OLFACTORY CUES MEDIATE MULTITROPHIC INTERACTIONS AMONG CUCUMBER PLANTS, CUCUMBER BEETLE LARVAE AND ENTOMOPATHOGENIC NEMATODES

A Thesis

by

JOHN MICHAEL GRUNSEICH

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Chair of Committee,	Anjel Helms
Committee Members,	Micky Eubanks
	Michael Kolomiets
Head of Department,	Phillip Kaufman

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ABSTRACT

Olfactory cues mediate a wide variety of ecological interactions among organisms at different trophic levels. There is abundant evidence that these cues play critical roles for organisms foraging for resources and defending against potential attackers. Some of the best-studied examples include plants producing volatile organic compounds to defend themselves against herbivores and natural enemies using prey-associated odors while hunting. While much of this research has focused on aboveground systems, there is growing recognition that olfactory cues also facilitate multitrophic interactions among soil-dwelling organisms. The overall purpose of this thesis was to examine how olfactory cues from plants and natural enemies guide the foraging decisions of herbivores and their natural enemies, focusing on a belowground tritrophic system.

First, I review the literature to examine how plant-associated microorganisms alter plant phenotypes to influence herbivore foraging behavior. Next, I investigate the roles of herbivore-induced plant volatiles (HIPVs) from roots of cucumber plants (*Cucumis sativus*) as foraging cues for a specialist herbivore, striped cucumber beetle (*Acalymma vittatum*) and its natural enemies, entomopathogenic nematodes (EPNs, *Heterorhabditis bacteriophora*). I predicted HIPVs from *A. vittatum*-damaged roots would attract EPNs, while repelling conspecific larvae that avoid competition, and increased risk of predation by EPNs. Finally, I evaluated how olfactory cues emitted by 3 species of EPNs with differing foraging strategies affect the behavior of their insect herbivore prey (*A. vittatum*) and competing EPNs. I hypothesized olfactory cues from the more sedentary ‘ambush’ EPN species (*Steinernema carpocapsae*) would be the most repulsive to prey and potential competitors, compared to cues from the active-hunting (*H. bacteriophora*) or intermediate-foraging (*Steinernema riobrave*) species.

In the second study, I found that 24 hours of wounding by *A. vittatum* herbivory, or mechanical damage, induced greater production of volatiles from *C. sativus* roots compared to undamaged controls, repelling foraging larvae and recruiting EPNs. However, after sustained herbivory for 7 days, larvae reduced HIPVs to levels indistinguishable from undamaged roots, while mechanically damaged roots continued to produce higher levels of volatiles. Attenuation of HIPVs impaired *C. sativus* indirect defenses by reducing recruitment of EPNs and deterrence of *A. vittatum* larvae.

In the final study, I found that foraging *A. vittatum* larvae avoided olfactory cues from the active-hunting EPN species, *Heterorhabditis bacteriophora*, but did not respond to cues from the ambush hunter, *S. carpocapsae*, or intermediate hunter, *S. riobrave*. In contrast, foraging *H. bacteriophora* EPNs were attracted to odors produced by the two *Steinernema* EPN species and did not respond to olfactory cues from conspecifics.

Taken together, these results suggest that *A. vittatum* larvae can navigate risk within the soil environment, first, by avoiding volatile cues associated with increased predation risk or competition (i.e., volatiles from herbivore-damaged plants or odors from EPN-infected) and, second, through direct attenuation of plant indirect defenses. Our findings also indicate that active-hunting ‘cruiser’ EPNs are attracted to multiple host-associated cues, including volatiles from herbivore-wounded *C. sativus* roots and odors from heterospefic EPN-infected insect cadavers, suggesting that these cues can provide information for foraging natural enemies about resource availability.

CONTRIBUTORS AND FUNDING SOURCES

This work was supervised by a thesis committee consisting of Professor Dr. Anjel Helms (advisor and committee chair) and Professor Dr. Eubanks or the Department of Entomology and Professor Dr. Kolomiets of the Department of Plant Pathology and Microbiology.

John Grunseich, Dr. Anjel Helms, and Dr. Jared Ali conceived the ideas and designed the methodology; John Grunseich, Morgan Thompson, Zack Gorman, Natalie Aguirre, and Alison Hay collected the data; John Grunseich and Dr. Anjel Helms analyzed the data. All authors contributed to writing the manuscripts.

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NOMENCLATURE

EPN	Entomopathogenic nematode
EPN IJs	EPN infective juveniles
VOC	Volatile organic compound
HIPV	Herbivore-induced plant volatiles
SR	*Steinernema riobrave*
SC	*Steinernema carpocapsae*
HB	*Heterorhabditis bacteriophora*
SAR	Systemic acquired resistance

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CHAPTER I

INTRODUCTION

Belowground herbivores and their natural enemies rely on chemical cues to locate resources and avoid predation within the soil environment (Johnson & Nielsen, 2012). Root herbivores shape populations of plants, soil-microbe communities and other herbivores directly through plant consumption or indirectly through induction of plant volatiles (Johnson & Rasmann, 2015). These Induced volatiles, also known as herbivore-induced plant volatiles (HIPVs), are produced in response to herbivory and often function as indirect defenses against herbivores. Chemical cues, such as HIPVs, drive many interactions between trophic levels (Johnson & Gregory, 2006). In our study we focused on the predator-prey interactions between the herbivore *Acalymma vittatum* and their natural enemies, entomopathogenic nematodes (EPNs) and how cucumber plants mediate these interactions (Figure 1).

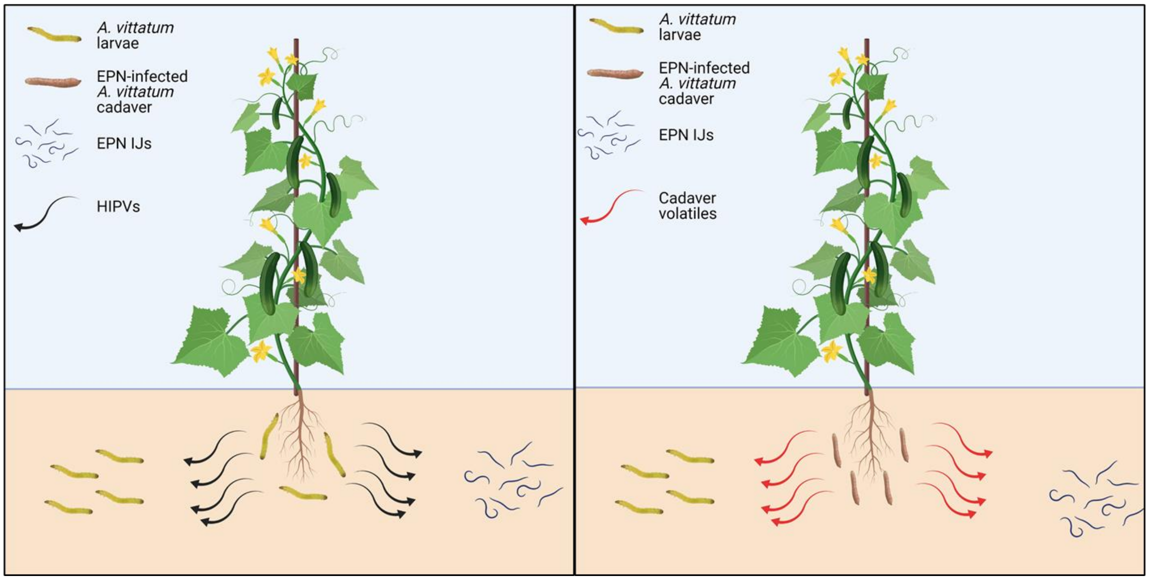

Figure 1 Herbivores and natural enemies interact with herbivore induced plant volatiles and EPN-infected insect cadavers following successful prey capture. These can mediate interactions among *A. vittatum* larvae, cucumber plants and EPNs.

The striped cucumber beetle, *A. vittatum*, is a major destructive pest in the eastern United States (C. Ellers-Kirk & Fleischer, 2006). Both the adult and larval life stages are economically important, as the larvae feed on roots, significantly reducing cucurbit root mass in the field, while adults feed aboveground on flowers, leaves, and fruits, also vectoring the causal agent of bacterial wilt disease (C. D. Ellers-Kirk, Fleischer, Snyder, & Lynch, 2000). Root-feeding herbivores are among the most economically devastating crop pests because their belowground infestations are challenging to detect and difficult to control (Johnson et al., 2016). Though most of the research has focused on *A. vittatum* aboveground, there is still much to study belowground (Johnson & Rasmann, 2015).An important aspect to study is how *A. vittatum* larvae use volatile cues to navigate within the soil as this will provide ecologically-relevant information and means for better control of the pest (Figure 1).

Entomopathogenic nematodes (EPNs) are obligate parasites of insects that live within soil. They belong to two families, having one genus each (Heterorhabditidae:*Heterorhabditis*) and Steinernematidae*:Steinernema*) and include about 60 known species (Johnson & Rasmann, 2015). Similarly to aboveground predators, foraging EPNs rely on both general cues, such as carbon dioxide, and host-specific herbivore-induced plant volatiles such as pregeijerene in citrus roots and E-β-caryophyllene in maize roots to locate their prey (Ali, Alborn, & Stelinski, 2010; Rasmann et al., 2005). Once located, EPNs invade their host via mouth, spiracles, or anus. After successful host invasion they release symbiotic bacteria that then kill the host through septicemia, typically after 48 hours. Biological control using EPNs is a promising strategy for sustainably managing root-feeding insects and there is currently interest in increasing their efficacy across diverse crop environment pests (Shapiro-Ilan, Hiltpold, & Lewis, 2018). By investigating how EPNs and their insect hosts respond to volatile cues within the environment, we will be able to understand their foraging decisions and how to modify current control methods for *A. vittatum.*

Cucumber plants (*Cucumis sativus)* are an important vegetable crop in the eastern United States (C. Ellers-Kirk & Fleischer, 2006). *C. sativus* is significantly impacted by

A. vittatum foraging, specifically as a seedling. These plants are not defenseless though and can produce secondary metabolites such as cucurbitacin and volatile organic compounds for defense against insect herbivores.

Interest in EPN and root-herbivore behavior in response to HIPVs has increased in the last decade, which lead to a better understanding of these interactions (Ali et al., 2010; Lackus, Lackner, Gershenzon, Unsicker, & Köllner, 2018; Robert, Erb, Hibbard, et al., 2012). There is also growing evidence that EPN-associated cues such as volatiles produced after successful prey capture from EPN-infected cadavers could potentially mediate many ecological interactions within the rhizosphere community (Gulcu, Hazir, & Kaya, 2012; Hu, Li, & Webster, 1999; Hu & Webster, 2000; Kaplan et al., 2012, 2020; Lu et al., 2017). The overall goal of this thesis was to examine how HIPVs and cadaver volatiles shape predator-prey interactions, which will provide valuable information to further develop our understanding of belowground tritrophic interactions. By improving our understanding of these interactions, we may be able to use EPNs more effectively as biological control organisms of root feeding herbivores, such as *Acalymma vittatum*.

CHAPTER II

THE ROLE OF PLANT-ASSOCIATED MICROBES IN MEDIATING HOST-PLANT SELECTION BY INSECT HERBIVORES[1]

INTRODUCTION

Insects need food resources that provide sufficient nutrients for growth, development, and reproduction. Insect herbivores require food plants to fuel these processes and must forage to find suitable host plants within diverse ecological backgrounds (Behmer, 2009; Moore, Andrew, Külheim, & Foley, 2014; Wetzel, Kharouba, Robinson, Holyoak, & Karban, 2016). To locate and assess the quality of potential host plants, insect herbivores typically rely on plant-produced cues that provide information about relevant plant traits (Bruce, Wadhams, & Woodcock, 2005). An additional layer of complexity in herbivore foraging arises from plant and herbivore interactions with microorganisms. All plants associate with beneficial and pathogenic microbes and these microbes can play important roles in modifying plant traits that indirectly influence host-plant selection by insect herbivores (Biere & Bennett, 2013; Hassani, Durán, & Hacquard, 2018). For this review, we define insect herbivore forging behavior as the location and selection of food plants and we focus on studies evaluating host-plant preference or colonization. We also

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[1] Reprinted with permission from "The Role of Plant-Associated Microbes in Mediating Host-Plant Selection by Insect Herbivores" by John Grunseich, Morgan N. Thompson, Natalie M. Aguirre, and Anjel M. Helms, 2019. *Plants*, 9(1), 6. doi: 10.3390/plants9010006

include measures of herbivore oviposition preference, as oviposition is a mechanism of host-plant selection by gravid females for future offspring (De Moraes, Mescher, & Tumlinson, 2001; Kariyat et al., 2013). Moreover, we also discuss the role of dispersal behavior and subsequent host-plant selection following herbivore contact with microbe-associated plants.

Insect herbivores are equipped with a range of sensory systems, allowing them to perceive and interpret information from their environment encoded as visual, olfactory, and gustatory cues (described in further detail below). Here, we focus on this subset of cues due to their prominence in the literature and importance in mediating host-plant selection by insect herbivores. Herbivores typically use plant-associated cues during foraging (Bruce et al., 2005) and oviposition (Reeves, 2011) as these cues can provide information related to plant location (Couty et al., 2006), identity, nutritional quality (Bruce & Pickett, 2011), and defensive status (De Moraes et al., 2001). Cues from different sensory modalities often play different roles throughout the host-plant selection process, from initial location of plants or habitats (Jönsson, Rosdahl, & Anderson, 2007; Pan, Xiu, & Lu, 2015) to selection of individual plants or tissues (Couty et al., 2006; Silva & Clarke, 2020; Wenninger, Stelinski, & Hall, 2009). Many insect species rely on visual cues for locating plants over large distances, especially if they are capable of long-range dispersal (Turlure, Schtickzelle, Van Dyck, Seymoure, & Rutowski, 2016). In contrast, gustatory cues require plant contact and provide information about suitable tissues for feeding or oviposition (Backus, Cervantes, Guedes, Li, & Wayadande, 2019).

The use of different cues varies among insect herbivore species (Hassell & Southwood, 1978) and particular cues may be more useful in certain habitats, like soil environments (Schumann, Ladin, Beatens, & Hiltpold, 2018), or during certain times of the day, such as diurnal, nocturnal, or crepuscular activity (Shiojiri, Ozawa, & Takabayashi, 2006). Although visual, olfactory, and gustatory cues vary in relative importance during host-plant selection among different herbivore species and environmental conditions, these cues are often used in combination by foraging or ovipositing insects (Silva & Clarke, 2020).

Interactions between plants and microbes are ubiquitous and can range from beneficial to parasitic or pathogenic. There is growing recognition that plant-associated microbes play important roles in modulating plant phenotypes and shaping interactions between plants and insects (Partida-Martínez & Heil, 2011; Pineda, Dicke, Pieterse, & Pozo, 2013; Porter et al., 2020; Shikano, Rosa, Tan, & Felton, 2017). For example, increasing evidence indicates that microbes alter plant-produced cues that subsequently influence the oviposition and foraging behavior of insect herbivores (Eigenbrode, Bosque-Pérez, & Davis, 2018; Franco, Moura, Vivanco, & Silva-Filho, 2017; K. E. Mauck, De Moraes, & Mescher, 2016). In this review, we discuss different ways that beneficial and pathogenic plant-associated microbes modify visual, olfactory, and gustatory cues in plants, focusing on microbes that spend at least a portion of their lifecycle on a plant. Furthermore, we examine how these microbe-mediated changes indirectly influence host-plant selection by insect herbivores (Figure 2).

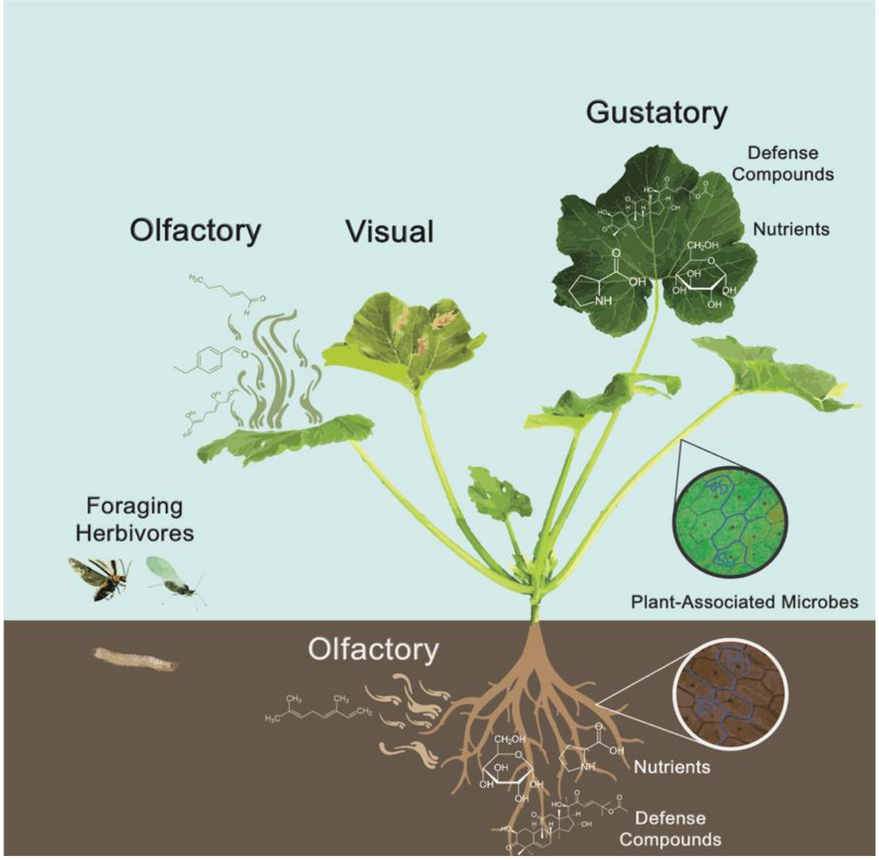
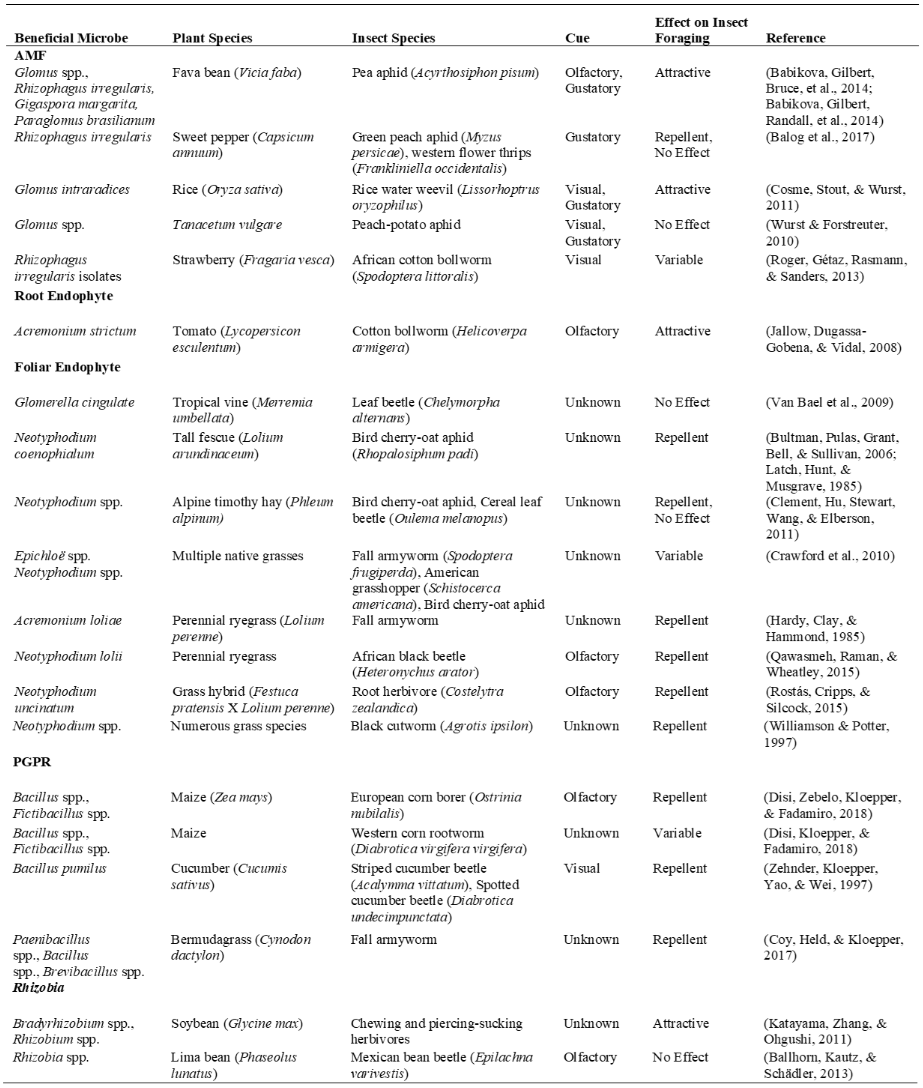


Figure 2 Beneficial and pathogenic microbes interact with above- and belowground plant tissues. These microbes can modify plant traits, such as visual, olfactory, and gustatory cues that insect herbivores use to locate and evaluate potential host plants. Plant olfactory cues are plant-produced volatile organic compounds. Plant visual cues are physical traits, such as plant size, shape, and color. Plant gustatory cues include nutrients, like sugars and amino acids, as well as plant defensive metabolites. Image by Alejandro J. Barroso, the figure is used with permission of the designer and has not been published elsewhere.

