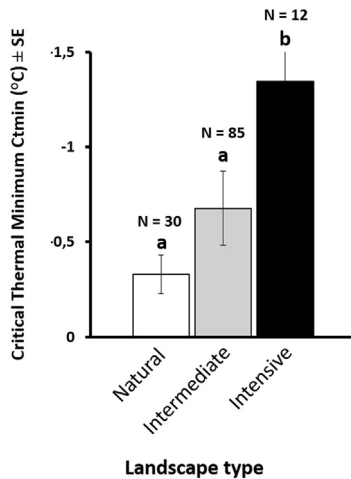


Figure 4 Average critical thermal minimum of braconid parasitoids of aphids in winter, depending on the type of landscape, ($Ctmin \pm$ standard error). The number of individuals tested is given for each category. The letters show significant differences between landscapes ($\alpha = 0.05$).

thermotolerance of some ectotherm species but not all, depending on their behavioural thermoregulation capacities. It suggests that landscape management could be used to favour some species to increase ecosystem services.



7. CONCLUSION

This chapter has given an overview of the multiple ways, biological processes and scales at which entomophagous insects interact with the plants of their herbivorous hosts or prey, and more widely with the vegetal community they live in. In conclusion, we would like to point out recent focuses and emerging approaches that will contribute to innovative management of natural enemies.

There is a complex food web centred on the plant and current researches investigate biochemical and population functioning of trophic networks between plants, herbivorous, primary and secondary entomophagous insects and pathogens as well as symbionts microorganisms. Identification of plant quality changes in response to interacting plant-dwelling organisms is important for understanding the outcome on fitness components of natural enemies like odour-guided host selection and development (Pashalidou et al., 2015). Studies of multitrophic interactions are called for in the context of sustainable agriculture. They can use high-throughput technologies for exhaustive identification of molecular changes at play during these trophic interactions. Such knowledge encompassing ecological and molecular aspects facilitates the possibility of our breeding plants for traits beneficial to entomophagous insects.

Increasing researches consider how plant communities, their spatio-temporal landscape and surrounding micro- and macro-climates condition the abundance and diversity of natural enemies' communities. These studies benefit from improving tools and methods to acquire and manage big data sets and from current progress in mathematical modelling. Ability to develop scenarios that depend on multiple environmental factors will help manage agricultural landscapes and forest habitats for efficient conservation of biological control and maintenance of ecosystem services. Including species' genetic diversity data in the models will help to simulate spatially explicit eco-evolutionary dynamics in complex food webs (Moya-Larano, 2011).

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REFERENCES

- Afshen, S., Wang, X., Li, R., Zhu, C.-S., & Lou, Y.-G. (2008). Differential attraction of parasitoids in relation to specificity of kairomones from herbivores and their by-products. *Insect Science*, *15*, 381–397.
- Agrawal, A. (2000a). Mechanisms, ecological consequences and agricultural implications of tri-trophic interactions. *Current Opinion in Plant Biology*, *3*, 329–335.
- Agrawal, A. A. (2000b). Benefits and costs of induced plant defense for *Lepidium virginicum* (Brassicaceae). *Ecology*, *81*, 1804–1813.
- Agrawal, A. A., Karban, R., & Colfer, R. G. (2000). How leaf domatia and induced plant resistance affect herbivores, natural enemies and plant performance. *Oikos*, *89*, 70–80.
- Alford, L., Andrade, T. O., Georges, R., Burel, F., & Van Baaren, J. (2014). Could behaviour and not physiological thermal tolerance determine winter survival of aphids in cereal fields? *PLoS One*, *9*, e114982.
- Al-Zyoud, F., Tort, N., & Sengonca, C. (2005). Influence of host plant species on *Bemisia tabaci* (Genn.) (Hom., Aleyrodidae) on some of the biological and ecological characteristics of the entomophagous *Serangium parcesetosum* Sicard (Col., Coccinellidae). *Journal of Pest Science*, *78*, 25–30.
- Appel, H. M., Maqbool, S. B., Raina, S., Jagadeeswaran, G., Acharya, B. R., Hanley, J. C., Jr., ... Schultz, J. C. (2014). Transcriptional and metabolic signatures of *Arabidopsis* responses to chewing damage by an insect herbivore and bacterial infection and the consequences of their interaction. *Frontiers in Plant Science*, *5*, 441.
- Araj, S. E., & Wratten, S. D. (2015). Comparing existing weeds and commonly used insectary plants as floral resources for a parasitoid. *Biological Control*, *81*, 15–20.
- Argent, R. M. (1992). The influence of a plant canopy on shelter effect. *Journal of Wind Engineering and Industrial Aerodynamics*, *44*, 2643–2653.
- Baeder, J. M., & King, B. H. (2004). Associative learning of color by males of the parasitoid wasp *Nasonia vitripennis* (Hymenoptera: Pteromalidae). *Journal of Insect Behavior*, *17*, 201–213.
- Barbosa, P., Gross, P., & Kemper, J. (1991). Influence of plant allelochemicals on the tobacco hornworm and its parasitoid *Cotesia congregata*. *Ecology*, *72*, 1567–1575.
- Barbosa, P., Saunders, J. A., Kemper, J., Trumbule, R., Olechno, J., & Martinat, P. (1986). Plant allelochemicals and insect parasitoids: Effects of nicotine on *Cotesia congregata* (Say) (Hymenoptera: Braconidae) and *Hyposoter annulipes* (Cresson) (Hymenoptera: Ichneumonidae). *Journal of Chemical Ecology*, *12*, 1319–1328.
- Barron, A. B. (2001). The life and death of Hopkins' host-selection principle. *Journal of Insect Behavior*, *14*, 725–737.
- Belz, E., Kölliker, M., & Balmer, O. (2013). Olfactory attractiveness of flowering plants to the parasitoid *Microplitis mediator*: potential implications for biological control. *BioControl*, *58*, 163–173.
- Benelli, G., & Canale, A. (2012). Learning of visual cues in the fruit fly parasitoid *Psytallia concolor* (Szepligetü) (Hymenoptera: Braconidae). *BioControl*, *57*, 767–777.
- Bianchi, F. J. A., Booij, C. J. H., & Tscharntke, T. (2006). Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 1715–1727.