Beneficial Plant-Associated Microbes

Plants often form mutualistic relationships with microorganisms. These beneficial plant-associated microbes interact with both above- and belowground plant organs and can live endophytically, within plant tissues, or ectophytically, depending on the species of microbe and the specificity or type of interaction (Gibert, Tozer, & Westoby, 2019). Here we focus on beneficial soil bacteria, especially plant growth-promoting rhizobacteria (PGPR), including nitrogen-fixing Rhizobia, as well as beneficial fungi like arbuscular mycorrhizal fungi (AMF), and foliar and root endophytes, as these are among the best-characterized microbes mediating plant-insect interactions to date. Beneficial microbes often alter plant growth or pest resistance traits that affect the performance and preference of insect herbivores. Microbes, like rhizobia or AMF, that increase plant nutrient acquisition, can also increase the nutritional quality of these plants for insect herbivores (Ballhorn, Elias, Balkan, Fordyce, & Kennedy, 2017; Wilkinson, Ferrari, Hartley, & Hodge, 2019). Moreover, the aptly named PGPR and fungi that enhance plant growth can provide greater amounts of available food resources for insect herbivores (Pineda, Zheng, van Loon, Pieterse, & Dicke, 2010). In contrast, certain species of beneficial microbes have also been observed to heighten plant defense responses via induced systemic resistance (ISR). ISR primes plants to mount faster or stronger defenses against a broad range of diseases or herbivores (Schoenherr, Rizzo, Jackson, Manosalva, & Gomez, 2019). This differs from systemic acquired resistance (SAR), which is initiated by plant infection with pathogenic microbes (discussed below).

For an extensive review of molecular mechanisms underlying ISR and how they contrast with SAR, we direct readers to (Pieterse et al., 2014). ISR can enhance direct plant defenses, like toxic or repellent compounds, as well as indirect defenses, like volatile compounds or food rewards that attract natural enemies to kill herbivores. In this review, we limit our discussion of beneficial plant-associated microbes to their influence on herbivore foraging and oviposition. For a recent review of how beneficial plant-associated microbes alter insect predator and parasitoid behavior, see (Tao, Hunter, & de Roode, 2017).



Beneficial Microbe	Plant Species	Insect Species	Cue	Effect on Insect Foraging	Reference
AMF					
Glomus spp., *Rhizophagus irregularis, Gigaspora margarita, Paraglomus brasilianum*	Fava bean (*Vicia faba*)	Pea aphid (*Acyrthosiphon pisum*)	Olfactory, Gustatory	Attractive	(Babikova, Gilbert, Bruce, et al., 2014; Babikova, Gilbert, Randall, et al., 2014)
Rhizophagus irregularis	Sweet pepper (*Capsicum annuum*)	Green peach aphid (*Myzus persicae*), western flower thrips (*Frankliniella occidentalis*)	Gustatory	Repellent, No Effect	(Balog et al., 2017)
Glomus intraradices	Rice (*Oryza sativa*)	Rice water weevil (*Lissorhoptrus oryzophilus*)	Visual, Gustatory	Attractive	(Cosme, Stout, & Wurst, 2011)
Glomus spp.	*Tanacetum vulgare*	Peach-potato aphid	Visual, Gustatory	No Effect	(Wurst & Forstreuter, 2010)
Rhizophagus irregularis isolates	Strawberry (*Fragaria vesca*)	African cotton bollworm (*Spodoptera littoralis*)	Visual	Variable	(Roger, Gétaz, Rasmann, & Sanders, 2013)
Root Endophyte					
Acremonium strictum	Tomato (*Lycopersicon esculentum*)	Cotton bollworm (*Helicoverpa armigera*)	Olfactory	Attractive	(Jallow, Dugassa-Gobena, & Vidal, 2008)
Foliar Endophyte					
Glomerella cingulate	Tropical vine (*Merremia umbellata*)	Leaf beetle (*Chelymorpha alternans*)	Unknown	No Effect	(Van Bael et al., 2009)
Neotyphodium coenophialum	Tall fescue (*Lolium arundinaceum*)	Bird cherry-oat aphid (*Rhopalosiphum padi*)	Unknown	Repellent	(Bultman, Pulas, Grant, Bell, & Sullivan, 2006; Latch, Hunt, & Musgrave, 1985)
Neotyphodium spp.	Alpine timothy hay (*Phleum alpinum)*	Bird cherry-oat aphid, Cereal leaf beetle (*Oulema melanopus*)	Unknown	Repellent, No Effect	(Clement, Hu, Stewart, Wang, & Elberson, 2011)
Epichloë spp. *Neotyphodium* spp.	Multiple native grasses	Fall armyworm (*Spodoptera frugiperda*), American grasshopper (*Schistocerca americana*), Bird cherry-oat aphid	Unknown	Variable	(Crawford et al., 2010)
Acremonium loliae	Perennial ryegrass (*Lolium perenne*)	Fall armyworm	Unknown	Repellent	(Hardy, Clay, & Hammond, 1985)
Neotyphodium lolii	Perennial ryegrass	African black beetle (*Heteronychus arator*)	Olfactory	Repellent	(Qawasmeh, Raman, & Wheatley, 2015)
Neotyphodium uncinatum	Grass hybrid (*Festuca pratensis* X *Lolium perenne*)	Root herbivore (*Costelytra zealandica*)	Olfactory	Repellent	(Rostás, Cripps, & Silcock, 2015)
Neotyphodium spp.	Numerous grass species	Black cutworm (*Agrotis ipsilon*)	Unknown	Repellent	(Williamson & Potter, 1997)
PGPR					
Bacillus spp., *Fictibacillus* spp.	Maize (*Zea mays*)	European corn borer (*Ostrinia nubilalis*)	Olfactory	Repellent	(Disi, Zebelo, Kloepper, & Fadamiro, 2018)
Bacillus spp., *Fictibacillus* spp.	Maize	Western corn rootworm (*Diabrotica virgifera virgifera*)	Unknown	Variable	(Disi, Kloepper, & Fadamiro, 2018)
Bacillus pumilus	Cucumber (*Cucumis sativus*)	Striped cucumber beetle (*Acalymma vittatum*), Spotted cucumber beetle (*Diabrotica undecimpunctata*)	Visual	Repellent	(Zehnder, Kloepper, Yao, & Wei, 1997)
Paenibacillus spp., *Bacillus* spp., *Brevibacillus* spp.	Bermudagrass (*Cynodon dactylon*)	Fall armyworm	Unknown	Repellent	(Coy, Held, & Kloepper, 2017)
Rhizobia					
Bradyrhizobium spp., *Rhizobium* spp.	Soybean (*Glycine max*)	Chewing and piercing-sucking herbivores	Unknown	Attractive	(Katayama, Zhang, & Ohgushi, 2011)
Rhizobia spp.	Lima bean (*Phaseolus lunatus*)	Mexican bean beetle (*Epilachna varivestis*)	Olfactory	No Effect	(Ballhorn, Kautz, & Schädler, 2013)

Table 1 Beneficial Plant-Associated Microbes Modifying Plant Cues That Influence Insect Herbivore Foraging and Oviposition Behavior.

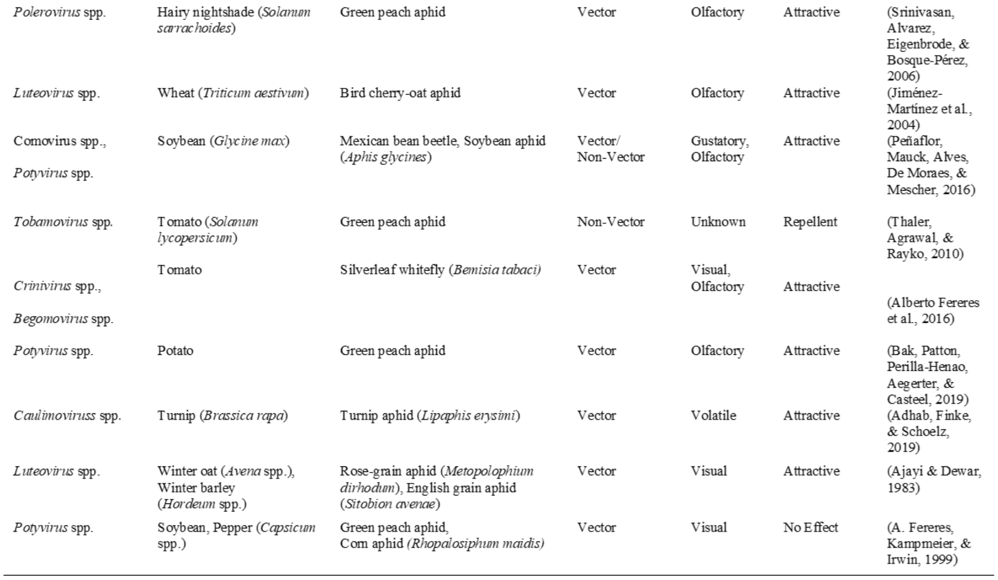
Pathogenic Plant-Associated Microbes

Plant-pathogenic microbes frequently cause disease symptoms that alter plant growth and/or chemistry and can influence the performance or behavior of insect herbivores. For example, plant pathogen infection often reduces plant growth (Burdon, Thrall, & Ericson, 2006; Chesnais et al., 2019; Jiang et al., 2017) or causes color changes (Y. Li, Cui, Cui, & Wang, 2016; Moericke, 1969) or physical deformations to plant tissues (Navas, Friess, & Maillet, 1998). Pathogen infection can also cause tissue damage that reduces photosynthate production which, coupled with the uptake of nutrients by the pathogen, can alter nutrient or resource availability for insect herbivores (Fernandez-Conradi, Jactel, Robin, Tack, & Castagneyrol, 2018; Mann et al., 2012; K. E. Mauck, De Moraes, & Mescher, 2014). Plants respond to pathogen infection by activating physical and chemical defenses. This can include mechanisms to physically block or prevent the spread of infection, as well as production of antimicrobial compounds to fight the pathogen (Biggs, 1987; Dangl & Jones, 2001; Pearce, 1990). Plants typically tailor their defense responses to specific pathogens and activate different defense pathways or suites of defense traits against biotrophic (feeding on living plant tissue) or necrotrophic (feeding on dead plant tissue) phytopathogens. Plants exposed to biotrophic pathogens typically increase defenses through systemic acquired resistance (SAR), which is a physiological state of enhanced immunity against further infection in distal, uninfected plant tissues (Tubert-Broham, Sherman, Repasky, & Beuming, 2017). For an extensive review of molecular mechanisms underlying plant pathogen-mediated SAR, we direct readers to (Z. Q. Fu & Dong, 2013). Plant-pathogen infection can reduce or enhance the performance of subsequent insect herbivores, depending on whether plant defense traits against the specific pathogen also confer resistance to insect herbivores, or suppress anti-herbivore defenses through crosstalk between defense pathways (Thaler, Humphrey, & Whiteman, 2012).

Pathogenic plant microbes have evolved to establish quickly and spread widely in plant populations. Some phytopathogen species are vectored by herbivorous arthropods, like insects, while others spread through abiotic factors like wind or water (Eigenbrode et al., 2018; Perilla-Henao & Casteel, 2016). Vector-borne phytopathogens can be further characterized by their transmission types, depending on the time of feeding needed for the vector to acquire and transmit the pathogen (persistent, semipersistent, or nonpersistent), and whether the pathogen enters the hemocoel of its vector (circulative or noncirculative) (Eigenbrode et al., 2018; K. Mauck, Bosque-Pérez, Eigenbrode, De Moraes, & Mescher, 2012; K. E. Mauck, 2016). A pathogen's transmission strategy is often related to the nature of its interactions with herbivores. For example, some phytopathogen species, especially those that propagate within their vectors, can directly influence vector behavior or physiology (Killiny, Hijaz, Ebert, & Rogers, 2017; Pelz-Stelinski & Killiny, 2016). For a recent review discussing the direct effects of pathogens on their vectors, see (Eigenbrode et al., 2018). There is also accumulating evidence that

Pathogenic Microbe	Plant Species	Insect Species	Vector Status	Cue	Effect on Insect Foraging	Reference
Fungi						
Podosphaera pannosa	Rose (*Rosa chinensis*)	Beet armyworm (*Spodoptera exigua*)	Non-Vector	Olfactory	Repellent	(Yang, Li, & Yang, 2013)
Sclerotium rolfsii	Peanut (*Arachis hypogaea*)	Beet armyworm	Non-Vector	Olfactory, Gustatory	Attractive	(Cardoza, Lait, Schmelz, Huang, & Tumlinson, 2003; Cardoza, Teal, & Tumlinson, 2003)
Microbotryum violaceum	White campion (*Silene latifolia*)	Lychnis moth (*Hadena bicruris*)	Non-Vector	Olfactory	Repellent	(Dötterl, Jürgens, Wolfe, & Biere, 2009)
Melampsora allii-fragilis	Willow (*Salix x cuspidata*)	Willow leaf beetle (*Plagiodera versicolora*)	Non-Vector	Unknown	Attractive	(Simon & Hilker, 2005)
Phyllosticta paviae	Horse Chestnut (*Aesculus hippocastanum*)	Horse chestnut leaf miner (*Cameraria ohridella*)	Non-Vector	Visual	No Effect	(Jagiełło, Łakomy, Łukowski, & Giertych, 2019)
Botrytis cinerea	Grape (*Vitis vinifera*)	European grapevine moth (*Lobesia botrana*)	Vector	Olfactory	Repellent	(Tasin, Knudsen, & Pertot, 2012)
B. cinerea	Grape	Light brown apple moth (*Epiphyas postvittana*)	Vector	Visual, Olfactory	Repellent	(Rizvi, Raman, Wheatley, Cook, & Nicol, 2015)
Fusarium verticillioides	Maize (*Zea mays*)	African sugar-cane borer (*Eladana saccharina*)	Vector	Visual, Olfactory	Attractive	(Ako, Schulthess, Gumedzoe, & Cardwell, 2003)
Puccinia punctiformis	Creeping thistle (*Cirsium arvense*)	Weevil (*Apion onopordi*)	Vector	Unknown	Attractive	(Friedli & Bacher, 2001)
Ophiostoma novo-ulmi	American Elm (*Ulmus americana*)	Elm bark beetle (*Hylurgopinus rufipes*)	Vector	Olfactory	Attractive	(McLeod et al., 2005)
Bacteria						
Xanthomonas oryzae	Rice (*Oryza sativa*)	Brown rice planthopper (*Nilaparvata lugens*)	Non-Vector	Visual, Olfactory	Attractive	(Sun et al., 2016)
Erwinia tracheiphila	Wild Gourd *(Cucurbita pepo)*	Striped cucumber beetle (*Acalymma vittatum)*	Vector	Olfactory	Attractive	(Shapiro, De Moraes, Stephenson, & Mescher, 2012)
Candidatus Liberibacter asiaticus	Citrus (*Citrus* sp.)	Asian citrus psyllid (*Diaphorina citri*)	Vector	Olfactory, Gustatory	Attractive then Repellent	(Mann et al., 2012)
Candidatus Liberibacter solanacearum	Potato (*Solanum tuberosum*)	Potato Psyllid (*Bactericera cockerelli*)	Vector	Olfactory	Attractive then Repellent	(Davis, Horton, Munyaneza, & Landolt, 2012)
Xylella fastidiosa	Citrus (*Citrus sinensis*)	Sharpshooters, leafhoppers (*Dilobopterus costalimai, Oncometopia facialis*)	Vector	Visual	Repellent or No Effect	(Marucci, Lopes, Vendramim, & Corrente, 2005)
Phytoplasmas						
Candidatus Phytoplasma mali	Apple (*Malus domestica)*	Psyllid (*Cacopsylla picta)*	Vector	Olfactory	Attractive	(Mayer, Vilcinskas, & Gross, 2008a)
Candidatus Phytoplasma vitis	Grape	Leafhopper (*Scaphoideus titanus*)	Vector	Visual	Attractive	(Chuche, Boudon-Padieu, & Thiéry, 2016)
Viruses						
Cucomovirus spp.	Squash (*Cucurbita pepo*)	Green peach aphid (*Myzus persicae),* Melon aphid (*Aphis gossypii*)	Vector	Olfactory, Gustatory	Attractive then Repellent	(K. E. Mauck, De Moraes, & Mescher, 2010; K. E. Mauck et al., 2014)
Cucumovirus spp.	Squash	Squash Bug (Anasa tristis)	Non-Vector	Unknown	Repellent	(K. E. Mauck et al., 2010)
Tunrgovirus spp., *Waikavirus* spp.	Rice	Green rice leafhopper (*Nephotettix virescens*)	Vector	Gustatory	Attractive then Repellent	(Khan & Saxena, 1985)
Sadwavirus spp., *Closterovirus* spp.	Red raspberry (*Rubus idaeus*)	Large raspberry aphid (*Amphorophora idaei*)	Vector	Olfactory, Gustatory	Attractive then No Effect	(McMenemy et al., 2012)
Enamovirus spp.	Fava bean *(Vicia faba)*	Pea aphid (*Acyrthosiphon pisum*)	Vector	Visual	Attractive	(Hodge & Powell, 2010)
Enamovirus spp.	Pea (*Pisum sativum*)	Weevil (*Sitona lineatus*)	Non-Vector	Gustatory	Attractive	(Chisholm, Sertsuvalkul, Casteel, & Crowder, 2018)
Sobemovirus spp., *Comovirus* spp.	Common bean (*Phaseolus vulgaris*)	Mexican bean beetle (*Epilachna varivestis*)	Vector	Unknown	Attractive	(Musser, Hum-Musser, Felton, & Gergerich, 2003)
Polerovirus spp.	Potato	Green peach aphid	Vector	Olfactory	Attractive	(Alvarez et al., 2007; D. Rajabaskar, Ding, Wu, & Eigenbrode, 2013)

Table 2 Plant-Associated Pathogens Modifying Plant Cues That Influence Insect Herbivore Foraging Behavior and Oviposition Behavior.