- Bianchi, F. J. J. A., & Wäckers, F. L. (2008). Effects of flower attractiveness and nectar availability in field margins on biological control by parasitoids. *Biological Control*, *46*, 400–408.
- Blande, J. D., Holopainen, J. K., & Niinemets, U. (2014). Plant volatiles in polluted atmospheres: Stress responses and signal degradation. *Plant Cell and Environment*, *37*, 1892–1904.
- Bottrell, D. G., Barbosa, P., & Gould, F. (1998). Manipulating natural enemies by plant variety selection and modification: A realistic strategy? *Annual Review of Entomology*, *43*, 347–367.
- Braasch, J., & Kaplan, I. (2012). Over what distance are plant volatiles bioactive? Estimating the spatial dimensions of attraction in an arthropod assemblage. *Entomologia Experimentalis et Applicata*, *145*, 115–123.
- Brandenburg, A., Dell’Olive, A., Bshary, R., & Kuhlmeier, C. (2009). The sweetest thing: advances in nectar research. *Current Opinion in Plant Biology*, *12*, 486–490.
- Brown, J. H. (2014). Why are there so many species in the tropics? *Journal of Biogeography*, *41*, 8–22.
- Calatayud, P.-A., Polonia, M. A., Seligmann, C. D., & Bellotti, A. C. (2002). Influences of water-stressed cassava on *Phenacoccus herenii* and their associated parasitoids. *Entomologia Experimentalis et Applicata*, *102*, 163–175.
- Campbell, B. C., & Duffey, S. S. (1979). Tomatine and parasitic wasps: Potential incompatibility of plant antibiosis with biological control. *Science*, *205*, 700–702.
- Canale, A., Geri, S., & Benelli, G. (2014). Associative learning for host-induced fruit volatiles in *Psytthalia concolor* (Hymenoptera: Braconidae), a koinobiont parasitoid of tephritid flies. *Bulletin of Entomological Research*, *104*, 774–780.
- Carroll, M. J., Schmelz, E. A., Meagher, R. L., & Teal, P. E. (2006). Attraction of *Spodoptera frugiperda* larvae to volatiles from herbivore-damaged maize seedlings. *Journal of Chemical Ecology*, *32*, 1911–1924.
- Casas, J., & Djemai, I. (2002). Plant canopy architecture and multitrophic interactions. In T. Tschamtkke, & B. A. Hawkins (Eds.), *Multitrophic level interactions*. Cambridge, UK: Cambridge University Press.
- Chaplin-Kramer, R., O’Rourke, M. E., Blitzer, E. J., & Kremen, C. (2011). A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters*, *14*, 922–932.
- Chen, J. Q., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosfoske, K. D., Mroz, G. D., ... Franklin, J. F. (1999). Microclimate in forest ecosystem and landscape ecology – Variations in local climate can be used to monitor and compare the effects of different management regimes. *Bioscience*, *49*, 288–297.
- Colazza, S., Fucarino, A., Peri, E., Salerno, G., Conti, E., & Bin, F. (2004). Insect oviposition induces volatile emission in herbaceous plants that attracts egg parasitoids. *Journal of Experimental Biology*, *207*, 47–53.
- Colazza, S., Salemo, G., & Wajnberg, E. (1999). Volatile and contact chemicals released by *Nezara viridula* (Heteroptera: Pentatomidae) have a kairomonal effect on the egg parasitoid *Trissolcus basalus* (Hymenoptera: Scelionidae). *Biological Control*, *16*, 310–317.
- Conti, E., Salemo, G., Bin, F., Williams, H. J., & Vinson, S. B. (2003). Chemical cues from *Murgantia histrionica* eliciting host location and recognition in the egg parasitoid *Trissolcus brochymenae*. *Journal of Chemical Ecology*, *29*, 115–130.
- Cronin, J. T., & Reeve, J. D. (2005). Host parasitoid spatial ecology: A plea for a landscape-level synthesis. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 2225–2235.
- Cusumano, A., Weldegergis, B. T., Colazza, S., Dicke, M., & Fatouros, N. E. (2015). Attraction of egg-killing parasitoids toward induced plant volatiles in a multi-herbivore context. *Oecologia*, *179*, 163–174.

- Danci, A., Hrabar, M., Ikoma, S., Schaefer, P. W., & Gries, G. (2013). Learning provides mating opportunities for males of a parasitoid wasp. *Entomologia Experimentalis et Applicata*, *149*, 229–240.
- De Boer, J. G., & Dicke, M. (2006). Olfactory learning by predatory arthropods. *Animal Biology*, *56*, 143–155.
- De Rijk, M., Dicke, M., & Poelman, E. H. (2013). Foraging behaviour by parasitoids in multiherbivore communities. *Animal Behaviour*, *85*, 1517–1528.
- DeBach, P., & Rosen, D. (1991). *Biological control by natural enemies* (2nd ed.). Cambridge, UK: Cambridge University Press, 456 pp.
- Desurmont, G. A., Xu, H., & Turlings, T. C. (2016). Powdery mildew suppresses herbivore-induced plant volatiles and interferes with parasitoid attraction in *Brassica rapa*. *New Phytologist*, *210*, 1344–1356.
- Dicke, M. (2016). Induced plant volatiles: Plant body odours structuring ecological networks. *New Phytologist*, *210*, 10–12.
- Dicke, M., & Baldwin, I. T. (2010). The evolutionary context for herbivore-induced plant volatiles: beyond the “cry for help”. *Trends in Plant Science*, *15*, 167–175.
- Dicke, M., & Sabelis, M. W. (1988). Infochemicals terminology: based on cost-benefit analysis rather than origin of compounds? *Functional Ecology*, *2*, 131–139.
- Dicke, M., Sabelis, M. W., & De Jong, M. (1988). Analysis of prey preference in phytoseiid mites by using an olfactometer, predation models and electrophoresis. *Experimental & Applied Acarology*, *5*, 225–241.
- Dobson, H. E. M., & Bergström, G. (2000). Ecology and evolution of pollen odors. In A. Dafni, M. Hesse, & E. Pacini (Eds.), *Pollen and pollination*. Vienna, Autriche: Springer.
- Drezen, J.-M., Chevignon, G., & Huguet, L. F. (2014). Origin and evolution of symbiotic viruses associated with parasitoid wasps. *Current Opinion in Insect Science*, *6*, 35–43.
- Dyer, L. A. (1995). Tasty generalists and nasty specialists? Antipredator mechanisms in tropical lepidopteran larvae. *Ecology*, *76*, 1483–1496.
- Easterling, D. R., Evans, J. L., Groisman, P. Y., Karl, T. R., Kunkel, K. E., & Ambenje, P. (2000). Observed variability and trends in extreme climate events: A brief review. *Bulletin of the American Meteorological Society*, *81*, 417–425.
- Easterling, D. R., Horton, B., Jones, P. D., Peterson, T. C., Karl, T. R., Parker, D. E., ... Folland, C. K. (1997). Maximum and minimum temperature trends for the globe. *Science*, *277*, 364–367.
- Erb, M., & Robert, C. A. M. (2016). Sequestration of plant secondary metabolites by insect herbivores: molecular mechanisms and ecological consequences. *Current Opinion in Insect Science*, *14*, 8–11.
- Erb, M., Robert, C. A. M., Hibbard, B. E., & Turlings, T. C. J. (2011). Sequence of arrival determines plant-mediated interactions between herbivores. *Journal of Ecology*, *99*, 7–15.
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics*, *34*, 487–515.
- Farahani, H. K., Ashouri, A., Goldansaz, S. H., Shapiro, M. S., Pierre, J. S., & Van Baaren, J. (2016). Decrease of memory retention in a parasitic wasp: an effect of host manipulation by *Wolbachia*? *Insect Science* (in press).
- Gandolfi, M., Mattiacci, L., & Dorn, S. (2003). Preimaginal learning determines adult response to chemical stimuli in a parasitic wasp. *Proceedings of the Royal Society B: Biological Sciences*, *270*, 2623–2629.
- Gardiner, M. M., Landis, D. A., Gratton, C., DiFonzo, C. D., O’Neal, M., Chacon, J. M., ... Heimpel, G. E. (2009). Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. *Ecological Applications*, *19*, 143–154.
- Gareau, T. L., Letourneau, D. K., & Shennan, C. (2013). Relative densities of natural enemy and pest insects within California hedgerows. *Environmental Entomology*, *42*, 688–702.

- Gauld, I. D., & Bolton, B. (1988). *The Hymenoptera*. Oxford, GB: Oxford University Press, 332 pp.
- Gauld, I. D., Gaston, K. J., & Janzen, D. H. (1992). Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the “nasty” host hypothesis. *Oikos*, *65*, 353–357.
- Geervliet, J. B. F., Ariens, S., Dicke, M., & Vet, L. E. M. (1998). Long-distance assessment of patch profitability through volatile infochemicals by the parasitoids *Cotesia glomerata* and *C. rubecula* (Hymenoptera: Braconidae). *Biological Control*, *11*, 113–121.
- Geervliet, J. B. F., Vreugdenhil, A. I., Dicke, M., & Vet, L. E. M. (1998). Learning to discriminate between infochemicals from different plant–host complexes by the parasitoids *Cotesia glomerata* and *C. rubecula*. *Entomologia Experimentalis et Applicata*, *86*, 241–252.
- Gish, M., De Moraes, C. M., & Mescher, M. C. (2015). Herbivore-induced plant volatiles in natural and agricultural ecosystems: open questions and future prospects. *Current Opinion in Insect Science*, *9*, 1–6.
- Giunti, G., Canale, A., Messing, R. H., Donati, E., Stefanini, C., Michaud, J. P., & Benelli, G. (2015). Parasitoid learning: current knowledge and implications for biological control. *Biological Control*, *90*, 208–219.
- Godfray, H. C. J. (1994). In J. R. Krebs, & T. Clutton-Brock (Eds.), *Parasitoids: Behavioral and evolutionary ecology*. Princeton, USA: Princeton University Press, 473 pp.
- Gols, R., Bukovinszky, T., Hemerik, L., Harvey, J. A., Van Lenteren, J. C., & Vet, L. E. M. (2005). Reduced foraging efficiency of a parasitoid under habitat complexity: Implications for population stability and species coexistence. *Journal of Animal Ecology*, *74*, 1059–1068.
- Gols, R., Van Dam, N. M., Raaijmakers, C. E., Dicke, M., & Harvey, J. A. (2009). Are population differences in plant quality reflected in the preference and performance of two endoparasitoid wasps? *Oikos*, *118*, 733–743.
- Gómez, J. M., & Zamora, R. (1994). Top-down effects in a tritrophic system: Parasitoids enhance plant fitness. *Ecology*, *75*, 1023–1030.
- Hambäck, P. A., & Englund, G. (2005). Patch area, population density and the scaling of migration rates: the resource concentration hypothesis revisited. *Ecology Letters*, *8*, 1057–1065.
- Hanski, I. (2015). Habitat fragmentation and species richness. *Journal of Biogeography*, *42*, 989–993.
- Hare, J. D. (2002). Plant genetic variation in tritrophic interactions. In T. Tschamtké, & B. A. Hawkins (Eds.), *Multitrophic level interactions* (pp. 8–43). Cambridge, UK: Cambridge University Press.
- Hare, J. D. (2011). Ecological role of volatiles produced by plants in response to damage by herbivorous insects. In M. R. Berenbaum, R. T. Cardé, & G. E. Robinson (Eds.), *Annual review of entomology* (Vol. 56, pp. 161–180).
- Harvey, J. A. (2005). Factors affecting the evolution of development strategies in parasitoid wasps: The importance of functional constraints and incorporating complexity. *Entomologia Experimentalis et Applicata*, *117*, 1–13.
- Harvey, J. A., & Gols, R. (2011). Population-related variation in plant defense more strongly affects survival of an herbivore than its solitary parasitoid wasp. *Journal of Chemical Ecology*, *37*, 1081–1090.
- Hawkins, B. A. (1994). *Pattern and process in host-parasitoid interactions*. Cambridge: Cambridge University Press, 190 pp.
- Heil, M. (2008). Indirect defence via tritrophic interactions. *New Phytologist*, *178*, 41–61.
- Heil, M. (2015). Extrafloral nectar at the plant–insect interface: A spotlight on chemical ecology, phenotypic plasticity, and food webs. *Annual Review of Entomology*, *60*, 213–232.