Polerovirus spp.	Hairy nightshade (*Solanum sarrachoides*)	Green peach aphid	Vector	Olfactory	Attractive	(Srinivasan, Alvarez, Eigenbrode, & Bosque-Pérez, 2006)
Luteovirus spp.	Wheat (*Triticum aestivum*)	Bird cherry-oat aphid	Vector	Olfactory	Attractive	(Jiménez-Martínez et al., 2004)
Comovirus spp., *Potyvirus* spp.	Soybean (*Glycine max*)	Mexican bean beetle, Soybean aphid (*Aphis glycines*)	Vector/ Non-Vector	Gustatory, Olfactory	Attractive	(Peñaflor, Mauck, Alves, De Moraes, & Mescher, 2016)
Tobamovirus spp.	Tomato (*Solanum lycopersicum*)	Green peach aphid	Non-Vector	Unknown	Repellent	(Thaler, Agrawal, & Rayko, 2010)
Crinivirus spp., *Begomovirus* spp.	Tomato	Silverleaf whitefly (*Bemisia tabaci*)	Vector	Visual, Olfactory	Attractive	(Alberto Fereres et al., 2016)
Potyvirus spp.	Potato	Green peach aphid	Vector	Olfactory	Attractive	(Bak, Patton, Perilla-Henao, Aegerter, & Casteel, 2019)
Caulimoviruss spp.	Turnip (*Brassica rapa*)	Turnip aphid (*Lipaphis erysimi*)	Vector	Volatile	Attractive	(Adhab, Finke, & Schoelz, 2019)
Luteovirus spp.	Winter oat (*Avena* spp.), Winter barley (*Hordeum* spp.)	Rose-grain aphid (*Metopolophium dirhodum*), English grain aphid (*Sitobion avenae*)	Vector	Visual	Attractive	(Ajayi & Dewar, 1983)
Potyvirus spp.	Soybean, Pepper (*Capsicum* spp.)	Green peach aphid, Corn aphid *(Rhopalosiphum maidis)*	Vector	Visual	No Effect	(A. Fereres, Kampmeier, & Irwin, 1999)

Table 2 Continued

In this review, we limit our discussion of phytopathogens to their plant-mediated effects on insect herbivore behavior. We focus on plant-pathogenic fungi, bacteria, phytoplasmas, and viruses, as these represent some of the best-characterized examples of phytopathogens influencing interactions between plants and insects. In Table 2, we summarize literature that measured the indirect effects of plant-pathogenic microbes on the foraging or oviposition behaviors of vector and non-vector insect herbivores. We review what is known about how plant pathogens modify visual, olfactory, and gustatory cues in plants, also calling attention to ‘unknown’ cues and outstanding questions in pathogen-plant-insect research to propel future investigation.

VISUAL CUES

Visual cues, in the form of patterns, dimensions, and spectral quality, are perceived by insect optical sensory systems (Prokopy & Owens, 1983). Insect herbivores are equipped with compound eyes, ocelli and/or stemmata to detect visual cues, and use of these cues varies by species and eye morphology. Visual cues are light dependent and most commonly used by diurnal, aboveground organisms (Sétamou et al., 2012). Insect herbivores use visual cues for both long- and short-range plant location (Jönsson et al., 2007) as well as for assessing plant quality (Pan et al., 2015). Combinations of visual cues encoded as physical plant traits like size, shape, texture, reflectance, or color can convey a wide variety of information about plant location (Irwin, Strauss, Storz, Emerson, & Guibert, 2003), nutrition (Kozlov, Zverev, & Zvereva, 2018), and defense status (Karageorgou & Manetas, 2006).

Influence of Beneficial Microbes on Plant-Produced Visual Cues

Visual cues for insect herbivores related to host-plant quality are predominantly influenced by beneficial plant-associated microbes through enhanced or reduced plant growth or biomass. In general, beneficial microbes are predicted to increase plant biomass through enhanced nutrient acquisition (Pineda et al., 2010), decreased drought stress (Gontia-Mishra, Sapre, Sharma, & Tiwari, 2016; Vurukonda, Vardharajula, Shrivastava, & SkZ, 2016), or production of growth-related phytohormones (Contreras-Cornejo, Macías-Rodríguez, Cortés-Penagos, & López-Bucio, 2009; Spaepen, Vanderleyden, & Remans, 2007). Although the effects of beneficial microbes on plant growth and biomass are well-documented, surprisingly few studies have evaluated the influence of these effects on insect herbivore foraging and oviposition. Here, we highlight areas for possible future research by restricting our review to studies that considered the role of beneficial microbes in plant-insect interactions. For example, plant association with AMF was found to increase aboveground plant biomass by 87% across seven herbaceous plant species, and African cotton bollworm mass gain was higher on AMF-associated plants (Kempel, Schmidt, Brandl, & Schädler, 2010). This suggests that foraging or ovipositing insect herbivores could benefit from detecting plants with AMF through visual cues like increased size to enhance their performance or fitness, although AMF-induced positive growth effects may be difficult to disentangle from other abiotic or biotic factors. Microbe-stimulated plant biomass gains are also not likely to affect host-plant discrimination by all species of foraging herbivores or in all contexts (Wurst & Forstreuter, 2010). PGPR-stimulated plant biomass gains were correlated with reduced colonization of beetle herbivores in a field experiment with cucumber plants, although plant size was not likely the driving factor underlying these results (Zehnder, Kloepper, Yao, et al., 1997). Previous studies have also documented variation in plant responses to different species or isolates of beneficial microbes, which can affect insect foraging behavior. Recent work with strawberry demonstrated different AMF isolates had variable effects on multiple plant visual cues, including height, chlorophyll levels, and leaf thickness (Roger et al., 2013). African cotton bollworm larvae preferred plants without AMF in detached leaf assays, however, in whole plant bioassays, they preferred the largest plants regardless of AMF status (Roger et al., 2013). Overall, beneficial microbes can differentially alter plant growth and biomass, which can, in turn, influence the attraction or repellence of foraging insect herbivores in a context-dependent manner. In addition to plant size, herbivores can also recognize physical plant defense structures, which affect host-plant selection. For instance, insect herbivores can recognize and clip plant trichomes to more easily access leaf tissues, although this behavior slows feeding and reduces insect performance (Kariyat et al., 2018). Hence, herbivores may preferentially select plants producing fewer trichomes to increase foraging efficiency. Plant production of such physical defense structures as well as maintenance of microbial mutualisms can incur metabolic costs, indicating a potential trade-off for plants. A recent study found that tomato plants colonized by AMF had reduced trichome densities and increased herbivore performance (Malik, Ali, & Bever, 2018). Although not explicitly tested in this study, insect herbivores could potentially detect a decreased investment in physical defense structures in microbe-associated plants when making foraging or oviposition decisions to enhance their performance or fitness.

Influence of Pathogenic Microbes on Plant-Produced Visual Cues

Plant-pathogenic microbes often modify physical plant traits like size or shape that could provide visual cues for foraging or ovipositing insect herbivores. Plant pathogens also cause visible disease symptoms like mottled tissues (Adhab et al., 2019; Hodge &

Powell, 2010; Musser et al., 2003), necrotic regions (Adhab et al., 2019; Jagiełło et al., 2019), and other color changes that serve as visual cues for insect herbivores (Ajayi & Dewar, 1983; Alberto Fereres et al., 2016; Sun et al., 2016). Several vector-borne phytopathogens have been found to alter plant coloration in ways that enhance plant attraction to their insect vectors. For example, “flavescence dorée” phytoplasma causes yellowing in leaves of grape plants. In visual-based choice tests, leafhopper vectors preferred yellow, diseased plants over healthy, green individuals (Chuche et al., 2016; Chuche, Thiéry, & Mazzoni, 2011; Mazzoni et al., 2011). The spread of this pathogen depends on leafhoppers, and thus increased attraction to plant disease symptoms could increase pathogen transmission. In addition to phytoplasmas, several species of plant viruses (e.g., Luteoviridae) cause yellows diseases that result in yellowing of plant tissues (Bosque-Pérez & Eigenbrode, 2011; Y. Li et al., 2016). Several studies have shown that aphids and whiteflies, which vector many species of viruses, are attracted to the yellow color caused by virus infection (Alberto Fereres et al., 2016; Moericke, 1969). For example, aphids were attracted to visual symptoms of barley yellow dwarf virus on oat and barley in both field and laboratory experiments (Ajayi & Dewar, 1983). Another study reported that pea aphid vectors were attracted to yellowed leaves of fava bean plants infected with pea enation mosaic, bean yellow mosaic, or broad bean mottle viruses (Hodge & Powell, 2010). Aphids did not discriminate between healthy and infected plants when visual cues were removed, indicating that these viruses enhance vector attraction by modifying plant visual cues (Hodge & Powell, 2010).

There is also evidence that non-vector-borne phytopathogens modify plant visual cues. For example, the fungal pathogen, *Phyllosticta paviae*, which induces visible necrotic regions on leaves of infected horse chestnut trees, influences the preference of a non-vector herbivore (Jagiełło et al., 2019). Ovipositing leafminers selectively deposited eggs on uninfected leaves and healthy portions of infected leaves, suggesting the necrotic tissue provided visual cues that reduced herbivore oviposition. Similarly, oviposition by light brown apple moths was lower on grape leaves infected by the necrotrophic fungal pathogen, *Botrytis cinerea*, and the rate of oviposition was inversely related to visual symptoms of infection (Rizvi et al., 2015). Female moths may selectively avoid oviposition on infected plants to increase larval survival, as necrotrophic pathogens ultimately kill host-plant tissues. In contrast, another study reported that brown rice planthoppers preferred rice plants infected by the hemi-biotrophic bacterial pathogen, *Xanthomonas oryzae*. Attraction persisted at 15 days post-inoculation when visual disease symptoms were severe but olfactory cues of infected plants were not different from healthy plants, indicating visual cues played an important role in planthopper attraction (Sun et al., 2016). As non-vector herbivores, foraging planthoppers may detect and capitalize on weakened defenses of infected plants for their own benefit.

OLFACTORY CUES

Olfactory cues are volatile chemical compounds that insects perceive using receptors located on olfactory organs, including the antennae, labial and maxillary palps, and ovipositor (Touhara & Vosshall, 2009). Most insect herbivores rely on olfactory cues from plants during at least one stage of the foraging process. Many insect species use plant-produced volatile compounds to locate and evaluate potential host plants (Szendrei & Rodriguez-Saona, 2010) as these cues effectively transmit useful information over both short (Egonyu, Ekesi, Kabaru, Irungu, & Torto, 2013) and long (Ballhorn, Kautz, & Heil, 2013) distances in a variety of environments. Olfactory cues can be general indicators of plant presence, for example the respiratory biproduct CO2 (Schumann et al., 2018), or complex blends of volatile organic compounds (VOCs) that convey detailed information about plant identity (Bruce et al., 2005), nutrient content (Goff & Klee, 2006), defense status, or risk of predation by natural enemies (Helms et al., 2019; Low, McArthur, Fisher, & Hochuli, 2014). Plants emit characteristic blends of VOCs that vary by plant species, genotype, developmental stage, and tissue (Maffei, 2010). The production of plant volatiles is a dynamic process altered by pathogen infection, mechanical wounding or feeding by different herbivore species, resulting in quantitative or qualitative changes in volatile profile (Maffei, 2010). These induced VOC blends convey additional information to herbivores about changes in environmental conditions. Plant VOCs also play important roles in direct defense against herbivores and pathogens, as some volatile compounds have toxic or anti-microbial properties (Brzozowski, Mazourek, & Agrawal, 2019) or deter foraging or oviposition by herbivores (Unsicker, Kunert, & Gershenzon, 2009). Plant volatiles induced by herbivore or pathogen attack also provide indirect protection for plants by recruiting herbivore natural enemies

(Clavijo McCormick, Unsicker, & Gershenzon, 2012) or beneficial microbes (Schulz-Bohm et al., 2018). In summary, foraging or ovipositing herbivores interpret a diversity of information through olfactory cues to select acceptable host plants.

Influence of Beneficial Microbes on Plant-Produced Olfactory Cues

Plant associations with beneficial microbes can alter production of plant volatiles and modify host-plant selection by insect herbivores. For example, AMF associations with fava bean suppressed plant VOC emissions (specifically, naphthalene, (S)-linalool, (*E*)-caryophyllene, and (R)-germacrene D) and increased attraction of aphids to plants with AMF (Babikova, Gilbert, Bruce, et al., 2014; Babikova, Gilbert, Randall, et al., 2014). Additionally, microbially altered plant VOCs can influence female herbivore oviposition. For instance, in tomato, root endophyte colonization quantitatively reduced VOC production—except for trans-β-caryophyllene, which plants produced in higher quantities when associating with endophytes—and resulted in increased cotton bollworm oviposition on endophyte-associated plants (Jallow et al., 2008). In contrast, PGPR association modified the VOC profile of maize plants, suppressing production of (*E*)-5-methyl-2-methylene-2-hexen-1-ol and decreasing European corn borer oviposition (Disi, Kloepper, et al., 2018). Foliar endophytes in perennial ryegrass also deterred host selection in female African black beetles, increasing 2-ethyl-1-hexanol acetate and decreasing dodecane emissions (Qawasmeh et al., 2015). Another study reported no difference in constitutive VOC production by lima bean plants with *Rhizobia* compared to unassociated plants. However, following plant wounding, the VOC blend emitted by *Rhizobia*-associated plants differed from that of unassociated plants and was less attractive to Mexican bean beetles (Ballhorn, Kautz, & Schädler, 2013). In addition to these explicit tests for foraging behavior and host-plant selection, we also highlight other studies which noted microbe-induced changes in plant VOCs and suggest these systems serve as avenues of future investigation on herbivore foraging and oviposition behavior (Fontana, Reichelt, Hempel, Gershenzon, & Unsicker, 2009; Leitner, Kaiser, Hause, Boland, & Mithöfer, 2010; T. Li, Blande, Gundel, Helander, & Saikkonen, 2014; Meier & Hunter, 2019).

In contrast to foraging by aboveground herbivores, soil-dwelling herbivores often rely primarily on olfactory cues to locate host plants (Johnson & Nielsen, 2012). Beneficial plant-associated microbes can alter belowground olfactory cues, which attract or repel belowground herbivores, depending on the interaction. For instance, an aboveground foliar endophyte of a grass hybrid increased belowground CO2 and suppressed root volatile emissions, repelling a foraging root herbivore (Rostás et al., 2015). PGPR associating with maize roots were recently shown to alter root VOC profiles, including *E*-β-caryophyllene production (Chiriboga et al., 2018; Disi, Mohammad, Lawrence, Kloepper, & Fadamiro, 2019). However, maize roots only enhanced production of *E*-β-caryophyllene following root herbivore damage, suggesting ISR-mediated priming of defenses in roots following herbivory(Chiriboga et al., 2018). The volatile compound, *E*-

β-caryophyllene, is involved in host-plant selection by root-feeding western corn rootworm larvae, suggesting PGPR-colonized maize roots could be more attractive to subsequent herbivores (Disi, Kloepper, et al., 2018; Robert, Erb, Duployer, et al., 2012). Root herbivore reliance on olfactory cues indicates microbe-modified plant cues are likely to have a significant impact on belowground interactions.

Influence of Pathogenic Microbes on Plant-Produced Olfactory Cues

Olfactory cues from plants are frequently altered by pathogen infection, and these changes depend on the plant and pathogen species, as well as the progression of disease symptoms (Dheivasigamani Rajabaskar, Wu, Bosque-Pérez, & Eigenbrode, 2013; Werner, Mowry, Bosque-Pérez, Ding, & Eigenbrode, 2009). Plant production of volatile compounds may be modified by pathogenic microbes to influence vector behavior and benefit pathogen spread and can also affect the behavior of non-vector herbivores. For example, a non-vector species, European grapevine moth, avoided laying eggs on grape plants infected with the necrotrophic fungal pathogen, *Botrytis cinerea*, as infected plants emitted greater amounts of herbivore-repellent 3-methyl-1-butanol (Tasin et al., 2012). A similar experiment showed that beet armyworm moths, a non-vector of biotrophic rose powdery mildew, were repelled by volatiles from infected rose plants (Yang et al., 2013). Another study reported that infection with anther smut fungus reduced floral VOCs (specifically, lilac aldehyde) in white campion flowers which deterred *Hadena bicruris* moths. These moths do not vector anther smut fungus. Their larvae, which are seed predators of white campion, have reduced performance when feeding on seeds of infected plants (Dötterl et al., 2009). Based on the current literature, it appears that some species of non-vector herbivores detect pathogen-altered plant olfactory cues and avoid infected plants. This could benefit both the pathogen and non-vector herbivore through decreased competition for shared plant resources.

In contrast to phytopathogen interactions with non-vector herbivores, insect-vectored phytopathogens modify the olfactory cues of their host plants to increase vector attraction and enhance their transmission (Eigenbrode et al., 2018; K. E. Mauck et al., 2016). The first documented example of such manipulation revealed that potato plants infected with potato leafroll virus had altered VOCs that more strongly attracted the insect vector, green peach aphid, compared to uninfected plants (Eigenbrode, Ding, Shiel, & Berger, 2002). Subsequent studies of other virus-plant-vector species combinations have reported similar findings of virus modification of plant VOCs with enhanced vector attraction to infected plants. This phenomenon has been observed for viruses with different transmission mechanisms including persistently, non-persistently, and semi-persistently transmitted viruses (Jiménez-Martínez et al., 2004; K. E. Mauck et al., 2010; Srinivasan et al., 2006; Tao et al., 2017). In addition to plant viruses, recent evidence suggests that insect-vectored bacterial pathogens also alter plant olfactory cues to enhance their transmission. For example, wild gourd plants infected with bacterial wilt emitted increased foliar VOCs (e.g., hexenal, E-2-hexenol, and ocimene) and reduced floral VOCs (e.g., 1,4-methoxybenzene). The insect vector, striped cucumber beetle, was more attracted to foliage of infected plants but dispersed to aggregate in healthy flowers, which increases bacterial transmission in this pathosystem (Shapiro et al., 2012). Another study reported that citrus trees infected with the pathogenic bacteria, *Candidatus Liberibacter* asiaticus, produced a different blend of VOCs (specifically, increased methyl salicylate and decreased methyl anthranilate and D-limonene) than non-infected plants and were initially more attractive to the citrus psyllid vector (Mann et al., 2012). This attraction was also observed in apple trees infected with the phytoplasma, *Candidatus Phytoplasma* mali. Infected apple trees released greater amounts of the compound E-β-caryophyllene which was highly attractive to the vector psyllid in field and laboratory experiments (Mayer, Vilcinskas, & Gross, 2008b; Mayer et al., 2008a). In general, these studies suggest that vector-borne phytopathogens commonly induce olfactory changes in plants that exaggerate existing host location cues to enhance vector attraction and increase subsequent pathogen transmission.

GUSTATORY CUES

Gustatory cues are non-volatile chemical compounds that insects perceive using gustatory receptors located on organs such as the antennae, mouthparts, tarsi, and ovipositor (Mitchell, Itagaki, & Rivet, 1999). Insect herbivores often use plant gustatory cues to evaluate the nutrient content or defense status of potential host plants to make foraging or oviposition decisions (Backus et al., 2019). Use of plant gustatory cues by herbivores in terrestrial environments requires physical contact and is typically involved in assessment of plant quality following initial location (Sisterson, 2008). Plant gustatory cues are often altered by plant interactions with herbivores or microorganisms and thus provide herbivores with ecologically relevant information related to plant quality (Machado, Arce, Ferrieri, Baldwin, & Erb, 2015). Examples of gustatory cues commonly used by insect herbivores include plant defensive secondary metabolites (Nishida, 2014) or plant nutrients (Moran & Thompson, 2001) like sugars and amino acids. Furthermore, we recognize that herbivores often detect gustatory cues through feeding, which itself damages plant tissues, introduces oral secretions, and triggers changes in plant metabolites (Acevedo, Rivera-Vega, Chung, Ray, & Felton, 2015). Therefore, we predict that interactions between microbe-altered and herbivore-induced gustatory cues will frequently occur.