- Heil, M., & Karban, R. (2010). Explaining evolution of plant communication by airborne signals. *Trends in Ecology & Evolution*, *25*, 137–144.
- Heinz, K. M., & Parella, M. P. (1994). Poinsettia (*Euphorbia pulcherrima* Willd. Ex Koltz.) cultivar-mediated differences in performance of five natural enemies of *Bemisia argentifolii* Bellows and Perring, n. sp. (Homoptera: Aleyrodidae). *Biological Control*, *4*, 305–318.
- Hilker, M., & Fatouros, N. E. (2015). Plant responses to insect egg deposition. *Annual Review of Entomology*, *60*, 493–515.
- Holt, R. D., Lawton, J. H., Polis, G. A., & Martinez, N. D. (1999). Trophic rank and the species-area relationship. *Ecology*, *80*, 1495–1504.
- Hunter, M. D. (2003). Effects of plant quality on the population ecology of parasitoids. *Agricultural and Forest Entomology*, *5*, 1–8.
- Inbar, M., & Gerling, D. (2008). Plant-mediated interactions between whiteflies, herbivores, and natural enemies. *Annual Review of Entomology*, *53*, 431–448.
- IPCC. (2013). In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, et al. (Eds.), *Climate change 2013: The physical science basis: Final draft underlying scientific-technical assessment: Working group I contribution to the IPCC fifth assessment report*. Cambridge, UK and New York: Cambridge University Press, 1535 pp. (Summary for Policymakers, 28 pp.).
- Jaloux, B. (2004). *La discrimination interspécifique par Eupelmus vuillei (Hymenoptera: Eupelmidae) des hôtes parasites par Dinarmus basalis (Hymenoptera: Pteromalidae)* (PhD thesis). Univ. François Rabelais, Tours. <https://tel.archives-ouvertes.fr/tel-001108221> (HAL Id: tel-001108221).
- Jamont, M., Crépeillère, S., & Jaloux, B. (2013). Effect of extrafloral nectar provisioning on the performance of the adult parasitoid *Diaeretiella rapae*. *Biological Control*, *65*, 271–277.
- Jervis, M., & Kidd, N. (1996). Phytophagy. In M. Jervis, & N. Kidd (Eds.), *Insect natural enemies. Practical approaches to their study and evaluation*. London, UK: Chapman & Hall.
- Kaiser, L., Couty, A., & Cortesero, A.-M. (2013). La plante, un biotope de choix pour les entomophages (QUAE-IRD. Chap. 31). In N. Sauvion, P.-A. Calatayud, D. Thiery, & F. Marion-Poll (Eds.), *Des insectes et des plantes* (pp. 513–536).
- Kaiser, L., Perez-Maluf, R., Sandoz, J. C., & Pham-Delegue, M. H. (2003). Dynamics of odour learning in *Leptopilina boulardi*, a hymenopterous parasitoid. *Animal Behaviour*, *66*, 1077–1084.
- Kaplan, I. (2012a). Attracting carnivorous arthropods with plant volatiles: the future of biocontrol or playing with fire? *Biological Control*, *60*, 77–89.
- Kaplan, I. (2012b). Trophic complexity and the adaptive value of damage-induced plant volatiles. *PLoS Biology*, *10*(11), e1001437.
- Kaplan, I., Carrillo, J., Garvey, M., & Ode, P. J. (2016). Indirect plant-parasitoid interactions mediated by changes in herbivore physiology. *Current Opinion in Insect Science*, *14*, 112–119.
- Kareiva, P. (1987). Habitat fragmentation and the stability of predator-prey interactions. *Nature*, *326*, 388–390.
- Karl, T. R., Knight, R. W., & Baker, B. (2000). The record breaking global temperatures of 1997 and 1998: Evidence for an increase in the rate of global warming? *Geophysical Research Letters*, *27*, 719–722.
- Karowe, D. N., & Schoonhoven, L. M. (1992). Interactions among three trophic levels: the influence of host plant on performance of *Pieris brassicae* and its parasitoid, *Cotesia glomerata*. *Entomologia Experimentalis et Applicata*, *62*, 241–251.
- Kessler, A., Halitschke, R., & Baldwin, I. T. (2004). Silencing the jasmonate cascade: induced plant defenses and insect populations. *Science*, *305*, 665–668.
- Kester, K. M., & Barbosa, P. (1991). Postemergence learning in the insect parasitoid, *Cotesia congregata* (Say) (Hymenoptera: Braconidae). *Journal of Insect Behavior*, *4*, 727–742.

- Kimani-Njogu, S. W., & Overholt, W. A. (1997). Biosystematics of the *Cotesia flavipes* species complex (Hymenoptera: Braconidae), parasitoids of the gramineous stemborers. *Insect Science and Its Application*, *17*, 119–130.
- Komonen, A., Penttila, R., Lindgren, M., & Hanski, I. (2000). Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos*, *90*, 119–126.
- Koppik, M., Hoffmeister, T. S., Brunkhorst, S., Kiess, M., & Thiel, A. (2015). Intraspecific variability in associative learning in the parasitic wasp *Nasonia vitripennis*. *Animal Cognition*, *18*, 593–604.
- Kruidhof, H. M., Pashalidou, F. G., Fatouros, N. E., Figueroa, I. A., Vet, L. E. M., Smid, H. M., & Huigens, M. E. (2012). Reward value determines memory consolidation in parasitic wasps. *PLoS One*, *7*(8), e39615.
- Kruidhof, H. M., Roberts, A. L., Magdaraog, P., Munoz, D., Gols, R., Vet, L. E. M., ... Harvey, J. A. (2015). Habitat complexity reduces parasitoid foraging efficiency, but does not prevent orientation towards learned host plant odours. *Oecologia*, *179*, 353–361.
- Kruidhof, H. M., Smid, H., Thiel, A., Hoffmeister, T. S., & Vet, L. E. M. (2014). Olfactory conditioning of natural enemies: potential benefits for pest control in greenhouse crops. *IOBC-WPRS Bulletin*, *102*, 121–126.
- Lampert, E. C., Dyer, L. A., & Bowers, M. D. (2010). Caterpillar chemical defense and parasitoid success: *Cotesia congregata* parasitism of *Ceratonia catalpae*. *Journal of Chemical Ecology*, *36*, 992–998.
- Lampert, E. C., Dyer, L. A., & Bowers, M. D. (2014). Dietary specialization and the effects of plant species on potential multitrophic interactions of three species of nymphaline caterpillars. *Entomologia Experimentalis et Applicata*, *153*, 207–216.
- Lampert, E. C., Zangerl, A. R., Berenbaum, M. R., & Ode, P. J. (2008). Tritrophic effects of xanthotoxin on the polyembryonic parasitoid *Copidosoma sosares* (Hymenoptera: Encyrtidae). *Journal of Chemical Ecology*, *34*, 783–790.
- Lampert, E. C., Zangerl, A. R., Berenbaum, M. R., & Ode, P. J. (2011). Generalist and specialist host-parasitoid associations respond differently to wild parsnip (*Pastinaca sativa*) defensive chemistry. *Ecological Entomology*, *36*, 52–61.
- Langellotto, G. A., & Denno, R. F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. *Oecologia*, *139*, 1–10.
- Lee, J. C., Heimpel, G. E., & Leibe, G. L. (2004). Comparing floral nectar and aphid honeydew diets on the longevity and nutrient levels of a parasitoid wasp. *Entomologia Experimentalis et Applicata*, *111*, 189–199.
- Lucchetta, P., Bernstein, C., Thery, M., Lazzari, C., & Desouhant, E. (2008). Foraging and associative learning of visual signals in a parasitic wasp. *Animal Cognition*, *11*, 525–533.
- Luo, S. P., Michaud, J. P., Li, J. C., Liu, X. X., & Zhang, Q. W. (2013). Odor learning in *Microplitis mediator* (Hymenoptera: Braconidae) is mediated by sugar type and physiological state. *Biological Control*, *65*, 207–211.
- Marino, P. C., & Landis, D. A. (1996). Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecological Applications*, *6*, 276–284.
- Marino, P. C., Landis, D. A., & Hawkins, B. A. (2006). Conserving parasitoid assemblages of North American pest Lepidoptera: Does biological control by native parasitoids depend on landscape complexity? *Biological Control*, *37*, 173–185.
- Mathur, V., Wagenaar, R., Caissard, J. C., Reddy, A. S., Vet, L. E., Cortesero, A. M., & Van Dam, N. M. (2013). A novel indirect defense in Brassicaceae: Structure and function of extrafloral nectaries in *Brassica juncea*. *Plant, Cell and Environment*, *36*, 528–541.
- McAuslane, H. J., Simmons, A. M., & Jackson, D. M. (2000). Parasitism of *Bemisia argentifolii* on collard with reduced or normal leaf wax. *Florida Entomologist*, *83*, 428–437.