Influence of Beneficial Microbes on Plant-Produced Gustatory Cues

Beneficial microbes can directly increase nutrient acquisition in plants, thereby enhancing the quality of food resources available for insect herbivores. For example, AMF association increased phosphorus and nitrogen levels in rice, which enhanced attraction of ovipositing female rice water weevils (Cosme et al., 2011). In another study, however, AMF-inoculated *T. vulgare* plants also had increased phosphorus and nitrogen concentrations, but this increase had no effect on aphid preference (Wurst & Forstreuter, 2010). Associations with beneficial microbes can also alter the production of plant defense compounds, suggesting the possibility of interactions between plant nutrients and defense compounds that can influence herbivore host-plant selection. For instance, plant inoculation with AMF differentially altered plant nutrients (levels of nitrogen and phosphorous), as well as defense compounds (foliar cardenolides and latex exudation), depending on the species of milkweed (*Asclepias* spp.) (Tao, Ahmad, de Roode, & Hunter, 2016). A milkweed specialist herbivore, the monarch butterfly (*Danaus plexippus*), prefers to oviposit on plants with low levels of cardenolides, suggesting that AMF colonization has the potential to modify monarch oviposition preferences (Jones & Agrawal, 2019).

Microbe-altered plant defenses also deter or attract insect herbivores depending on their ability to physiologically process particular compounds. For instance, PGPR-associated cucumber plants had decreased levels of cucurbitacin C, a bitter defense compound produced by cucurbits (Zehnder, Kloepper, Tuzun, et al., 1997). Cucurbitacins, although toxic to most generalist herbivores, are attractive and stimulate feeding in some coevolved herbivore species like spotted cucumber beetles. Previous research suggests PGPR-mediated reduction of cucurbitacin C, which reduced beetle feeding damage, could also decrease attraction in foraging or ovipositing beetles (Zehnder, Kloepper, Yao, et al., 1997). In contrast, another study reported that cotton plants (*Gossypium hirsutum*) treated with PGPR had increased levels of the defense compound gossypol and increased expression of genes that regulate its production, resulting in decreased performance of beet armyworm larvae on PGPR plants (Zebelo, Song, Kloepper, &

Fadamiro, 2016). As a generalist herbivore, beet armyworm may avoid PGPR-associated cotton plants with increased gossypol that reduce its performance.

Recent evidence also indicates that beneficial microbes alter plant responses to herbivore damage, which may have cascading effects on insect herbivore behavior. For example, AMF-associated P. lanceolata plants differed in constitutive levels of chemical defenses depending on the AMF species. AMF-associated plants also had reduced induction of defense compounds (e.g., iridoid glycosides) following herbivory, which could influence host-plant selection by subsequent herbivores (Bennett, Bever, & Deane Bowers, 2009). The continued exploration into species-level or genotypic variation in plant responses to beneficial microbes, and perhaps herbivores, will provide greater insight into the mechanisms driving host-plant selection by insect herbivores on microbe-associated plants.

Influence of Pathogenic Microbes on Plant-Produced Gustatory Cues

Pathogenic microbes modify plant gustatory cues through changes in defensive metabolites or plant nutritional quality. Altered levels of plant nutrients, including nitrogen, phosphorus, calcium, sugar, and amino acids, can influence host-plant quality for subsequent vector and non-vector insect herbivores (Jensen, 1972; K. E. Mauck et al., 2010, 2014; Orlob & Arny, 1961). For example, peanut plants infected with white mold fungus had elevated levels of soluble sugars and were more attractive to ovipositing beet armyworm moths(Cardoza, Lait, et al., 2003; Cardoza, Teal, et al., 2003). Recognizing enhanced nutrient content in diseased plants suggests a general benefit for insect herbivores, including non-vectors, as plant-derived nutrients are essential for herbivore growth and development. However, studies of how plant pathogens affect gustatory cues used by non-vector herbivores are not well represented in the literature. We propose that gustation plays an important role in influencing non-vector foraging and oviposition on pathogen-infected plants and merits further study. Similar to visual and olfactory cues, there are numerous examples suggesting vector-borne phytopathogens alter plant gustatory cues to modify vector behavior and promote their transmission success (Carmo-Sousa, Moreno, Garzo, & Fereres, 2014; Khan & Saxena, 1985; Mann et al., 2012; K. E. Mauck et al., 2010). For example, infection of squash plants with cucumber mosaic virus (CMV) disrupted carbohydrate and amino acid ratios in phloem, and enhanced plant defense responses, reducing plant quality for the vector herbivore, green peach aphid (K. E. Mauck et al., 2014). Aphids detected these altered gustatory cues and rapidly dispersed to healthy plants after initial feeding on CMV-infected plants (K. E. Mauck et al., 2010). In another study, rice plants infected with tungro disease had increased free sugars and reduced soluble proteins. Vector leafhoppers preferentially fed on infected plants for up to 24 h before dispersing and settling on non-infected plants (Khan & Saxena, 1985). We note that gustatory cues primarily affected dispersal behavior in these systems, while initial host-plant attraction was typically mediated by changes in olfactory cues. Hence, pathogens may benefit from modifying suites of foraging cues that play different roles in vector attraction to infected plants and subsequent dispersal to healthy plants.

Plants co-infected with multiple vector-borne pathogens are a common occurrence in natural and agricultural ecosystems. In these cases, multiple pathogens may alter different cues within a single, shared host plant and change foraging behaviors of multiple vector species. One recent study investigated how soybean plants singly or co-infected with two plant viruses influenced plant attraction and palatability for two insect herbivore species. Soybean plants co-infected with bean pod mottle virus (BPMV) and soybean mosaic virus (SMV) were equally attractive to Mexican bean beetles and soybean aphids compared to healthy control plants. However, when plants were individually infected with either virus, the vector of BPMV (Mexican bean beetle) was more attracted to the virus-infected plants, which had higher levels of glucose. The vector of SMV, soybean aphid, was more attracted to SMV-infected, but not BPMV-infected plants, compared to healthy plants. This was correlated with lower levels of defense-related phytohormones (e.g., jasmonic acid) produced by SMV-infected and BPMV+SMV co-infected plants, altering plant attractiveness in a virus and vector-specific manner (Peñaflor et al., 2016). Although this is a single example, plant-pathogen co-infection is also likely to modify plant gustatory cues in other pathosystems and influence pathogen transmission dynamics.

CONCLUSIONS AND PERSPECTIVES FOR FUTURE RESEARCH

In nature, plants frequently interact with beneficial and pathogenic microorganisms. Here we reviewed the current literature and discussed different ways plant-associated microbes alter plant traits and indirectly influence plant interactions with insect herbivores. Both beneficial and pathogenic plant-associated microbes can modify visual, olfactory, and gustatory cues of their host plants in ways that affect the foraging and oviposition behavior of subsequent insect herbivores. Overall, our review revealed a limited number of studies have explicitly quantified the influence of plant-associated microbes on plant traits and the corresponding influence on herbivore host-plant selection. Among studies identifying specific plant cues mediating herbivore behavior, olfactory cues were most widely reported for both beneficial and plant-pathogenic species. This finding could reflect the relative importance of olfactory cues for mediating herbivore foraging decisions or could be the result of publication bias where many studies chose to focus on olfactory-based cues.

The majority of research in this area, to date, has focused on vector-borne phytopathogens altering plant cues for herbivore vectors. In general, vector-borne pathogenic microbes modified plant cues and the behavior of herbivore vectors in ways predictive of enhanced pathogen transmission, suggesting pathogen manipulation of both host plants and vectors (Table 2). On the other hand, non-vectored phytopathogens variably affected plant cues and insect herbivore behavior. Commonly, non-vector herbivore preference for infected or uninfected plants was correlated with herbivore performance on those plants. In contrast, beneficial plant microbes had inconsistent effects on plant visual, olfactory, and gustatory cues and the influence of these cues on herbivore behavior varied greatly among the combinations of microbe-plant-herbivore species studied (Table 1). Outcomes may vary so widely due to the facultative nature of plant interactions with beneficial microbes, dynamically oscillating to and from mutualism, which indirectly shape plant-insect interactions. We also note that very few studies have examined how plant microbes alter cues in belowground plant tissues and how these changes influence the behavior of soil-dwelling herbivores. Future research is needed to expand our current knowledge on the mechanisms of how plant-associated microbes indirectly influence herbivore behavior through modified plant cues, evaluating multiple plant cues to form a better understanding of these tripartite interactions.

Within the current literature, the majority of studies have focused on microbe-plant-herbivore interactions in agriculturally important crop plants and have rarely considered the influence of plant domestication or plant genetic variation on these interactions. Some notable exceptions include, a comparison of plant infection with potato leafroll virus in cultivated potato and wild solanaceous hairy nightshade plants. These studies found higher attraction of the vector herbivore, green peach aphid, to wild over cultivated plants, as well as increased attraction for virus-infected plants of both species

(Eigenbrode et al., 2002; Srinivasan et al., 2006). Another recent study examined the effects of turnip yellows virus (genus *Tymovirus*) across a spectrum of domestication from cultivated false flax (Camelina sativa), a wild congener (*C. microcarpa*), and a hybrid of these two species. This study identified differences in plant susceptibility to virus infection and attraction of the vector, green peach aphid, among plant species (Chesnais et al., 2019). In general, plant domestication is correlated with reduced plant resistance to herbivores, although there is not a clear pattern for differences in specific resistance traits among plant species (Whitehead, Turcotte, & Poveda, 2017). This highlights the need for additional comparative studies of microbe-plant-herbivore interactions in domesticated plant species and their wild relatives to uncover broader patterns of how plant domestication affects microbially mediated changes in plant traits that influence herbivore behavior.

Most studies of microbe–plant–herbivore interactions to date have focused on tripartite interactions within controlled environmental conditions. A few exceptions include studies that have considered abiotic factors like soil nutrients (Vannette & Hunter, 2011) or drought stress (de Bobadilla et al., 2017). There is abundant evidence that abiotic factors, such as water or nutrient availability (Gershenzon, 1984), solar radiation (Dillon, Chludil, Reichelt, Mithöfer, & Zavala, 2018), and temperature (Hahn, Agrawal, Sussman, & Maron, 2019) influence plant physiology and defensive traits. Abiotically mediated changes in plant defenses affect the outcomes of plant interactions with beneficial and pathogenic microbes, in addition to herbivores. For example, if stressful abiotic conditions result in reduced plant defenses, plant-associated microbes might exert a stronger influence over plant phenotypes that affect subsequent herbivores. Alternatively, reduced plant defensive potential could result in reduced responsiveness of plant traits to microbial-induced changes, especially for olfactory cues like plant volatiles or gustatory cues like defensive metabolites. Moreover, abiotic conditions also disrupt plant interactions with beneficial microbes (Pineda et al., 2013). For example, plant-AMF associations shift from beneficial to parasitic in higher nutrient environments (Johnson, Graham, & Smith, 1997) and such shifts are likely to influence plant traits and subsequent interactions with herbivores. Future studies including abiotic variation are needed to better understand microbe-plant-herbivore tripartite interactions in a more realistic context and to gain insights into how such interactions might be affected in a changing climate (Pineda et al., 2013) .

Additional areas of microbe-plant-herbivore interactions that deserve more attention in future work are plant associations with multiple beneficial and/or pathogenic microbes, as well as the influences of insect-associated microbial symbionts. As discussed above, a recent study determined that co-infections or co-associations of multiple microbe species within a host plant are likely to affect the outcomes of herbivore foraging (Peñaflor et al., 2016). Additionally, although outside the scope of this review, insect herbivores often rely on microbial symbionts to overcome host-plant defenses (Ben-Yosef, Pasternak, Jurkevitch, & Yuval, 2015), obtain nutrients (Body, Kaiser, Dubreuil, Casas, & Giron, 2013), or biosynthesize nutrients the insect needs but the plant does not provide (Hansen & Moran, 2014). Future studies combining these distinct areas of microbial research (plant-associated and insect-associated) will further advance our understanding of the role microbes play in plant-insect interactions. We especially advocate for research on the interactive effects of plant-associated and insect-associated microbes on insect herbivore foraging and oviposition. Finally, future studies comprising a greater number and diversity of microbial and/or insect-herbivore species sharing a common host plant will provide a more realistic view of multipartite interactions and have the potential to reveal new ecological patterns within these interactions.

CHAPTER III

RISKY ROOTS AND CAREFUL HERBIVORES: SUSTAINED HERBIVORY BY A ROOT-FEEDING HERBIVORE ATTENUATES INDIRECT PLANT DEFENCES[2]

INTRODUCTION

Chemical information plays key roles in ecological interactions across trophic levels, as organisms forage for food while attempting to avoid competition and natural enemies (Mescher & De Moraes, 2015; Raguso et al., 2015). Insect herbivores frequently rely on olfactory cues from plants to find and evaluate hosts for feeding or oviposition, as plant-produced volatiles provide ecologically relevant information about plant identity, nutritional content, and defense status (Bruce & Pickett, 2011; De Moraes et al., 2001; Grunseich, Thompson, Aguirre, & Helms, 2020). It is well known that herbivore feeding triggers the production of distinct herbivore-induced plant volatiles (HIPVs), which can directly repel herbivores (Bernasconi, Turlings, Ambrosetti, Bassetti, & Dorn, 1998; De Moraes et al., 2001; Ray et al., 2020) or indirectly protect plants by attracting natural enemies that kill herbivores (Aartsma, Bianchi, van der Werf, Poelman, & Dicke, 2017; Allmann & Baldwin, 2010; De Moraes, Lewis, Pare, Alborn, & Tumiinson, 1998; De Moraes et al., 2001; Kessler & Heil, 2011; T. C.J. Turlings, Tumlinson, & Lewis, 1990).

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[2] Reprinted with permission from "Risky roots and careful herbivores: Sustained herbivory by a root-feeding herbivore attenuates indirect plant defences" by John Grunseich, Morgan N. Thompson, Allison A. Hay, Zachary Gorman, Michael V. Kolomiets, Micky D. Eubanks, and Anjel M. Helms, 2020. *Functional Ecology*, 34(9), 1779-1789

Herbivore avoidance of HIPVs is theorized to be a mechanism to enhance their survival or fitness by evading competition, induced plant defenses, and increased risk of predation by natural enemies (Bernasconi et al., 1998; De Moraes et al., 2001; Kariyat et al., 2013). Here, we test this prediction in a belowground tritrophic system, to investigate the roles of volatiles from plant roots in guiding foraging decisions by herbivores and their natural enemies.

The majority of research on chemically mediated plant-insect interactions has focused on aboveground systems, however, there is growing recognition that volatiles from plant roots facilitate a diversity of ecological interactions belowground (Johnson & Gregory, 2006; Johnson & Nielsen, 2012; Rasmann, Hiltpold, & Ali, 2012; van Dam, Weinhold, & Garbeva, 2016; Wenke, Kai, & Piechulla, 2010). These include plant allelopathy (Huang, Gfeller, & Erb, 2019), growth promotion (Gfeller et al., 2019), and protection against pathogen infection (Lackus et al., 2018). Similar to aboveground plant tissues, roots also modify their production of volatiles in response to stressors, such as pathogen infection (Schulz-Bohm et al., 2018) or herbivory (Abraham, Giacomuzzi, & Angeli, 2015; Pierre et al., 2011). Although our understanding of herbivore-induced root volatiles and their roles in belowground interactions is limited, increasing evidence suggests that HIPVs from plant roots can influence foraging by herbivores (Robert, Erb, Duployer, et al., 2012) and their natural enemies (Ali et al., 2010; Rasmann et al., 2005; Tonelli et al., 2016). One of the best-studied examples is the production of HIPVs from maize roots following herbivory by western corn rootworm larvae (*Diabrotica virgifera virgifera*) (Köllner et al., 2008; Rasmann et al., 2005; Robert, Erb, Hibbard, et al., 2012; Robert, Veyrat, et al., 2012). Maize root HIPVs attract *D. virgifera* larvae, which experience enhanced performance on plants with conspecific herbivory (Robert, Erb, Duployer, et al., 2012; Robert, Veyrat, et al., 2012), and recruit entomopathogenic nematodes (EPNs), which are natural enemies of root-feeding insects (Hiltpold, Erb, Robert, & Turlings, 2011; Rasmann et al., 2005). This suggests that root herbivores can face critical trade-offs when using root HIPVs as foraging cues while also avoiding natural enemies. Our knowledge of these trade-offs in belowground systems and across different plant, herbivore, and natural enemy communities, however, remains limited, and additional research is needed to elucidate the ecological and evolutionary outcomes.

As emphasized in the above examples, plant volatile production is a dynamic process where volatile blends are modified in response to environmental changes and blend compositions fluctuate over time. Diurnal rhythms of constitutive and induced volatile production are well-documented (De Moraes et al., 2001; Naranjo-Guevara, Peñaflor, Cabezas-Guerrero, & Bento, 2017; Ted C.J. Turlings & Erb, 2018), with more recent studies investigating the role of plant circadian clocks in regulating these changes (Arimura et al., 2008; Joo et al., 2019). Emitted blends of HIPVs also change throughout the duration of herbivory. For example, some compounds are emitted rapidly following initiation of damage, while production of other compounds may be delayed by several hours (Erb et al., 2015; Joo et al., 2018; Ponzio, Gols, Pieterse, & Dicke, 2013). Some studies have observed stronger production of HIPVs with increased herbivore damage (Boer, Hordijk, Posthumus, & Dicke, 2008; Marcel Dicke, Van Loon, & Soler, 2009; Maeda & Takabayashi, 2001), while others have reported suppression of HIPVs with continuous feeding (Alba, Glas, Schimmel, & Kant, 2011; Desurmont et al., 2014; Takai et al., 2018). The temporal dynamics of plant volatile production influence the outcomes of ecological interactions, including the timing and magnitude of natural enemy or pollinator recruitment (Balao, Herrera, Talavera, & Dötterl, 2011; Joo et al., 2018; Kant, Ament, Sabelis, Haring, & Schuurink, 2004). A few studies have investigated production of root volatiles at multiple timepoints (Crespo et al., 2012; Danner et al., 2015; Deasy, Shepherd, Alexander, Birch, & Evans, 2016; van Dam, Samudrala, Harren, & Cristescu, 2012), however, it is currently not understood how root HIPVs change during sustained herbivory, and temporal variation in root HIPVs has not been correlated with ecological interactions.

The goal of this study was to investigate how belowground insect herbivores use olfactory cues from plant roots to navigate the conflict of locating suitable host plants while avoiding predation. Here, we examined the role of HIPVs from roots of cucumber plants (*Cucumis sativus*) in mediating foraging decisions by larvae of the specialist cucumber beetle (*Acalymma vittatum*) and their entomopathogenic nematode (EPN) natural enemies. We predicted that cucumber roots emit HIPVs in response to herbivory from *A. vittatum* larvae and that these HIPVs function as an indirect defense by recruiting larvae-killing EPNs (Ali et al., 2010; Ali, Alborn, & Stelinski, 2011; C. D. Ellers-Kirk et al., 2000; Rasmann et al., 2005). Due to the role of HIPVs in plant defense, we hypothesized that *A. vittatum* larvae avoid cues from conspecific-damaged roots to avoid induced indirect plant defenses that could reduce larval performance or survival. To characterize the temporal dynamics of these interactions, we quantified changes in root HIPVs following short-term (24 h) and sustained (7 d) herbivory and we investigated the influence of these changes on *A. vittatum* and EPN behavior. We predicted that cucumber root HIPVs change over time with sustained herbivory by *A. vittatum* larvae, influencing the attraction of both herbivores and natural enemies. By linking herbivore and natural enemy responses to root HIPVs, we shed light on how the challenges of foraging, while avoiding competition and predation, guide herbivore behavior. Through examining these interactions over time, we can determine the ecological consequences and significance of the temporal dynamics of induced plant defenses.

MATERIAL AND METHODS

Plants, insects and nematodes

Cucumber plants (*C. sativus* cv. Max Pack) were grown from seed (Johnny's Selected Seeds, USA) and used in experiments after 3-4 weeks of growth. Plants were grown in individual pots in topsoil mix (Hyponex Corporation, USA) with 3 g Osmocote®

fertilizer (15-9-12 N-P-K; Scotts, USA) and were kept in an insect-free, climate-controlled growth room with supplemental lighting (16 h light: 8 h dark; 22°C: 29°C; 56% RH, Fluence, USA). Striped cucumber beetles (*A. vittatum*) were maintained in a laboratory colony on cultivated squash (*Cucurbita pepo* cv. Raven) that was periodically supplemented with wild-caught adults. Entomopathogenic nematodes (EPNs; *Heterorhabditis bacteriophora*) used in this study are commercially available generalists used for biological control of *A. vittatum* (C. D. Ellers-Kirk et al., 2000). EPNs were cultured in last-instar wax moth larvae *(Galleria mellonella*) at 27°C. Infective juveniles were harvested in White traps (White, 1927) and used within 24 h of emergence.

Collection and analysis of root volatiles

To determine how herbivory by *A. vittatum* larvae affects production of olfactory cues from cucumber roots, we used dynamic headspace sampling to characterize the volatile profiles emitted by damaged and control roots after 24 h and 7 d (Ali et al., 2010). Prior to collections, seedlings were transplanted into individual glass pots (5 cm diameter) containing clean sand (10% water W/V) and allowed to acclimate for 24 h. One group of plants (n = 11) each received 5 second-instar *A. vittatum* larvae for 24 h, one group (n = 9) received mechanical wounding (roots pierced with a metal spatula once every 8 hours for 24 h), and another group was kept as undamaged controls (n = 11). Collections were repeated with plants damaged by 5 second-instar *A. vittatum* larvae for 7 d (n = 11), plants with 7 d mechanical wounding (n = 5), and 7 d controls (n = 11). VOCs were also collected from chambers containing only clean sand as negative controls. Vacuum pumps were used to gently pull air over roots (100 ml min^{-1}) and through an adsorbent filter trap containing 60 mg of HaySep® Q (Hayes Separations, Inc, USA) for 8 h (14:00-22:00). Compounds were eluted from filter traps using 150 µl dichloromethane. A 5 µl aliquot of standard solution containing nonyl acetate (80 ng μl^{-1}) was added to each sample. Roots were harvested, washed, and dried, and root dry mass was recorded. After each collection, larvae were recovered and confirmed to be feeding.

VOCs were analyzed using an Agilent 7890B gas chromatograph and 5977B mass spectrometer with a splitless injector held at 250°C and helium as the carrier gas. After sample injection (1 µl), the column (HP-5MS 30 m x 0.250 mm-ID, 0.25 µm film thickness, Agilent Technologies, USA) was held at 40°C for 5 min before the temperature was increased at 20°C min^{-1} to 250°C. Compounds were ionized by electron impact ionization at 70 eV and mass spectra were acquired by scanning from 40 to 300 m/z at 5.30 scans s^{-1}. Tentative identification of target compounds was achieved by comparison with mass spectral libraries (NIST17, Adams2 (Allured Publishing Corporation), and a University of Göteborg library), and structure assignments were confirmed where possible by comparison of mass spectra and retention times with authentic standards (Helms et al., 2019). Compounds were quantified relative to standard concentrations and calculated as ng g^{-1} dried root mass.

Larval preference assays

We conducted dual-choice experiments using belowground olfactometers to assess the effect of olfactory cues from cucumber roots on larval foraging behavior (Robert, Erb, Duployer, et al., 2012). One day after collecting root volatiles (24 h or 7 d), the same plants were used for larval preference experiments (48 h and 8 d). An initial experiment was conducted to verify that *A. vittatum* larvae prefer olfactory cues from cucumber roots over sand (n = 11). A second experiment was conducted to determine whether larvae differentiate between volatiles from undamaged cucumber roots and HIPVs from roots damaged by conspecifics for 48 h (n = 26). Finally, a third assay was conducted to determine whether larvae prefer volatile cues from undamaged roots or cues from roots damaged by conspecifics for 8 d (n = 20). Olfactometers were assembled 30 min prior to experiments and covered to exclude light. Pots were connected with a central glass arm (13 cm) and wire mesh barriers were used to prevent larval movement into pots and larval contact with roots. Five second-instar larvae were added to each center arm, recovered after 20 min, and their positions recorded. Treatment orientations were randomized to account for potential directional bias. Larvae were recovered from herbivory treatments to confirm active feeding.

EPN preference assays

To determine whether EPNs use cucumber root HIPVs while foraging for insect hosts, dual-choice experiments were performed using belowground olfactometers. Cucumber seedlings were transplanted into glass pots in 1:1 sand: topsoil mix (10% water W/V) and allowed to acclimate for 24 h. Plants were each damaged by 5 second-instar *A. vittatum* larvae (n = 12) for 24 h or 7 d, or were kept as undamaged controls (n = 12). Separate pairwise comparisons were conducted to determine EPN preference for 1) volatile cues from undamaged roots vs. HIPVs from roots damaged by larvae for 24 h, and 2) volatile cues from undamaged roots vs. cues from roots damaged by larvae for 7 d. Olfactometers were assembled with a central arm (36 cm) 1h prior to experiments and covered to exclude light and olfactometer orientation was randomized among trials. Wire 400 mesh screen (MSC Industrial Supply, USA) barriers prevented EPNs from moving into pots. EPN infective juveniles (2,500) were added to the center of each arm and their positions were recorded after 48 h (Willett, Alborn, Duncan, & Stelinski, 2015). EPNs were extracted from sand using an adapted Baermann funnel method (MacMillan, Blok, Young, Crawford, & Wilson, 2006). After experiments, beetle larvae from damage treatments were recovered and confirmed to be feeding.

Larval performance assays

We conducted larval performance experiments to quantify the influence of prior conspecific herbivory on *A. vittatum* larvae (Robert, Erb, Hibbard, et al., 2012). Cucumber seedlings were transplanted into sand and allowed to acclimate for 24 h. In the first experiment, plants were damaged by 5 second-instar *A. vittatum* larvae for 24 h (n = 23) or kept as undamaged controls (n = 23). After 24 h damage, larvae were removed, and all plants were transplanted into new, individual pots. A second cohort of second-instar *A. vittatum* larvae were weighed and individual larvae were placed on each plant. Larvae were allowed to feed for 24 h, then were removed and reweighed. Following these methods, a second bioassay was conducted to compare larval performance on plants damaged for 7 d (n = 12) and undamaged plants (n = 12).

Root consumption assay

To determine whether herbivory by *A. vittatum* larvae affects the availability of resources for conspecifics (resource competition), we quantified the influence of herbivory on root loss/growth and plant mortality. Roots of 3-week old cucumber seedlings were washed, and initial root mass was recorded. Seedlings were transplanted into individual pots with a 1:1 sand: topsoil mixture. One group of plants each received 5 second-instar *A. vittatum* larvae (n = 7), while a second group was kept as undamaged controls (n = 7). Larvae fed for 9 days, then were recovered and seedling mortality and root mass were recorded (Harrington, Mexal, & Fisher, 1994).

EPN infection assays

To confirm that EPNs locate and kill *A. vittatum* larvae, we quantified larval infection rates using 2-choice infection assays (Zhang et al., 2019). Seedlings were transplanted into belowground olfactometers as previously described. One damaged plant (with 5 second-instar *A. vittatum* larvae) and one control plant were paired (n = 8). After 24 h of herbivory, 2,500 EPNs were added to the central chamber of each olfactometer and allowed to move within the arena and into pots for 72 h. Larvae were then recovered from the pots and monitored for EPN infection and mortality.

Statistical analyses

Statistical analyses were performed using the software program R (R Version 3.6.1, R Development Core Team, 2019). Root volatile data were analyzed by conducting non-metric multidimensional scaling (NMDS) ordinations in the package vegan to visualize blend differences (Oksanen et al., 2012). Permutational multivariate analysis of variance (PERMANOVA) was conducted to quantify differences in VOC blends at different timepoints (Clavijo Mccormick, Gershenzon, & Unsicker, 2014). Random forest analysis was used to identify compounds with the greatest contribution to variation among treatments (Ranganathan & Borges, 2010; Ray et al., 2020). One-way ANOVAs and Dunn’s Tests were used to compare the individual compounds and total VOC production. Preference data were analyzed using generalized log-linear models (GLM) with quasi-likelihood functions to compensate for over-dispersion (Robert, Erb, Duployer, et al., 2012). Larval performance and root biomass data were analyzed using one-way ANOVA comparisons.

RESULTS

Herbivory from *A. vittatum* larvae initially induces, but ultimately attenuates volatile production in cucumber roots

Herbivory by larvae or mechanical wounding for 24 h induced distinct volatile blends from cucumber roots compared to control plants (Figure 3A; PERMANOVA $F_{2, 28}$= 6.35, $R^2 = 0.31$, $p < 0.001$). In contrast, the root HIPV blend after 7 d of sustained herbivory was not different from that of undamaged roots, while volatile production from mechanically damaged roots remained higher (Figure 3B; PERMANOVA $F_{2, 24} = 5.29$, $R^2 = 0.31$, $p < 0.001$). Undamaged cucumber roots emitted relatively small quantities of VOCs and herbivory or mechanical damage (24 h) induced higher total volatile production (Figure 3C). Herbivory and wounding at 24 h comparatively increased the abundance of several compounds that were already emitted in undamaged controls but did not induce production of any new compounds from cucumber roots. Random forest analysis revealed that 3 monoterpenes (Camphene, Sabinene, and α-Pinene) contributed most to the variation among treatments (Figure S1) and their abundances were higher in damaged roots compared to controls (Figure 3C). After 7 d, compound abundances remained higher for mechanically wounded, but not herbivore-damaged roots (Figure

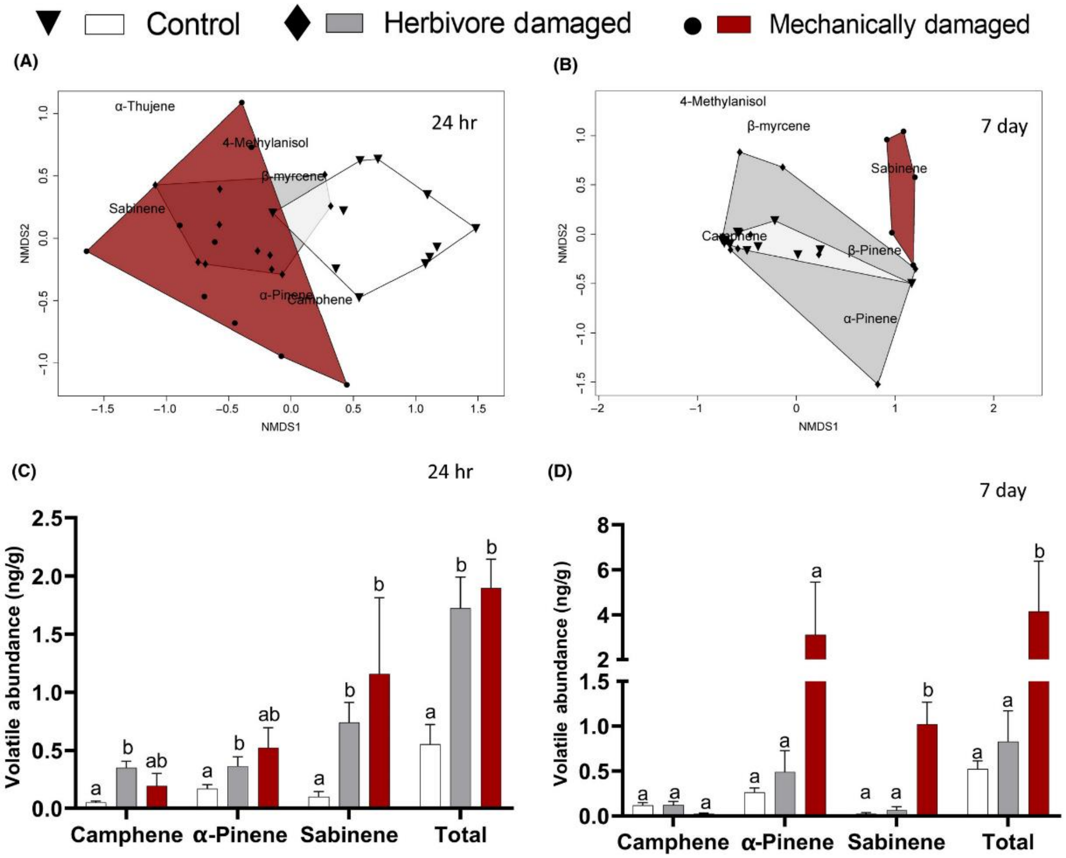

Figure 3 (A) Herbivory by *Acalymma vittatum* larvae or mechanical wounding for 24 hr induced similar volatile blends that differed from undamaged roots. (B) After 7 days of herbivory, volatile blends were not different for damaged and control roots while mechanically wounded root volatiles remained different. (C) Herbivory or wounding of cucumber roots (24 hr) increased production of monoterpenes (Camphene, Sabinene and α-Pinene) and total volatiles. (D) After 7 days, induced volatile production was attenuated in herbivore-damaged but not mechanically wounded roots. Different letters indicate significant differences among treatments ($p \leq 0.05$). Means ± *SE* are presented

3D). Herbivory by larvae or mechanical wounding for 24 h induced distinct volatile blends from cucumber roots compared to control plants (Figure 3A; PERMANOVA $F_{2, 28}$= 6.35, R^2 = 0.31, $p < 0.001$). In contrast, the root HIPV blend after 7 d of sustained herbivory was not different from that of undamaged roots, while volatile production from mechanically damaged roots remained higher (Figure 3B; PERMANOVA $F_{2, 24}$ = 5.29, R^2 = 0.31, $p < 0.001$). Undamaged cucumber roots emitted relatively small quantities of VOCs and herbivory or mechanical damage (24 h) induced higher total volatile production (Figure 3C). Herbivory and wounding at 24 h comparatively increased the abundance of several compounds that were already emitted in undamaged controls but did not induce production of any new compounds from cucumber roots. Random forest analysis revealed that 3 monoterpenes (Camphene, Sabinene, and α-Pinene) contributed most to the variation among treatments (Figure S1) and their abundances were higher in damaged roots compared to controls (Figure 3C). After 7 d, compound abundances remained higher for mechanically wounded, but not herbivore-damaged roots (Figure 3D).

Acalymma vittatum larvae initially avoid plants with conspecific herbivory

A. vittatum larvae showed a strong preference for cucumber root volatiles compared to sand (Figure 4; GLM $T_{1,10}$ = -7.02, $p < 0.001$). Larvae also preferred volatiles from undamaged roots over HIPVs from roots damaged by conspecifics for 48 h (Figure 4;

GLM $T_{1,51} = 2.78$, $p = 0.007$). However, larval preference was not different between damaged and control roots after 8 d of herbivory (Figure 4; GLM $T_{1,35} = -0.58$, $p = 0.56$).

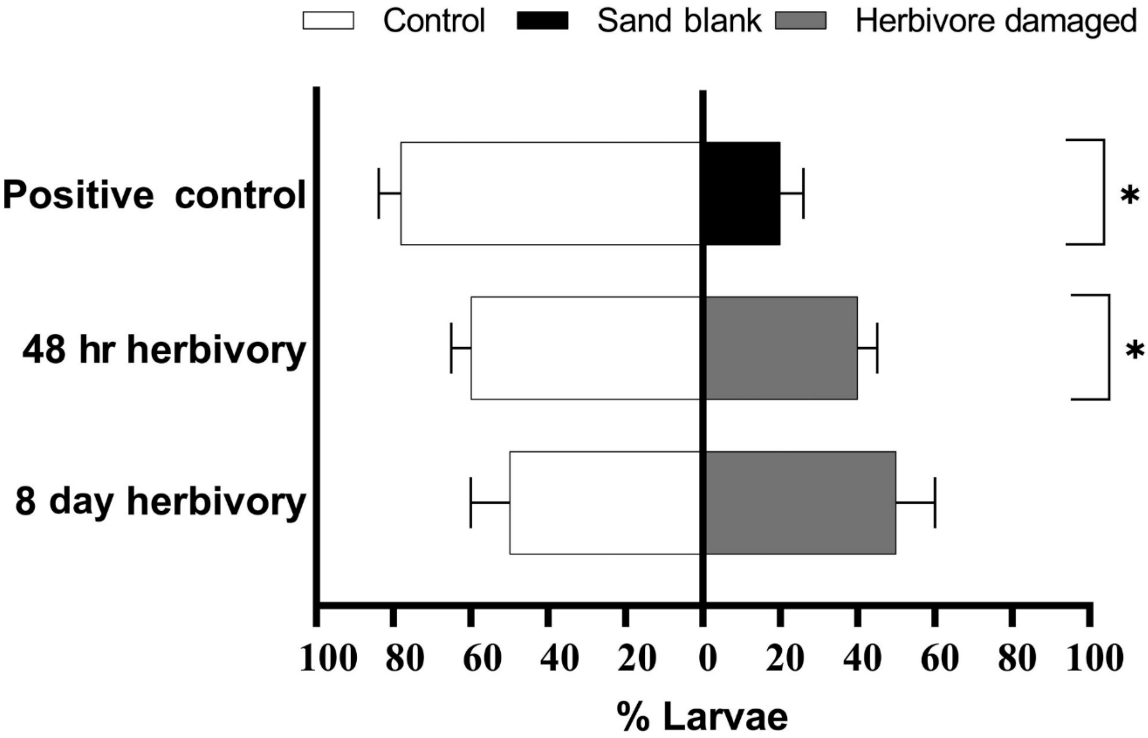

Figure 4 *Acalymma vittatum* attraction to cucumber roots was modulated by conspecific herbivory. Larvae preferred volatiles from undamaged roots compared to sand or roots with 48 hr conspecific herbivory. After 8 days of herbivory, larvae did not discriminate between damaged and undamaged root volatiles (*$p \leq 0.05$). Means ± *SE* are presented

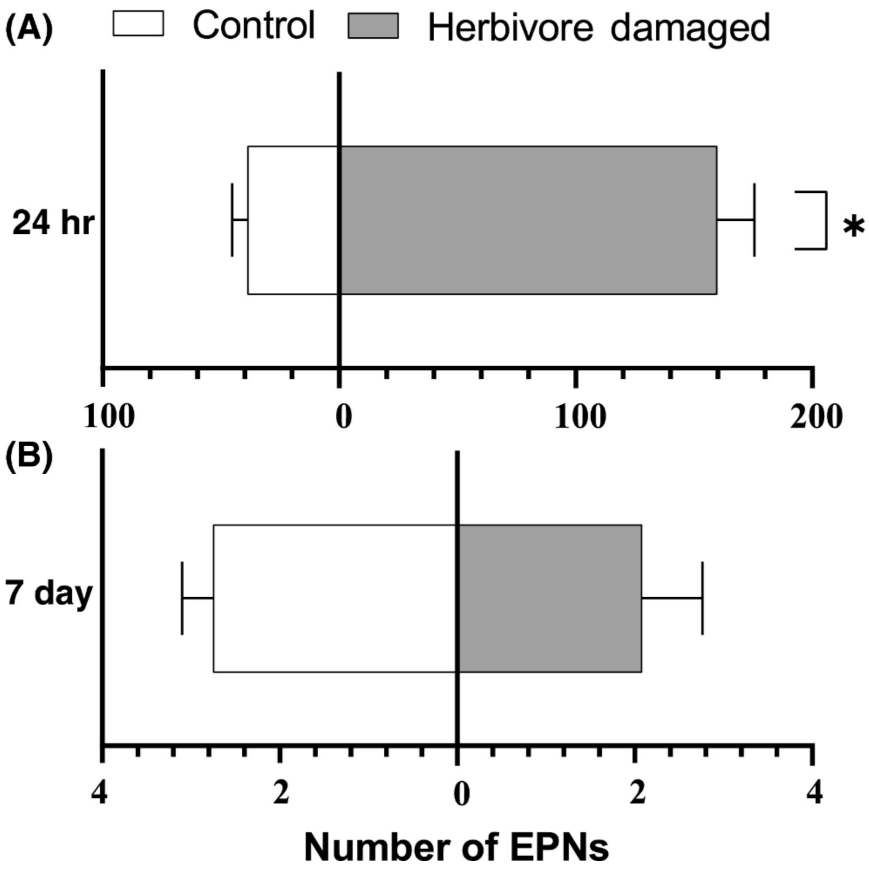

Figure 5 (A) Entomopathogenic nematodes (EPNs) preferred cucumber root volatiles after 24 hr of herbivory. (B) After 7 days herbivory, no difference in attraction was observed (*$p \leq 0.05$). Means ± *SE* are presented

EPNs are initially attracted to herbivore-damaged roots

More EPNs were attracted to roots with 24 h of herbivory compared to undamaged control roots (Figure 5A; GLM $T_{1,11} = 7.13$, $p < 0.001$). However, after 7 d of herbivory, no attraction was observed, with few EPNs choosing either treatment (Figure 5B; GLM $T_{1,11} = 0.87$, $p = 0.39$).