- McCormick, A. C., Unsicker, S. B., & Gershenson, J. (2012). The specificity of herbivore-induced plant volatiles in attracting herbivore enemies. *Trends in Plant Science*, *17*, 303–310.
- McGovern, J. L., Zangerl, A. R., Ode, P. J., & Berenbaum, M. R. (2006). Furanocoumarins and their detoxification in a tri-trophic interaction. *Chemoecology*, *16*, 45–50.
- Meiners, T., & Hilker, M. (2000). Induction of plant synomones by oviposition of a phytophagous insect. *Journal of Chemical Ecology*, *26*, 221–232.
- Meiners, T., & Peri, E. (2013). Chemical ecology of insect parasitoids: Essential elements for developing effective biological control programmes. In E. Wajnberg, & S. Colazza (Eds.), *Chemical ecology of insect parasitoids* (pp. 191–224). Chichester, UK: John Wiley & Sons, Ltd.
- Mery, F. (2013). Natural variation in learning and memory. *Current Opinion in Neurobiology*, *23*, 52–56.
- Mooney, K. A., & Singer, M. S. (2012). Plant effects on herbivore–enemy interactions in natural systems. In T. Ohgushi, O. Schmitz, & R. D. Holt (Eds.), *Trait-mediated indirect interactions: Ecological and evolutionary perspectives* (pp. 107–130). Cambridge, UK: Cambridge University Press.
- Moujahed, R., Frati, F., Cusumano, A., Salerno, G., Conti, E., Peri, E., & Colazza, S. (2014). Egg parasitoid attraction toward induced plant volatiles is disrupted by a non-host herbivore attacking above or belowground plant organs. *Frontiers in Plant Science*, *5*, 601.
- Moya-Larano, J. (2011). Genetic variation, predator–prey interactions and food web structure. *Philosophical Transactions of the Royal Society of London, Series B*, *366*, 1425–1437.
- Mumm, R., & Dicke, M. (2010). Variation in natural plant products and the attraction of bodyguards involved in indirect plant defense. *Canadian Journal of Zoology*, *88*, 628–667.
- Nair, A., & Van Nouhuys, S. (2016). Spatial and temporal genetic structure at the fourth trophic level in a fragmented landscape. *Proceedings of the Royal Society B: Biological Sciences*, *283*.
- Ngumbi, E., Jordan, M., & Fadamiro, H. (2012). Comparison of associative learning of host-related plant volatiles in two parasitoids with different degrees of host specificity, *Cotesia marginiventris* and *Microplitis croceipes*. *Chemoecology*, *22*, 207–215.
- Nishida, R. (2002). Sequestration of defensive substances from plants by *Lepidoptera*. *Annual Review of Entomology*, *47*, 57–92.
- Nordlund, D. A., Jones, R. L., & Lewis, W. J. (1981). *Semiochemicals: Their role in pest control*. New York, USA: John Wiley.
- Nordlund, D. A., & Lewis, W. J. (1976). Terminology of chemical releasing stimuli in intra-specific and interspecific interactions. *Journal of Chemical Ecology*, *2*, 211–220.
- Ode, P. J. (2006). Plant chemistry and natural enemy fitness: Effects on herbivore and natural enemy interactions. *Annual Review of Entomology*, *51*, 163–185.
- Ode, P. J. (2013). Plant defences and parasitoid chemical ecology. In E. Wajnberg, & S. Colazza (Eds.), *Chemical ecology of insect parasitoids* (pp. 11–36). West Sussex, UK: Wiley-Blackwell.
- Ode, P. J., Berenbaum, M. R., Zangerl, A. R., & Hardy, I. C. W. (2004). Host plant, host plant chemistry and the polyembryonic parasitoid *Copidosoma sosares*: Indirect effects in a tritrophic interaction. *Oikos*, *104*, 388–400.
- Ode, P. J., Harvey, J. A., Reichelt, M., Gershenson, J., & Gols, R. (2016). Differential induction of plant chemical defenses by parasitized and unparasitized herbivores: consequences for reciprocal, multitrophic interactions. *Oikos*, *125*, 1398–1407.
- O'Dowd, D. J., & Willson, M. F. (1991). Associations between mites and leaf domatia. *Trends in Ecology & Evolution*, *6*, 179–182.
- Oliai, S. E., & King, B. H. (2000). Associative learning in response to color in the parasitoid wasp *Nasonia vitripennis* (Hymenoptera: Pteromalidae). *Journal of Insect Behavior*, *13*, 55–69.