Prior conspecific herbivory does not affect the performance of *A. vittatum* larvae

No differences in larval performance were observed on damaged or control roots at either 24 hours or 7 days. Percent mass gain of larvae was not different when feeding on control plants or plants damaged for 24 h (Figure 6; ANOVA, $F_{1,44} = 0.03$, $p = 0.87$) or 7 d (Figure 6; ANOVA, $F_{1,22} = 0.72$, $p = 0.42$).

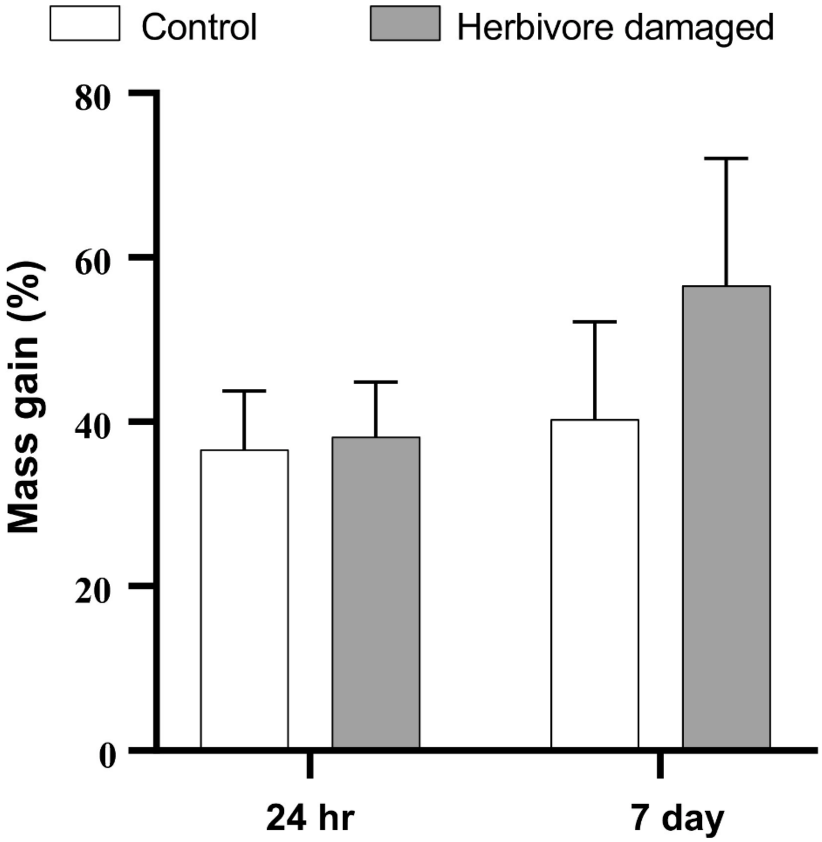

Figure 6 Larval performance was not different on roots damaged by conspecifics or control roots at 24 hr or 7 days. Means ± *SE* are presented

Herbivory by *A. vittatum* larvae reduces root biomass and increases plant mortality

After 9 days of continuous herbivory, cucumber root biomass was reduced compared to controls (Figure 7; ANOVA, $F_{1,7} = 13.05$, $p < 0.001$). We also observed 42% mortality among damaged plants and no mortality for control plants.

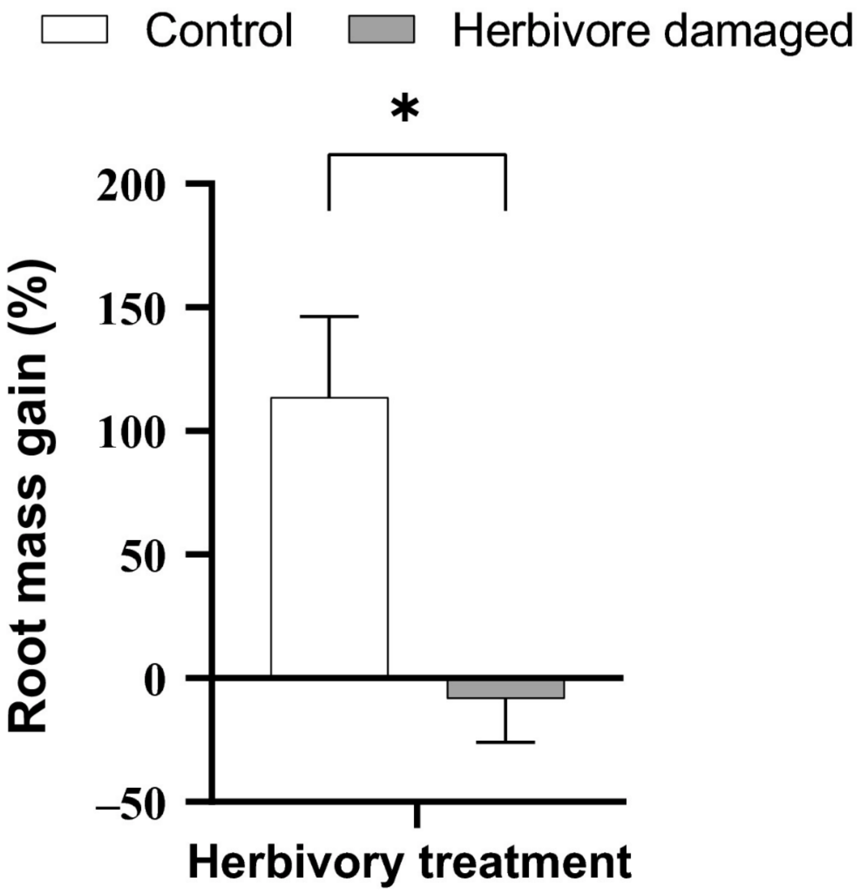

Figure 7 Cucumber root mass was reduced after 9 days of herbivory (*$p \leq 0.05$). Means ± *SE* are presented

EPNs infect and kill *A. vittatum* larvae

We observed that 71% of larvae recovered from the two-choice infection assays were infected and killed by EPNs.

DISCUSSION

This study demonstrates that olfactory cues from plant roots guide the foraging decisions of herbivores and their natural enemies, by helping herbivores assess their risk of competition and predation, and helping natural enemies locate prey. We found that HIPVs from cucumber roots initially (after 24 h) function as direct and indirect plant defenses by repelling *A. vittatum* larvae and attracting beneficial EPNs that kill larvae. Furthermore, our study revealed that root HIPV emissions change over the course of herbivory, which modifies their roles in belowground multi-trophic interactions. Initial feeding by *A. vittatum* larvae (24 h) induced a distinct blend of HIPVs, but after 7 days of sustained herbivory, root volatile production was reduced to levels indistinguishable from controls. This reduction in HIPVs attenuated the avoidance of conspecific larvae and attraction of EPNs. These findings suggest that *A. vittatum* larvae ultimately reduce or suppress production of root HIPVs, thereby disrupting plant defenses and altering chemically mediated interactions belowground.

HIPVs as honest signals of reward and risk

Plant-produced volatile compounds mediate ecological interactions at multiple trophic levels, communicating messages of risk and reward to herbivores and their natural enemies. HIPVs are widely recognized as indirect defenses through their attraction of natural enemies (Ali et al., 2010; Allmann & Baldwin, 2010; Hiltpold et al., 2011; Naranjo-Guevara et al., 2017; Rasmann et al., 2005). In this role, HIPVs are honest signals of reward, exposing herbivores—which are often cryptic—to foraging predators and parasitoids seeking them as food for themselves or their offspring. Just as HIPVs make prey more apparent to natural enemies, foraging herbivores can also use HIPVs to assess the possibility of encountering natural enemies (Joo et al., 2018; Shiojiri et al., 2006), although this has not been previously investigated belowground, where volatile compounds are dominant foraging cues (Johnson & Nielsen, 2012). In our study, we found that root HIPVs initially attract EPNs and repel *A. vittatum* larvae after short-term herbivory. This is one of a growing number of studies demonstrating that the functions of belowground HIPVs are analogous to aboveground HIPV-mediated defenses (Pearse et al., 2020), and suggests that herbivores can use these cues to avoid increased predation risk across a variety of ecological contexts.

HIPVs also directly defend plants against herbivores, reducing herbivore performance through toxic or deterrent properties (Brzozowski et al., 2019; Veyrat, Robert, Turlings, & Erb, 2016). Furthermore, volatile production is often correlated or metabolically linked to other defenses (Christensen et al., 2013). This includes cucurbitacins in cucumber, although the variety used in this study produces extremely low levels of cucurbitacins (Agrawal, Janssen, Bruin, Posthumus, & Sabelis, 2002). When HIPVs directly reduce herbivore performance or signal production of other defenses, they communicate direct risks for foraging herbivores (Bernasconi et al., 1998; Ray et al., 2020). Although no differences in larval performance were observed in this study, we found that after 9 days of larval herbivory, all damaged plants lost root mass and 42% of these plants eventually died. Thus, HIPVs may also serve as indicators of resource competition for belowground herbivores (De Moraes et al., 2001; Valladares, Coll-Aráoz, Alderete, Vera, & Fernández, 2020; Zakir et al., 2013).

Attenuation of indirect plant defenses

One hypothesis to explain our finding of reduced root HIPVs with sustained herbivore damage is that defenses are suppressed by microbes or effector molecules in *A. vittatum* oral secretions. Plant defense suppression by herbivore oral secretions has been observed in aboveground tissues for several plant and herbivore species (Chung et al., 2013; Sarmento et al., 2011; Schausberger, 2018; Takai et al., 2018). For example, effector molecules in saliva of *Helicoverpa zea* larvae were found to suppress production of defenses like nicotine in tobacco (*Nicotiana tabacum*) (Musser et al., 2002). Similarly, bacteria in oral secretions from Colorado potato beetle larvae (*Leptinotarsa decemlineata*) suppressed anti-herbivore defenses in tomato plants (*Solanum* *lycopersicum*) (Chung et al., 2013). While there is some evidence for herbivore manipulation of root defenses, suppression of belowground indirect defenses by root herbivores has not been previously documented (Robert et al., 2013). Future research is needed to identify the mechanisms underlying root HIPV reduction by *A. vittatum* larvae and to determine whether defense suppression occurs or is widespread in belowground plant-herbivore interactions.

Alternative hypotheses to explain our finding of reduced HIPVs with sustained herbivore damage are that plants attenuate root HIPVs to reduce attraction of subsequent herbivores or that they shift defensive strategies over time. Previous studies have found that HIPVs can simultaneously attract natural enemies and subsequent herbivores (Ali et al., 2011; Marcel Dicke & Baldwin, 2010; El-Sayed, Knight, Basoalto, & Suckling, 2018; Orre, Wratten, Jonsson, & Hale, 2010), indicating a trade-off for plants between indirect defense and herbivore attraction. Here we observed EPN attraction to root HIPVs but did not assess whether this attraction extends to other herbivore species. While reducing HIPVs, plants could also invest in alternative defense strategies following sustained herbivory. We did not, however, observe a reduction in herbivore performance as evidence of induced plant defenses after 7 days. Our findings suggest that plants can balance the costs and benefits of defense and herbivory by modifying HIPVs over relatively short time scales (7 d), initially increasing indirect defenses, then reducing possible attraction of subsequent herbivores.

CONCLUSION

This work highlights the critical functions of root HIPVs in mediating multitrophic interactions among plants, herbivores, and natural enemies in belowground ecosystems. Our findings indicate that plants produce HIPVs for indirect defense, as EPNs use these cues to locate prey, and herbivores use HIPVs to avoid antagonistic interactions with natural enemies and conspecifics. This work also sheds light on the temporal dynamics of belowground chemically mediated interactions, revealing that olfactory cues and their ecological functions can shift over relevant time scales.

CHAPTER IV

OLFACTORY CUES FROM PREDATORY ENTOMOPATHOGENIC NEMATODES VARY ACROSS SPECIES AND HUNTING STRATEGIES, TRIGGERING DIFFERENT BEHAVIOURAL RESPONSES IN PREY AND COMPETITORS

INTRODUCTION

A major goal among ecologists is to better predict the outcomes of trophic interactions and their cascading consequences for community ecology and ecosystem function (Culshaw-Maurer, Sih, & Rosenheim, 2020; Descombes et al., 2020; J. Miller, Ament, & Schmitz, 2014). Growing evidence in the study of predator-prey interactions points to environmental (e.g. climate and habitat) and species (e.g. predator and prey) traits as playing key roles in disentangling this complexity (Luttbeg, Hammond, Brodin, & Sih, 2020; Rosenheim, Glik, Goeriz, & Rämert, 2004; Wirsing, Heithaus, Brown, Kotler, & Schmitz, 2021). Behavioural traits of both predators and prey are of increasing interest, particularly the role these traits play in non-consumptive effects. Non-consumptive effects—in contrast to ‘consumptive effects’, which describe the capture and killing of prey by predators—encompass modified prey behaviour, morphology, and/or physiology in response to perceived predation risk (Hermann & Landis, 2017; Thaler, McArt, & Kaplan, 2012). For instance, prey may reduce foraging activity or escape to different habitats to circumvent predators (Heithaus, Wirsing, Burkholder, Thomson, & Dill, 2009; Hermann & Thaler, 2014), highlighting the challenge prey face in evading predation while also locating suitable food resources (Sih, 1980). Predators also face foraging challenges as they compete with other predators for prey, without falling victim to predation themselves. To forage for prey, predators employ different hunting behaviours or modes. Some predators are active hunters that move through the environment to locate and pursue prey, while others adopt a sit-and-wait or ambush strategy, remaining stationary and attacking prey that move within close range (J. Miller et al., 2014; Schmitz, 2008). Current theory predicts prey should most readily recognize and respond to cues from ambush predators that represent an immediate threat (Kats & Dill, 1998; Preisser, Orrock, & Schmitz, 2007), and predators should avoid cues from potential competitors, particularly those that will outcompete or predate them (Chase et al., 2002; Mestre, Narimanov, Menzel, & Entling, 2020; Rosenheim, 1998). Here we test this prediction by examining prey responses to chemical cues from different species of natural enemies that employ a range of hunting strategies, and we evaluate how these olfactory cues affect the foraging behaviour of an active-hunting predator.

Trophic interactions are often mediated by chemical information, which provides a mechanistic link to observed behaviours. It has been well documented, for example, that insect herbivores use plant-produced chemical cues to select suitable hosts, while their natural enemies typically rely on herbivore-associated cues to locate prey (Bruce & Pickett, 2011; Grunseich, Thompson, Aguirre, et al., 2020; Pearse et al., 2020). Many species (e.g. plants and herbivores) have evolved to recognize chemical cues associated with their enemies to help them predict and avoid attack (Helms et al., 2017; Hermann & Thaler, 2014; Kats & Dill, 1998; Kempraj, Park, & Taylor, 2020, Karban et al. 2016). In this way, predators are often faced with the challenge of having their presence betrayed to potential prey by the chemical signals and cues they produce. Predator semiochemicals, like pheromones (e.g. sex attractants or territorial marking pheromones) and kairomones (e.g. metabolic biproducts), can persist in the environment for varying lengths of time, revealing the presence, identity, and abundance of emitting predators (Banks, Daly, & Bytheway, 2016; M. Dicke & Grostal, 2001; Kats & Dill, 1998). Predators can also eavesdrop on chemical cues from other predators to assess prey availability and gauge possible competition (Banks et al., 2016; Cusumano, Harvey, Bourne, Poelman, & Boer, 2020; Mestre, Bucher, & Entling, 2014; Poelman et al., 2012; Stowe, Turlings, Loughrin, Lewis, & Tumlinson, 1995). Despite our current understanding of chemically mediated predator-prey interactions, we are lacking a systematic empirical evaluation of how chemical cues can be linked to species traits, like predator hunting mode, that affect predator and prey behaviour. Evaluating these trophic interactions in a belowground soil environment, where chemical cues are the dominant type of communication between trophic levels, can help fill this knowledge gap.

Entomopathogenic nematodes (EPNs), in the genera *Steinernema* and *Heterorhabditis*, are important natural enemies of soil-dwelling insects and are emerging as model organisms for studies of belowground multi-trophic interactions (Campos-Herrera, Barbercheck, Hoy, & Stock, 2012; Rasmann, Ali, Helder, & van der Putten, 2012). Different species of EPNs exhibit a range of hunting modes, from cruisers that actively move through soil (e.g. *Heterorhabditis bacteriophora*) to sit-and-wait ambush predators (e.g. *Steinernema carpocapsae*) (Griffin, 2012; Lewis, Campbell, Griffin, Kaya, & Peters, 2006; Ruan et al., 2018). EPNs are also associated with species-specific symbiotic bacteria that aid the free-living infective juveniles in infecting and killing their insect hosts (Ciche, Darby, Ehlers, Forst, & Goodrich-Blair, 2006; Lewis et al., 2006). The insect-EPN-bacteria complex (i.e. infected host cadaver), produces a suite of chemical compounds including pheromones, insecticidal compounds, antimicrobials, and scavenging deterrents that influence EPN foraging behaviour, infectivity, and survival (Gulcu et al., 2012; Hu et al., 1999; Hu & Webster, 2000; Kaplan et al., 2012, 2020; Lu et al., 2017). Another recent discovery revealed EPN-infected insect cadavers emit olfactory cues that influence the behaviour of their insect prey. These infected cadavers produce blends of volatile compounds distinct from the odours of dead insects, suggesting cadaver volatiles can reliably indicate increased predation risk to prey (Helms et al., 2019; Zhang et al., 2019). Although some EPN olfactory cues may be conserved, there is emerging evidence for species-level specificity in their volatile blends and the corresponding insect responses (Helms et al., 2019; Zhang et al., 2019).

The goal of this study was to investigate how olfactory cues from entomopathogenic nematodes with different hunting strategies influence the behaviour of their herbivore prey and other EPNs. We characterized the volatile compounds produced by insect cadavers infected with 3 different EPN species, each employing a different hunting strategy (*H. bacteriophora*: active, *S. riobrave*: intermediate, *S. carpocapsae*: ambusher), to evaluate potential differences and conserved olfactory cues. We also investigated how EPN volatile blends change depending on insect host species, using one species that is a standard rearing host for EPNs and one ecologically relevant root-feeding species. We predicted the EPN cues would vary by species, with the two more closely related *Steinernema* species producing more similar olfactory cues compared to *H. bacteriophora*, regardless of insect host species. We also examined how these cues affect the foraging behaviour of an insect herbivore, striped cucumber beetle (*Acalymma vittatum*). Based on previous studies, we predicted that *A. vittatum* larvae would detect odours from EPN-infected cadavers as a warning of increased predation risk and avoid foraging near these cues, with the ambusher species eliciting the strongest response (Culshaw-Maurer et al., 2020; Kats & Dill, 1998; Luttbeg et al., 2020). Finally, we evaluated how foraging *H. bacteriophora* EPNs respond to olfactory cues produced by the three EPN species. Previous work indicates that *H. bacteriophora* rely on prey-associated volatile cues when foraging (Grunseich, Thompson, Hay, et al., 2020), and non-volatile pheromones from host cadavers have been shown affect dispersal in other EPN species (Kaplan et al., 2020; Oliveira-Hofman et al., 2019). We predicted that *H. bacteriophora* would avoid cues from cadavers infected with other EPN species as a mechanism for avoiding interspecific competition. By linking predator olfactory cues to hunting modes, we examine how prey perceive predation risk and how predators recognize competition while foraging for critical resources. Our study suggests hunting mode has a significant context-dependent influence on belowground predator-prey and competitive interactions, calling attention to the cascading consequences ultimately shaping these ecological communities.