- Olson, D. L., & Nechols, J. R. (1995). Effect of squash leaf trichome exudate and honey on adult feeding, survival, and fecundity of the squash bug (Heteroptera: Coreidae) egg parasitoid *Gryon pennsylvanicum* (Hymenoptera: Scelionidae). *Biological Control*, *24*, 454–458.
- Opitz, S. W., & Müller, C. (2009). Plant chemistry and insect sequestration. *Chemoecology*, *19*, 117–154.
- Papaj, D. R., Snellen, H., Swaans, K., & Vet, L. E. M. (1994). Unrewarding experiences and their effect on foraging in the parasitic wasp *Leptopilina heterotoma* (Hymenoptera: Eucolidae). *Journal of Insect Behavior*, *7*, 465–481.
- Papaj, D. R., & Vet, L. E. M. (1990). Odor learning and foraging success in the parasitoid, *Leptopilina heterotoma*. *Journal of Chemical Ecology*, *16*, 3137–3150.
- Pashalidou, F. G., Frago, E., Griese, E., Poelman, E. H., Van Loon, J. J. A., Dicke, M., & Fatouros, N. E. (2015). Early herbivore alert matters: Plant-mediated effects of egg deposition on higher trophic levels benefit plant fitness. *Ecology Letters*, *18*, 927–936.
- Patt, J. M., Hamilton, G. C., & Lashomb, J. H. (1997). Foraging success of parasitoid wasps on flowers: Interplay of insect morphology, floral architecture and searching behavior. *Entomologia Experimentalis et Applicata*, *83*, 21–30.
- Patt, J. M., Hamilton, G. C., & Lashomb, J. H. (1999). Responses of two parasitoid wasps to nectar odors as a function of experience. *Entomologia Experimentalis et Applicata*, *90*, 1–8.
- Petschenka, G., & Agrawal, A. A. (2016). How herbivores coopt plant defenses: Natural selection, specialization, and sequestration. *Current Opinion in Insect Science*, *14*, 17–24.
- Pieterse, C. M. J., Van der Does, D., Zamioudis, C., Leon-Reyes, A., & Van Wees, S. C. M. (2012). Hormonal modulation of plant immunity. *Annual Review of Cell and Developmental Biology*, *28*, 489–521.
- Pincebourde, S., & Casas, J. (2006). Leaf miner-induced changes in leaf transmittance cause variations in insect respiration rates. *Journal of Insect Physiology*, *52*, 194–201.
- Pincebourde, S., van Baaren, J., Rasmann, S., Rasmont, P., Rodet, G., Martinet, B., & Calatayud, P.-A. (2016). Plant–insect interactions in a changing world. In N. Sauvion, D. Thiery, & P.-A. Calatayud (Eds.), *Insect-plant Interactions* (Vol. 81). (in this volume).
- Poelman, E. H., Bruinsma, M., Zhu, F., Weldegergis, B. T., Boursault, A. E., Jongema, Y., ... Dicke, M. (2012). Hyperparasitoids use herbivore-induced plant volatiles to locate their parasitoid host. *PLoS Biology*, *10*, e1001435.
- Poelman, E. H., & Dicke, M. (2014). Plant-mediated interactions among insects within a community ecological perspective. In C. Voelckel, & G. Jander (Eds.), *Annual plant reviews* (Vol. 47). Chichester, UK: John Wiley & Sons, Ltd.
- Poelman, E. H., Zheng, S.-J., Zhang, Z., Heemskerk, N. M., & Cortesero, A.-M. (2011). Parasitoid-specific induction of plant responses to parasitized herbivores affects colonization by subsequent herbivores. *Proceedings of the National Academy of Sciences B: Biological Sciences*, *108*, 19647–19652.
- Poirié, M., Colinet, D., & Gatti, J.-L. (2014). Insights into function and evolution of parasitoid wasp venoms. *Current Opinion in Insect Science*, *6*, 52–60.
- Ponzio, C., Gols, R., Weldegergis, B. T., & Dicke, M. (2014). Caterpillar-induced plant volatiles remain a reliable signal for foraging wasps during dual attack with a plant pathogen or non-host insect herbivore. *Plant, Cell and Environment*, *37*, 1924–1935.
- Powell, S. J., & Bale, J. S. (2006). Effect of long-term and rapid cold hardening on the cold torpor temperature of an aphid. *Physiological Entomology*, *31*, 348–352.
- Price, P. W., Bouton, C. E., Gross, P., McPheron, B. A., Thompson, J. N., & Weis, A. E. (1980). Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology, Evolution and Systematics*, *11*, 41–65.

- Pumarino, L., Sileshi, G. W., Gripenberg, S., Kaartinen, R., Barrios, E., Muchame, M. N., ... Jonsson, M. (2015). Effects of agroforestry on pest, disease and weed control: a meta-analysis. *Basic and Applied Ecology*, *16*, 573–582.
- Quénol, H., & Beltrando, G. (2006). Microclimate in forest ecosystem and landscape ecology. *Climatologie*, *3*, 9–23.
- Quicke, D. L. J. (1988). Host relationships in the Braconinae — How little we know! *Queensland Entomological Society News Bulletin*, *16*, 85–92.
- Quicke, D. L. J. (1997). *Parasitic wasps*. London, UK: Chapman and Hall, 488 pp.
- Quicke, D. L. J. (2015). *The braconid and ichneumonid parasitoid wasps: Biology, systematics, evolution and ecology*. Chichester, UK: John Wiley & Sons, Ltd, 704 pp.
- Quintero, C., Lampert, E. C., & Bowers, M. D. (2014). Time is of the essence: direct and indirect effects of plant ontogenetic trajectories on higher trophic levels. *Ecology*, *95*, 2589–2602.
- Rand, T. A., Waters, D. K., Blodgett, S. L., Knodel, J. J., & Harris, M. O. (2014). Increased area of a highly suitable host crop increases herbivore pressure in intensified agricultural landscapes. *Agriculture, Ecosystems & Environment*, *186*, 135–143.
- Rani, P. U., Kumari, S. I., Sriramakrishna, T., & Sudhakar, T. R. (2007). Kairomones extracted from rice yellow stem borer and their influence on egg parasitization by *Trichogramma japonicum* Ashmead. *Journal of Chemical Ecology*, *33*, 59–73.
- Ratzka, A., Vogel, H., Kliebenstein, D. J., Mitchell-Olds, T., & Kroymann, J. (2002). Disarming the mustard oil bomb. *Proceedings of the National Academy of Sciences of the United States of America (PNAS)*, *99*, 11223–11228.
- Rezende, M. Q., Venzon, M., Perez, A. L., Cardoso, I. M., & Janssen, A. (2014). Extrafloral nectaries of associated trees can enhance natural pest control. *Agriculture, Ecosystems & Environment*, *188*, 198–203.
- Robinson, K. A., Jonsson, M., Wratten, S. D., Wade, M. R., & Buckley, H. L. (2008). Implications of floral resources for predation by an omnivorous lacewing. *Basic and Applied Ecology*, *9*, 172–181.
- Romero, G. Q., & Benson, W. W. (2005). Biotic interactions of mites, plants and leaf domatia. *Current Opinion in Plant Biology*, *8*, 436–440.
- Rostas, M., Ruf, D., Zabka, V., & Hildebrandt, U. (2008). Plant surface wax affects parasitoid's response to host footprints. *The Science of Nature — Naturwissenschaften*, *95*, 997–1002.
- Rusch, A., Chaplin-Kramer, R., Gardiner, M. M., Hawro, V., Holland, J., Landis, D., ... Winqvist, C. (2016). Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. *Agriculture, Ecosystems & Environment*, *221*, 198–204.
- Schuman, M. C., & Baldwin, I. T. (2016). The layers of plant responses to insect herbivores. *Annual Review of Entomology*, *61*, 373–394.
- Sime, K. (2002). Chemical defense of *Battus philenor* larvae against attack by the parasitoid *Trogus pennator*. *Ecological Entomology*, *27*, 237–345.
- Simpson, M., Gurr, G. M., Simmons, A. T., Wratten, S. D., James, D. G., Leeson, G., ... Orre-Gordon, G. U. S. (2011). Attract and reward: Combining chemical ecology and habitat manipulation to enhance biological control in field crops. *Journal of Applied Ecology*, *48*, 580–590.
- Singer, M. S., Mace, K. C., & Bernays, E. A. (2009). Self-medication as adaptive plasticity: Increased ingestion of plant toxins by parasitized caterpillars. *PLoS One*, *4*, e4796.
- Smallegange, R. C., Van Loon, J. J. A., Blatt, S. E., Harvey, J. A., & Dicke, M. (2008). Parasitoid load affects plant fitness in a tritrophic system. *Entomologia Experimentalis et Applicata*, *128*, 172–183.
- Smid, H., & Vet, L. E. M. (2016). The complexity of learning, memory and neural processes in an evolutionary ecological context. *Current Opinion in Insect Science*, *15*, 61–69.