MATERIALS AND METHODS

Nematodes, insects and plants

The entomopathogenic nematodes used in this study (*Heterorhabditis bacteriophora*, *Steinernema riobrave,* and *Steinernema carpocapsae*) (Arbico Organics, Tucson, USA) are generalists with different hunting strategies that infect *Acalymma vittatum*(C. D. Ellers-Kirk et al., 2000). EPNs were cultured in last-instar wax moth larvae (*Galleria mellonella*) at 27°C. Infective juveniles (IJs) were harvested in White traps. To generate EPN-infected insect cadavers for experiments, we added ~250 IJs to third-instar *A. vittatum* larvae or last-instar *G. mellonella* on moistened filter paper in 35 mm Petri dishes. Cadavers used in all experiments were 6 days post-infection for *G. mellonella* and 2 days post-infection for *A. vittatum* (approximately 2 days before IJ emergence). Control cadavers for all experiments were freeze killed and kept under the same conditions as EPN cadavers prior to experiments. Striped cucumber beetles (*A. vittatum*) were maintained in a laboratory colony on cultivated squash (*Cucurbita pepo* cv. Raven). Cucumber plants (*Cucumis sativus* cv. Max Pack) were grown from seed

(Johnny's Selected Seeds, Fairfield, USA) and used in experiments after 3-4 weeks. Plants were grown in individual pots in topsoil mix (Hyponex Corporation, Marysville, USA) with 3 g Osmocote® fertilizer (Scotts, Marysville, USA) and kept in a growth room with supplemental lighting (16 h light: 8 h dark; 22°C: 29°C; 57% RH).

Collection and analysis of EPN volatiles

To evaluate potential differences among EPN-produced olfactory cues, we characterized the volatiles emitted by three species of EPNs, each infecting two insect species (*A. vittatum* with *H. bacteriophora* n=14, *S. riobrave* n=10, and *S. carpocapsae* n=9; and *G. mellonella* with each species n=10). As controls, we analysed volatiles produced by freeze-killed *A. vittatum* (n=17) and *G. mellonella* (n=10) cadavers. We used solid-phase microextraction (SPME) to collect volatiles from the headspace of each cadaver treatment (Zhang et al., 2019). Individual cadavers were placed into 4 ml glass vials with a PTFE septum-containing lid. Vials were held at 35°C for 1 h, then a SPME fibre (100 µm, polydimethylsiloxane, Agilent Technologies, Palo Alto, USA) was inserted and exposed for 1 h for *G. mellonella* or 2 h for *A. vittatum* cadavers (adjusted for cadaver mass). Samples were analysed using an Agilent 7890B gas chromatograph and 5977B mass spectrometer with a splitless injector held at 250°C and helium as the carrier gas. The column (HP-5MS 30 m x 0.250 mm-ID, 0.25 µm film thickness, Agilent Technologies, Palo Alto, USA) was held at 60°C for 1 min then increased at 5°C min^{-1} until 200°C. Compounds were ionized by electron impact ionization at 70 eV and mass spectra were acquired by scanning from 40 to 300 m/z at 5.30 scans s^{-1}. Tentative identification of target compounds was achieved by comparison with mass spectral libraries (NIST17, Adams2 (Allured Publishing Corporation)), and structure assignments were confirmed where possible by comparisons of mass spectra and retention times with authentic standards. Compounds were quantified as relative abundance hr^{-1} g^{-1} cadaver.

A. vittatum **response to EPN olfactory cues – Belowground olfactometer**

We conducted dual-choice experiments using belowground olfactometers to assess how olfactory cues from EPN-infected insect cadavers influence the foraging behaviour of *A. vittatum* larvae. Two-choice olfactometers, consisting of two glass pots connected by a 13 cm-long glass arm with a central top opening were constructed. Individual *C. sativus* seedlings were transplanted into the glass olfactometer pots in clean (baked at 200°C for 24 h and cooled), moistened sand (10% water W/V) and allowed to acclimate for 24 h prior to experiments. These plants served as attractive cues for foraging *A. vittatum* larvae based on previous work (Grunseich, Thompson, Hay, et al., 2020). For each trial, three EPN-infected cadavers were inserted at the base of one pot, while the other pot received three control cadavers. This was repeated for every EPN-insect species pair described above (*A. vittatum* with *H. bacteriophora* n=9, *S. riobrave* n=9, and *S. carpocapsae* n=10; and *G. mellonella* with *H. bacteriophora* n=10, *S. riobrave* n=10, and *S. carpocapsae* n=12). To determine whether *A. vittatum* larvae respond to odours from dead insects, we compared larval preference for plants with control cadavers vs.

plants only for *A. vittatum* or *G. mellonella* cadavers (n=12). Olfactometers were assembled 30 minutes prior to experiments. We introduced 5 second-instar larvae into the central chamber and after 20 minutes, we recovered the larvae and recorded their locations.

A. vittatum **response to EPN cues – Petri dish assays**

To visually observe *A. vittatum* behavioural responses to cues from *H. bacteriophora*-infected cadavers, we conducted Petri-dish preference assays (Fig. S1). On opposite sides of glass Petri dishes (15 mm x 100 mm), we placed three 5 cm segments of *C. sativus* roots on moist filter paper. On one side, between the root segments, we placed *H. bacteriophora*-infected cadavers (3 *G. mellonella* or 5 *A. vittatum*). The other side received an equal number of control cadavers. Five second-instar *A. vittatum* larvae were placed in the centre and their locations and behaviour (1. feeding on roots, 2. hiding, 3. feeding on cadavers, i.e. “cannibalism”, or 4. foraging/moving) were recorded after 10, 30, and 60 min (*A. vittatum*, n=10*; G. mellonella*, n=9). Preference was determined by location in the arena. Larvae that did not move from the centre were recorded as “no-choice”.

H. bacteriophora **response to EPN olfactory cues – Belowground olfactometer**

To investigate the influence of olfactory cues from EPN-infected cadavers on the foraging behaviour of *H. bacteriophora* infective juveniles, we conducted two-choice preference assays with belowground olfactometers. *H. bacteriophora* use a “cruiser” foraging strategy and previous work indicates they are attracted to volatiles from roots of *A. vittatum*-damaged *C. sativus* (Grunseich, Thompson, Hay, et al., 2020). Two-choice belowground olfactometers, comprising two glass pots connected by a 36 cm-long glass arm with a central top opening were used in experiments. As above, *C. sativus* seedlings were transplanted into olfactometer pots and EPN-infected cadavers or control cadavers were placed on each side. To induce production of EPN-attracting root volatiles, each plant was treated with 5 second-instar *A. vittatum* larvae. After 24 h, 2500 EPN IJs were added to the central chamber. After 48 h, sand was collected from each side of the olfactometer and IJs were extracted using an adapted Baermann funnel method and counted (Grunseich, Thompson, Hay, et al., 2020). Larvae were recovered and confirmed to be feeding. This was repeated for both *G. mellonella* and *A. vittatum* infected with each of the three EPN species (*H. bacteriophora*, *S. riobrave*, and *S. carpocapsae*; n= 6).

Statistical analysis

Statistical analyses were conducted in the software program R (R Version 3.6.3, R Development Core Team, 2020). Non-metric multidimensional scaling (NMDS) ordinations were used to visualize volatile blend differences (package vegan, Oksanen et al., 2013). Permutational multivariate analysis of variance (PERMANOVA) was conducted to quantify differences among cadaver odours. One-way ANOVA and Tukey

Post-Hoc analyses were used to compare individual compounds produced by cadavers. Preference data were analysed using generalized log-linear models (GLM) with quasi-likelihood functions to compensate for overdispersion (Ali et al., 2010).

RESULTS

EPN olfactory cues vary across species with different foraging strategies and by insect host species

We identified differences in the volatile blends from *A. vittatum* and *G. mellonella* cadavers infected with the 3 EPN species (Table 3, Fig. 8, 9). We recovered 25 volatile compounds across all treatments, observing differences in the abundances of individual compounds within these blends (Table 4). Notably, we found a suite of seven sesquiterpenes that were only emitted by *H. bacteriophora*-infected *A. vittatum* cadavers, tentatively identified as alpha-copaene, beta-cubebene, gamma-cadinene, delta-cadinene, beta-copaene, gamma-muurolene, and delta-amorphene (Table 4). The compound 1-dodecene was only present for cadavers infected with *H. bacteriophora* for both insect host species (Table 4). Butylated hydroxytoluene and unknown 6 were emitted by all EPN-infected *A. vittatum* cadavers, but not by any *G. mellonella* cadavers (Table 4). The compound 1-nonene was emitted by cadavers infected with each of the 3 EPN species (Table 4). When comparing the overall volatile blends of *A. vittatum* cadavers, we found that the two *Steinernema* species were more similar to each other than *Heterorhabditis* and that all three were distinctly different from the freeze-killed controls (Fig. 8). The differences among volatile blends from *G. mellonella* cadavers were more pronounced, with little similarity between any EPN species (Fig. 9).

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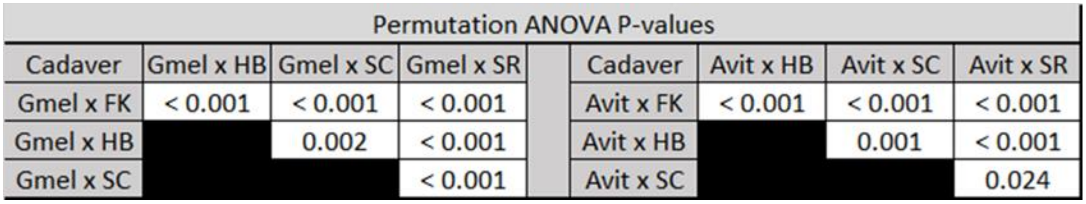

Permutation ANOVA P-values								
Cadaver	Gmel x HB	Gmel x SC	Gmel x SR		Cadaver	Avit x HB	Avit x SC	Avit x SR
Gmel x FK	< 0.001	< 0.001	< 0.001		Avit x FK	< 0.001	< 0.001	< 0.001
Gmel x HB		0.002	< 0.001		Avit x HB		0.001	< 0.001
Gmel x SC			< 0.001		Avit x SC			0.024

Table 3 Results (*p*-values) from individual PERMANOVA comparisons across all EPN treatments for each insect host species. Gmel = *G. mellonella;* Avit = *A. vittatum;* FK = Freeze-killed cadaver; HB = *H. bacteriophora;* SC = *S. carpocapsae;* SR = *S. riobrave*

Compound	**Insect Host Species**	**Control ± SE**	**HB ± SE**	**SR ± SE**	**SC ± SE**
Benzaldehyde (1)	*A. vittatum*	2020.67±1154.44	39478.80±26417.90	1295.87±1295.87	0.00±0.00
	G. mellonella	0.00±0.00	8.03±6.00	0.00±0.00	301.63±301.63
1-Nonene (2)	*A. vittatum*	0.00±0.00	2461.41±1347.87	34533.00±33614.01	1247.87±1247.87
	G. mellonella	0.00±0.00	292.47±76.54	2.64±2.64	502.98±201.87
1-Decene (3)	***A. vittatum***	**0.00±0.00^{a}**	**11490.70±4421.59^{b}**	**0.00±0.00^{a}**	**0.00±0.00^{a}**
	G. mellonella	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
5-Decene (4)	*A. vittatum*	0.00±0.00	1182.10±1182.10	0.00±0.00	0.00±0.00
	G. mellonella	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
1-Dodecene (5)	***A. vittatum***	**0.00±0.00^{a}**	**29642.19±12093.29^{b}**	**0.00±0.00^{a}**	**0.00±0.00^{a}**
	G. mellonella	**0.00±0.00^{a}**	**19.20±7.18^{b}**	**0.00±0.00^{a}**	**0.00±0.00^{a}**
Alpha-Copaene (6)	*A. vittatum*	0.00±0.00	3162.27±2570.29	0.00±0.00	0.00±0.00
	G. mellonella	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Beta-Cubebene (7)	*A. vittatum*	0.00±0.00	2302.09±1476.65	0.00±0.00	0.00±0.00
	G. mellonella	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Gamma-Cadinene (8)	*A. vittatum*	0.00±0.00	139615.18±101078.00	0.00±0.00	0.00±0.00
	G. mellonella	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00

Table 4 Individual compounds from *G. mellonella* and *A. vittatum* cadavers infected with *H. bacteriophora*, *S. riobrave*, or *S. carpocapsae* or uninfected controls. Means ± SE are presented. Different letters indicate significant differences among treatments ($p \leq 0.05$).

Compound	**Insect Host Species**	**Control ± SE**	**HB ± SE**	**SR ± SE**	**SC ± SE**
Butylated hydroxytoluene (9)	***A. vittatum***	**0.00±0.00^{a}**	**97477.40±32717.63^{b}**	**96315.80±33953.92^{b}**	**159668.21±41020.76^{b}**
	G. mellonella	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Delta-Cadinene (10)	***A. vittatum***	**0.00±0.00^{a}**	**3089.02±1417.72^{b}**	**0.00±0.00^{a}**	**0.00±0.00^{a}**
	G. mellonella	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Beta-Copaene (11)	***A. vittatum***	**0.00±0.00^{a}**	**2788.06±1451.82^{b}**	**0.00±0.00^{a}**	**0.00±0.00^{a}**
	G. mellonella	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Gamma-Muurolene (12)	*A. vittatum*	0.00±0.00	626.17±554.94	0.00±0.00	0.00±0.00
	G. mellonella	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Delta-Amorphene (13)	***A. vittatum***	**0.00±0.00^{a}**	**2695.87±1421.35^{b}**	**0.00±0.00^{a}**	**0.00±0.00^{a}**
	G. mellonella	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
Indole (14)	*A. vittatum*	0.00±0.00	2636.51±905.16	41827.25±36579.30	8818.59±7346.94
	G. mellonella	37.18±19.84	5993.101±1958.825	338.76±108.82	8271.36±4636.12
2,5-Dimethyl-pyrazine (15)	***A. vittatum***	**194.92±194.92^{a}**	**0.00±0.00^{a}**	**5091.06±5091.06^{a}**	**242229.74±124737.47^{b}**
	G. mellonella	0.00±0.00	1024.07±1024.07	374.16±157.14	0.00±0.00
Phenol (16)	*A. vittatum*	4947.44±3436.74	0.00±0.00	14496.68±13298.59	0.00±0.00
	G. mellonella	**25.93±17.30^{a}**	**2.07±2.07^{a}**	**648.36±232.89^{a}**	**4453.59±1980.68^{b}**

Table 4 Continued

Compound	**Insect Host Species**	**Control ± SE**	**HB ± SE**	**SR ± SE**	**SC ± SE**
Trimethyl-pyrazine (17)	*A. vittatum*	0.00±0.00	0.00±0.00	4267.04±4267.04	4680.5±1947.82
	G. mellonella	0.00±0.00	13.20±13.20	17.29±12.06	0.00±0.00
Phenyl ethyl alcohol (18)	***A. vittatum***	**30264.53±10882.72^{a}**	**3506.45±719.63^{bc}**	**29025.90±6550.20^{ac}**	**6246.55±2291.40^{ac}**
	G. mellonella	**522.86±203.37^{a}**	**249.91±42.06^{ac}**	**126.70±15.09^{bc}**	**118.332±25.12^{bc}**
Anisole (19)	*A. vittatum*	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
	G. mellonella	0.00±0.00	0.00±0.00	1882.12±367.74	0.00±0.00
Unknown 1 (20)	*A. vittatum*	17865.70±17865.70	0.00±0.00	0.00±0.00	0.00±0.00
	G. mellonella	460.48±460.48	0.00±0.00	12.04 ±8.61	262.29±146.39
Unknown 2 (21)	*A. vittatum*	0.00±0.00	74.63±74.63	18295.40±18295.40	0.00±0.00
	G. mellonella	192.01±192.01	0.00±0.00	66.00±30.09	40.12±40.12
Unknown 3 (22)	*A. vittatum*	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
	G. mellonella	**0.00±0.00^{a}**	**247.20±30.07^{b}**	**357.07±56.73^{b}**	**13.67±10.65^{a}**
Unknown 4 (23)	*A. vittatum*	0.00±0.00	0.00±0.00	733.11±733.11	0.00±0.00
	G. mellonella	**0.00±0.00^{a}**	**1559.06±207.40^{b}**	**2315.6±356.24^{b}**	**183.39±100.11^{a}**
Unknown 5 (24)	***A. vittatum***	**0.00±0.00^{a}**	**19148.88±7698.74^{b}**	**0.00±0.00^{a}**	**0.00±0.00^{a}**
	G. mellonella	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00

Table 4 Continued

Compound	Insect Host Species	Control ± SE	HB ± SE	SR ± SE	SC ± SE
Unknown 6 (25)	***A. vittatum***	**0.00±0.00**^{a}	**60483.30±17761.80**^{b}	**6604.47±6002.94**^{a}	**3916.16±3916.16**^{a}
	G. mellonella	00.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00

Table 4 Continued

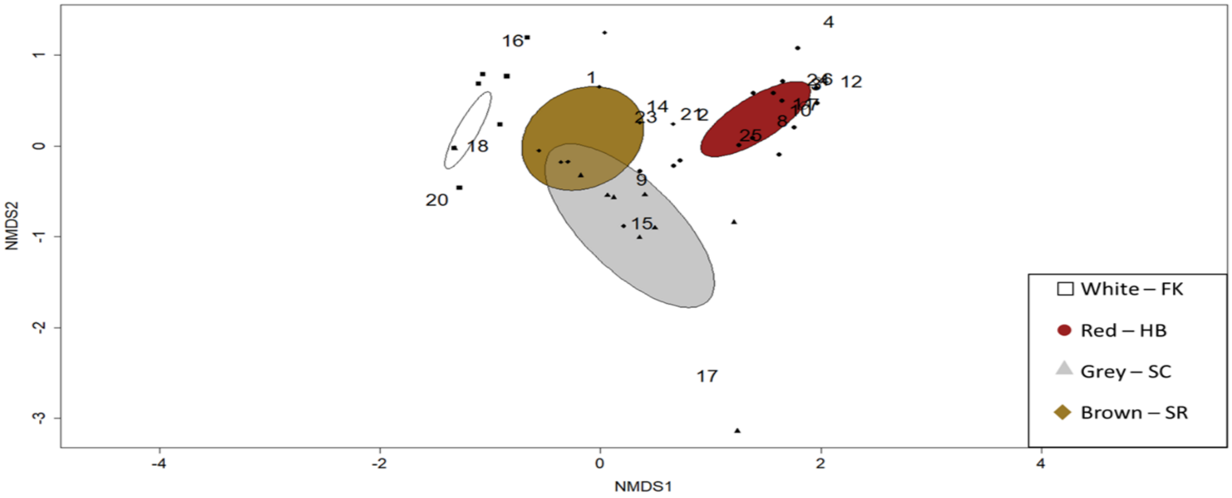

Figure 8 Distinct volatile blends were emitted by *A. vittatum* cadavers infected with 3 EPN species and freeze-killed controls. FK=Freeze-killed cadaver; HB=*H. bacteriophora*; SC=*S. carpocapsae*; SR=*S. riobrave.* Compounds listed in table 4.