- Smilanich, A. M., Dyer, L. A., Chambers, J. Q., & Bowers, M. D. (2009). Immunological cost of chemical defence and the evolution of herbivore diet breadth. *Ecology Letters*, *12*, 612–621.
- Smith, M. A., Rodriguez, J. J., Whitfield, J. B., Deans, A. R., Janzen, D. H., Hallwachs, W., & Hebert, P. D. N. (2008). Extreme diversity of tropical parasitoid wasps exposed by iterative integration of natural history, DNA barcoding, morphology, and collections. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 12359–12364.
- Stapel, J. O., Cortesero, A.-M., De Moraes, C. M., Tumlinson, J. H., & Lewis, W. J. (1997). Extrafloral nectar, honeydew and sucrose effects on searching behavior and efficiency of *Microplitis croceipes* (Hymenoptera: Braconidae) in cotton. *Environmental Entomology*, *26*, 617–623.
- Steidle, J. L. M., & Schöller, M. (1997). Olfactory host location and learning in the granary weevil parasitoid *Lariophagus distinguendus* (Hymenoptera: Pteromalidae). *Journal of Insect Behavior*, *10*, 331–342.
- Steidle, J. L. M., & Van Loon, J. J. A. (2003). Dietary specialization and infochemical use in carnivorous arthropods: testing a concept. *Entomologia Experimentalis et Applicata*, *108*, 133–148.
- Stiling, P., & Moon, D. C. (2005). Quality or quantity: The direct and indirect effects of host plants on herbivores and their natural enemies. *Oecologia*, *142*, 413–420.
- Suh, C. P. C., Orr, D. B., Van Duyn, J. W., & Borchert, M. D. (2002). Influence of cotton microhabitat on temperature and survival of *Trichogramma* (Hymenoptera: Trichogrammatidae) within cardboard capsules. *Environmental Entomology*, *31*, 361–366.
- Takasu, K., & Lewis, W. J. (1996). The role of learning in adult food location by the larval parasitoid, *Microplitis croceipes* (Hymenoptera: Braconidae). *Journal of Insect Behavior*, *9*, 265–281.
- Takasu, K., & Lewis, W. J. (2003). Learning of host searching cues by the larval parasitoid *Microplitis croceipes*. *Entomologia Experimentalis et Applicata*, *108*, 77–86.
- Takasu, K., Rains, G. C., & Lewis, W. J. (2007). Comparison of detection ability of learned odors between males and females in the larval parasitoid *Microplitis croceipes*. *Entomologia Experimentalis et Applicata*, *122*, 247–251.
- Tamo, C., Ricard, I., Held, M., Davison, A. C., & Turlings, T. C. J. (2006). A comparison of naive and conditioned responses of three generalist endoparasitoids of lepidopteran larvae to host-induced plant odours. *Animal Biology*, *56*, 205–220.
- Thaler, J. S. (1999). Jasmonate-inducible plant defences cause increased parasitism of herbivores. *Nature*, *399*, 686–688.
- Thiel, A., Schlake, S., & Kosior, D. (2013). *Omnia tempus habent*: habitat-specific differences in olfactory learning and decision making in parasitic wasps. *Animal Cognition*, *16*, 223–232.
- Thies, C., Steffan-Dewenter, I., & Tschamtkke, T. (2003). Effects of landscape context on herbivore and parasitism at different spatial scales. *Oikos*, *18*, 18–25.
- Tougeron, K., Van Baaren, J., Burel, F., & Alford, L. (2016). Comparing thermal tolerance across contrasting landscapes: first steps towards understanding how landscape management could modify ectotherm thermal tolerance. *Insect Conservation and Diversity*, *9*, 171–180.
- Trapero, C., Wilson, I. W., Stiller, W. N., & Wilson, L. J. (2016). Enhancing integrated pest management in GM cotton systems using host plant resistance. *Frontiers in Plant Science*, *7*, 500.
- Tschamtkke, T., Bommarco, R., Clough, Y., Crist, T. O., Kleijn, D., Rand, T. A., ... Vidal, S. (2008). Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, *45*, 238–253.

- Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., ... Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes — eight hypotheses. *Biological Reviews of the Cambridge Philosophical Society*, *87*, 661–685.
- Turlings, T. C. J., Loughrin, J. H., McCall, P. J., Rose, U. S. R., Lewis, W. J., & Tumlinson, J. H. (1995). How caterpillar damaged plants protect themselves by attracting parasitic wasps. *Proceedings of the National Academy of Sciences of the United States of America*, *92*, 4169–4174.
- Turlings, T. C. J., Tumlinson, J. H., & Lewis, W. J. (1990). Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science*, *250*, 1251–1253.
- Turlings, T. C. J., & Wäckers, F. L. (2004). Recruitment of predators and parasitoids by herbivore-damaged plants. In R. T. Cardé, & J. G. Millar (Eds.), *Advances in insect chemical ecology* (pp. 21–75). Cambridge, UK: Cambridge University Press.
- Turlings, T. C. J., Wäckers, F. L., Vet, L. E. M., Lewis, W. J., & Tumlinson, J. H. (1993). Learning of host-finding cues by hymenopterous parasitoids. In D. R. Papaj, & A. C. Lewis (Eds.), *Insect learning: Ecology and evolutionary perspectives* (pp. 51–78). New York: Chapman & Hall.
- Tylianakis, J. M., Tscharntke, T., & Klein, A.-M. (2006). Diversity, ecosystem function, and stability of parasitoid host interactions across a tropical habitat gradient. *Ecology*, *87*, 3047–3057.
- Van den Bosch, R. (1971). Biological control of insects. *Annual Review of Ecology, Evolution and Systematics*, *2*, 45–66.
- Van der Meijden, E., & Klinkhamer, P. G. L. (2000). Conflicting interests of plants and the natural enemies of herbivores. *Oikos*, *89*, 202–208.
- Van Driesche, R., Hoddle, M., & Center, T. (2008). *Control of pests and weeds by natural enemies: An introduction to biological control*. Oxford, UK: Blackwell Publishing, 473 pp.
- Van Emden, H. F., Sponagl, B., Baker, T., Ganguly, S., & Douloumpaka, S. (1996). Hopkins' "host selection principle", another nail in its coffin. *Physiological Entomology*, *21*, 325–328.
- Van Loon, J. J. A., De Boer, J. G., & Dicke, M. (2000). Parasitoid–plant mutualism: Parasitoid attack of herbivore increases plant reproduction. *Entomologia Experimentalis et Applicata*, *97*, 219–227.
- Van Nouhuys, S. (2005). Effects of habitat fragmentation at different trophic levels in insect communities. *Annales Zoologici Fennici*, *42*, 433–447.
- Van Nouhuys, S., & Hanski, I. (2002). Multitrophic interactions in space: Metacommunity dynamics in fragmented landscapes. In T. Tscharntke, & B. A. Hawkins (Eds.), *Multitrophic level interactions* (pp. 124–147). Cambridge: Cambridge University Press.
- Van Nouhuys, S., & Kaartinen, R. (2008). A parasitoid wasp uses landmarks while monitoring potential resources. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 377–385.
- Van Vugt, J., Hoedjes, K. M., Van de Geest, H. C., Schijlen, E., Vet, L. E. M., & Smid, H. M. (2015). Differentially expressed genes linked to natural variation in long-term memory formation in *Cotesia* parasitic wasps. *Frontiers in Behavioral Neuroscience*, *9*.
- Vet, L. E. M., & Dicke, M. (1992). Ecology of infochemical use by natural enemies in a tri-trophic context. *Annual Review of Entomology*, *37*, 141–172.
- Vet, L. E. M., & Van Opzeeland, K. (1984). The influence of conditioning on olfactory microhabitat and host location in *Asobara tabida* (Nees) and *A. rufescens* (Foerster) (Bracoonidae: Alysiinae) larval parasitoids of *Drosophilidae*. *Oecologia*, *63*, 171–177.
- Vogelweith, F., Moreau, J., Thiéry, D., & Moret, Y. (2015). Food-mediated modulation of immunity in a phytophagous insect: an effect of nutrition rather than parasitic contamination. *Journal of Insect Physiology*, *77*, 55–61.

- Wäckers, F. L. (2001). A comparison of nectar- and honeydew sugars with respect to their utilization by the hymenopteran parasitoid *Cotesia glomerata*. *Journal of Insect Physiology*, *47*, 1077–1084.
- Wäckers, F. L., & Lewis, W. J. (1999). A comparison of color-, shape- and pattern-learning by the hymenopteran parasitoid *Microplitis croceipes*. *Journal of Comparative Physiology A*, *184*, 387–393.
- Wäckers, F. L., & Steppuhn, A. (2003). Characterizing nutritional state and food source use of parasitoids collected in fields with high and low nectar availability. *IOBC-WPRS Bulletin*, *26*, 203–208.
- Wäckers, F. L., van Rijn, P. C. J., & Bruin, J. (2005). *Plant-provided food for carnivorous insects: A protective mutualism and its applications*. Cambridge, UK: Cambridge University Press.
- Wäckers, F. L., van Rijn, P. C., & Heimpel, G. E. (2008). Honeydew as a food source for natural enemies: Making the best of a bad meal? *Biological Control*, *45*(2), 176–184.
- Wajnberg, E., Bernstein, C., & Van Alphen, J. (2007). *Behavioural ecology of insect parasitoids: From theoretical approaches to field applications*. Dordrecht, Pays-Bas: Blackwell publishing.
- Wajnberg, E., & Colazza, S. (2013). *Chemical ecology of insect parasitoids*. New York, United States: John Wiley & Sons, 328 pp.
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., ... Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*, 389–395.
- Weevers, T. (1952). Flower color and their frequency. *Acta Botanica Neerlandica*, *1*, 81–92.
- Williams, T., Arrendondo-Bernal, H. C., & Rodríguez-del-Bosque, L. A. (2013). Biological pest control in Mexico. *Annual Review of Entomology*, *58*, 119–140.
- Wirta, H. K., Vesterinen, E. J., Hambäck, P. A., Weingartner, E., Rasmussen, C., Reneerkens, J., ... Roslin, T. (2015). Exposing the structure of an Arctic food web. *Ecology and Evolution*, *5*, 3842–3856.
- Wittstock, U., Agerbirk, N., Stauber, E. J., Olsen, C. E., Hippler, M., Mitchell-Olds, T., ... Vogel, H. (2004). Successful herbivore attack due to metabolic diversion of a plant chemical defense. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 4859–4864.
- Woods, H. A. (2013). Ontogenetic changes in the body temperature of an insect herbivore. *Functional Ecology*, *27*, 1322–1331.
- Yarnes, C. T., & Boecklen, W. J. (2006). Abiotic mosaics affect seasonal variation of plant resources and influence the performance and mortality of a leaf-miner in Gambel's oak (*Quercus gambelii*, Nutt.). *Ecological Research*, *21*, 157–163.
- Züst, T., & Agrawal, A. A. (2016). Population growth and sequestration of plant toxins along a gradient of specialization in four aphid species on the common milkweed, *Asclepias syriaca*. *Functional Ecology*, *30*, 547–555.