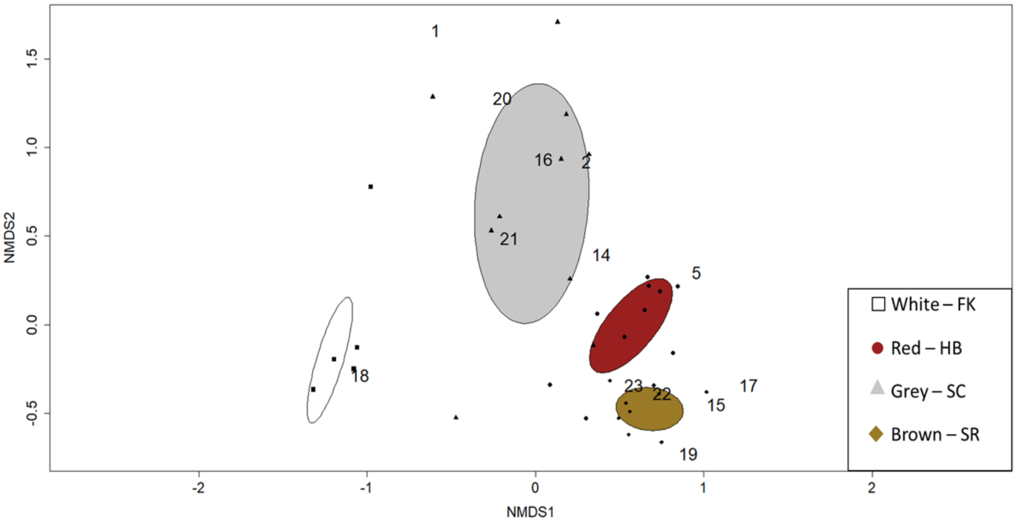

Figure 9 Distinct volatile blends were emitted by *G. mellonella* cadavers infected with 3 species of EPNs and freeze-killed controls. FK=Freeze-killed cadaver; HB=*H. bacteriophora*; SC=*S. carpocapsae*; SR=*S. riobrave.* Compounds listed in table 2. Compounds listed in table 4.

A. vittatum larvae avoid olfactory cues from *H. bacteriophora*-infected cadavers

Foraging *A. vittatum* larvae differentiated between odours from *H. bacteriophora*-infected and uninfected control cadavers for *A. vittatum* (Fig. 10; GLM $T_{1,8} = 10.96$, $p < 0.001$) and *G. mellonella* (Fig. 10; GLM $T_{1,9} = -3.96$, $p < 0.001$). Contrary to our predictions, however, they did not avoid volatile cues from the other two EPN species, regardless of insect host species (Fig. 10). Larvae did not differentiate between *S. riobrave*-infected or control *A. vittatum* cadavers (GLM $T_{1,8} = -1.136$, $p = 0.27$) or *G. mellonella* cadavers (GLM $T_{1,8} = 1.30$, $p = 0.22$) or *S. Carpocapsae*-infected or control cadavers for *A. vittatum* (GLM $T_{1,9} = 1.22$, $p = 0.24$) or *G. mellonella* (GLM $T_{1,11} = 1.29$, $p = 0.21$). Odours from freeze-killed cadavers also had no influence on *A. vittatum* foraging compared to plants only for *A. vittatum* (Fig. 10; GLM $T_{1,11} = 0.377$, $p = 0.71$) or *G. mellonella* (Fig. 10; GLM $T_{1,11} = 0.01$, $p = 1.00$)

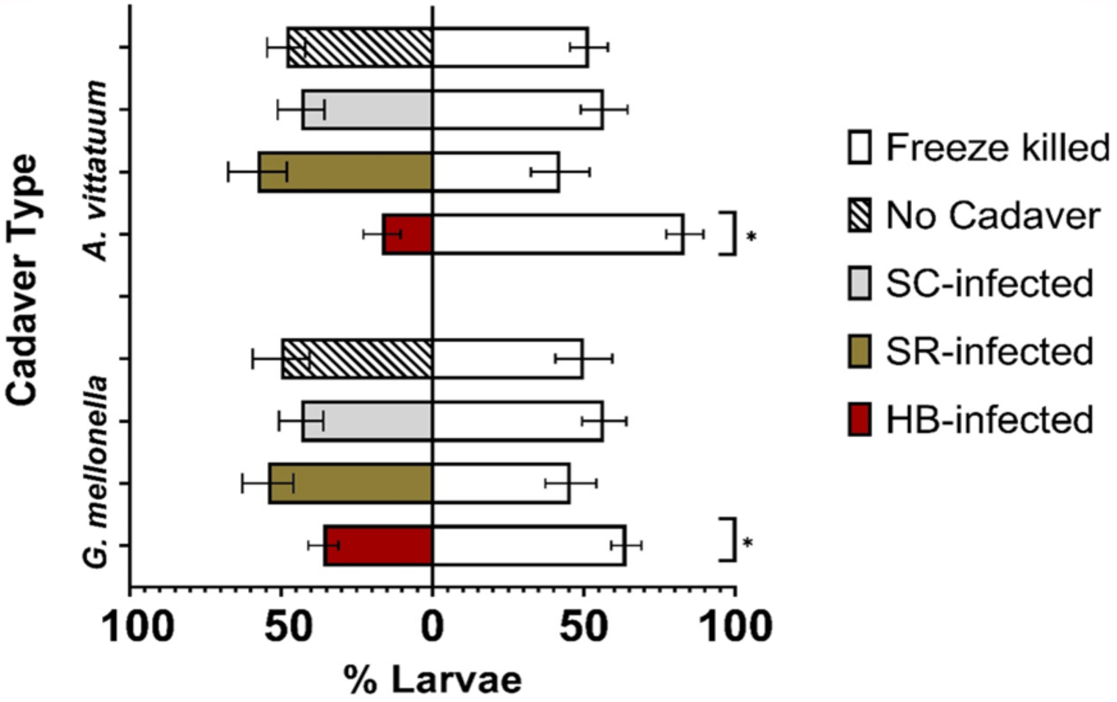

Figure 10 *A. vittatum* larvae avoided plants with olfactory cues from *H. bacteriophora*-infected cadavers. However, larval preference was not influenced by volatile cues from *S. carpocapsae*- or *S. riobrave*-infected cadavers or control cadavers. Means ± SE are presented. (*$p \leq 0.05$).

A. vittatum **larvae avoid insect cadavers infected with** ***H. bacteriophora*** **EPNs**

In Petri-dish preference assays, we observed a similar EPN avoidance response by *A. vittatum* larvae (Fig. 11). Larvae avoided *H. bacteriophora*-infected conspecifics and nearby roots throughout the duration of the experiment (10 min GLM $T_{1,18} = -4.11$, $p < 0.001$, 30 min GLM $T_{1,18} = -2.24$, $p = 0.037$, and 1 h GLM $T_{1,18} = -2.70$, $p = 0.014$). In addition to feeding on roots, *A. vittatum* larvae also consumed uninfected conspecific control cadavers, but not EPN-infected cadavers. In total, we observed "cannibalism" of 40.74% of freeze-killed *A. vittatum*. Foraging larvae did not discriminate between *H. bacteriophora*-infected and control *G. mellonella* cadavers until after 1 h of foraging (10 min GLM $T_{1,17} = 1.06$, $p = 0.30$, 30 min GLM $T_{1,17} = 1.76$ $p = 0.096$, 1 h GLM $T_{1,17} = -3.31$, $p = 0.004$).

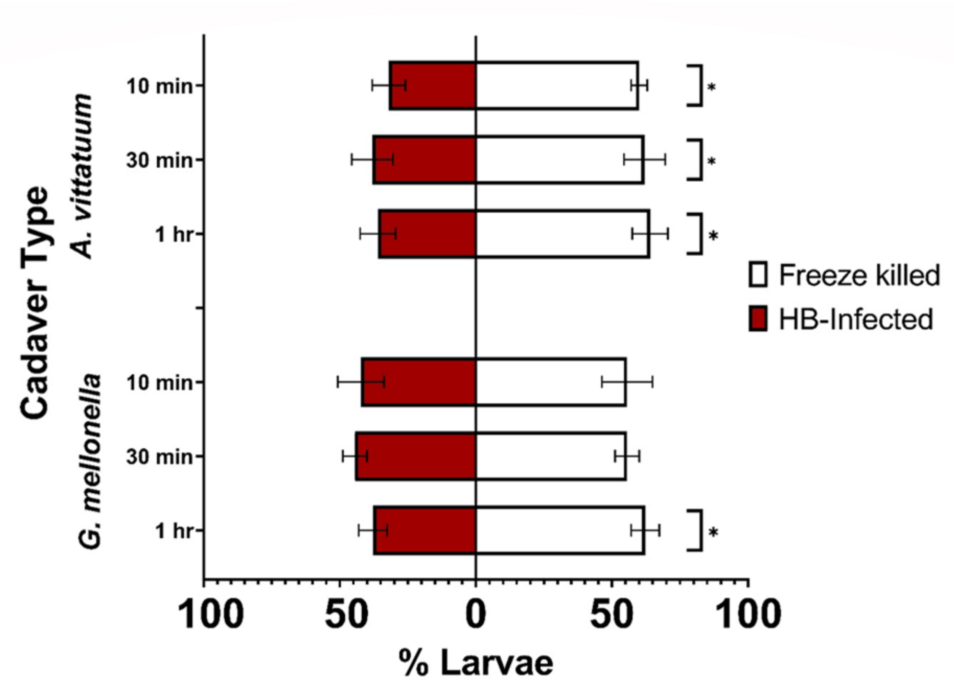

Figure 11 *A. vittatum* larvae avoided conspecific and *G. mellonella* cadavers infected with *H. bacteriophora*. Means ± SE are presented. (*$p \leq 0.05$).

H. bacteriophora **IJs are attracted to olfactory cues from heterospecific-infected cadavers**

Contrary to our predictions, we found that *H. bacteriophora* IJs were attracted to *S. carpocapsae*-infected *G. mellonella* cadavers (GLM $T_{1,5} = 3.98$, $p = 0.003$) (Fig. 12) and *S. carpocapsae*-infected *A. vittatum* cadavers (GLM $T_{1,5} = 2.65$, $p = 0.029$), as well as *S. riobrave*-infected cadavers regardless of host species (*G. mellonella*, GLM $T_{1,5} = 2.736$, $p = 0.025$; *A. vittatum*, GLM $T_{1,5} = 8.57$, $p < 0.001$). However, they did not prefer conspecific-infected cadavers over freeze-killed cadavers (*G. mellonella*, GLM $T_{1,5} = -0.32$, $p = 0.76$; *A. vittatum*, GLM $T_{1,5} = 0.125$, $p = 0.903$).

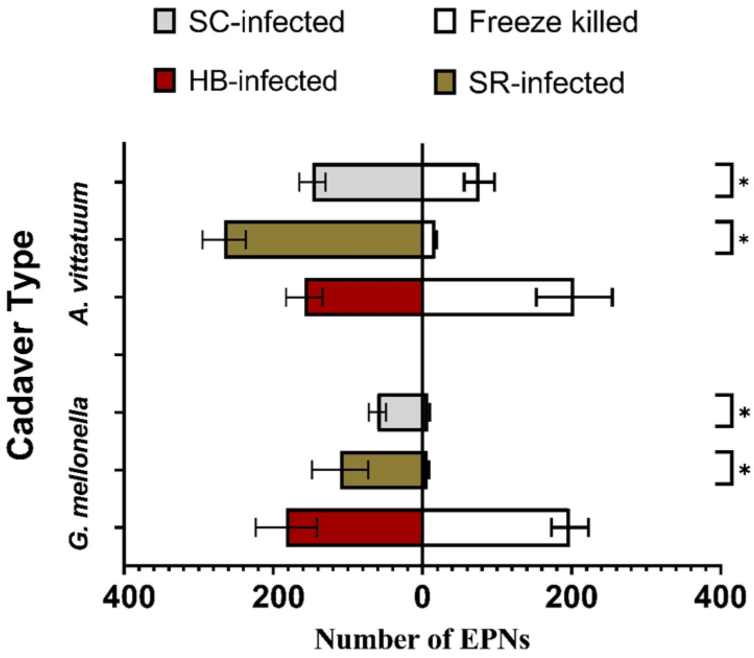

Figure 12 *H. bacteriophora* IJs preferred olfactory cues from *S. riobrave*- and *S. carpocapsae*-infected cadavers, while odours from *H. bacteriophora*-infected cadavers did not affect conspecific foraging. (*p ≤ 0.05). Means ± SE are presented.

DISCUSSION

The outcomes of trophic interactions are often affected by traits of the interacting species, with predator traits driving responses in both prey and competitors. However, our understanding of these traits and how they vary across predator species with different hunting modes, particularly in belowground soil environments, remains limited.

Here, we found predator olfactory cues varied across different hunting modes and host species, and we determined that cues from active hunters repelled foraging prey, while ambush and intermediate hunters had no effect on prey foraging. Further, active predators were attracted to heterospecific predator cues but showed no response to conspecific cues. Taken together, our findings indicate predator cues play an integral role in shaping both predator-prey and competitive interactions, highlighting the context dependency of olfactory-mediated trophic interactions, with possible cascading consequences for other community members.

Olfactory cues from EPN-infected cadavers are species specific

A growing number of studies provide evidence that predators produce specific chemical cues, that are detected by both prey and competitors (Kaplan et al., 2012, 2020). Here, we focused on olfactory cues from insect cadavers infected with EPNs, which represent a unique class of predator-associated semiochemicals, combining necromones from the dead insect host with predator kairomones (Helms et al., 2019; Zhang et al., 2019). This aligns with our findings that EPN-infected cadavers emit different blends of volatile compounds compared to dead and decomposing insects (Fig. 8, 9), and suggests they could provide a reliable indicator of EPN presence to susceptible insect prey or other competing predators.

A surprising finding in this study was that the three EPN species produced distinct blends of olfactory cues (Fig. 8, 9), with very little overlap across the various EPN-host species combinations (Table 4). Although species-level differences have been implicated from previous work (Y. Fu et al., 2020; Helms et al., 2019; Zhang et al., 2019), we expected to find a suite of conserved cues associated with EPN infection. However, only the compound 1-nonene was present for all EPN species combinations. Even the two *Steinernema* species, which we predicted would be more similar compared to *Heterorhabditis*, produced distinct volatile blends with relatively little compound overlap (Fig. 8, 9). Previous studies have documented other conserved EPN semiochemicals, including their ascaroside pheromones, which appear to be chemically similar across EPN and even plant-parasitic nematode species (Choe et al., 2012). This begs the question “why are EPN-produced volatiles so different among species?”. One possible explanation stems from the highly specific associations of different EPN species with different species of bacterial symbionts. *Steinernema* are known to form associations with *Xenorhabdus* sp. (e.g. *S. carpocapsae* with *X. nematophila* and *S. riobrave* with *X. cabanillasii*), while *Heterorhabditis* associate with *Photorhabdus* sp. (e.g. *H. bacteriophora* with *P. luminescens*) (Campos-Herrera et al., 2012; Lewis et al., 2006). These bacteria play critical roles in host infection, deterring other microorganisms or scavengers, and even mediating interspecific competition, often through synthesizing bioactive chemicals (Cai et al., 2017; Machado et al., 2020; Sicard et al., 2006). It is possible these different symbiont species are at least partially responsible for driving the high degree of interspecific variation among EPN volatile blends.

Another unexpected result was the dramatic difference in cadaver volatile blends from the two insect host species infected with the same species of EPNs. Remarkably, *A. vittatum* cadavers infected with *H. bacteriophora,* but not *G. mellonella* cadavers, produced seven sesquiterpenes as part of their volatile blends (Table 4). These compounds are not produced by *A. vittatum* alone or their host plant, and to our knowledge, this is the first report of terpene production from EPNs and/or their symbionts (Helms et al., 2019; Zhang et al., 2019). Such differences may stem from EPN symbionts aiding in the breakdown of host nutrients and secondary metabolites, as microbes grown on different substrates can change microbial metabolite profiles (Borjesson, Stollman, & Schnurer, 1990; Davis, Crippen, Hofstetter, & Tomberlin, 2013). However, further research is required to tease apart the exact contributions of EPN microbial symbionts to cadaver volatile blends

A. vittatum **larvae respond differently to olfactory cues from different EPN species**

In foraging for food resources, prey must simultaneously avoid predation (Sih, 1980) and many do so by adaptively responding to chemical cues associated with a heightened risk of predation. Our previous work suggests that *A. vittatum* larvae are “risk averse” and repelled by olfactory cues from herbivore-damaged plants, presumably because these cues also attract EPNs (Grunseich, Thompson, Hay, et al., 2020). Here, we evaluated whether larvae can also reduce their predation risk by avoiding olfactory cues produced directly by their EPN natural enemies. *A. vittatum* likely rely on avoidance or escape behaviour as a first level of defense against EPNs, which agrees with our findings that larvae were repelled by some EPN-associated olfactory cues (Fig. 10). Notably, we also observed “cannibalism” of uninfected control cadavers in our Petri dish assays. This agrees with our previous observations that in the absence of adequate food resources, *A. vittatum* larvae readily cannibalize conspecifics. Previous studies have also reported elevated incidence of cannibalism among prey exposed to increased predation risk, likely as a mechanism to enhance performance (Tigreros, Norris, Wang, & Thaler, 2017). Some insect herbivore species also directly defend against predation through sequestration of toxic host-plant compounds. *Diabrotica* species, for example, sequester plant toxins to defend against EPNs (Bruno et al., 2020; Robert et al., 2017), but this has not been reported for *A. vittatum*. Chemical defense against EPNs could also help explain why a recent study found that western corn rootworm larvae (*Diabrotica virgifera virgifera*) were not repelled by cues from EPN-infected conspecifics (Zhang et al., 2019).

Several recent studies have focused on how predator traits, including hunting modes, influence the outcomes of predator-prey interactions (Luttbeg et al., 2020; Pears, Emberts, & Bateman, 2018; Preisser et al., 2007). Current hypotheses related to prey perception of predation risk suggest prey should respond most strongly to cues from sedentary predators, as these cues indicate a more immediate threat compared to an active predator who is more likely to vacate a shared microhabitat relatively quickly (Kats & Dill, 1998; Kuijper, Schmidt, Behnke, & Wikenros, 2015; Preisser et al., 2007; Schmitz et al., 2008). Contrary to these predictions, we found that *A. vittatum* larvae avoided olfactory cues from the active-hunting species, *H. bacteriophora*, and did not respond to cues from the other two, more sedentary EPN species (Fig. 11, 12). Cadavers in experiments were standardized for age and size rendering it unlikely that our results are due to cue intensity. Additionally, all 3 EPN species kill *A. vittatum* and it does not appear that *H. bacteriophora* pose a greater infection risk than the other species. A possible explanation for why *A. vittatum* larvae avoided *H. bacteriophora*-infected cadavers, but not the other EPN species, is that these more sedentary *Steinernema* species face strong selection against production of olfactory cues that would repel their prey. This type of chemical crypsis has been predicted but little evidence has been identified to date (Kats & Dill, 1998; A. K. Miller, Maritz, McKay, Glaudas, & Alexander, 2015; Ruxton, 2009). Alternatively, since *A. vittatum* larvae are attracted to a select suite of specific host-plant terpenes (Grunseich, Thompson, Hay, et al., 2020), the contrasting terpenes produced by *H. bacteriophora*-infected cadavers could repel foraging larvae if they associate these compounds with non-host plants, a case of mistaken identity. However, this does not explain why larvae were also repelled by the non-terpene producing *G. mellonella* cadavers. The specific cues responsible for repelling *A. vittatum* and their roles in EPN ecology, as well as the potential for EPN olfactory crypsis, merit further investigation.

Foraging H. bacteriophora are attracted to olfactory cues from heterospecific EPN-infected cadavers

Many species of EPNs use chemical cues, often emitted by damaged plant roots, to locate their insect herbivore hosts (Ali et al., 2010; Grewal, Lewis, & Gaugler, 1997; Rasmann et al., 2005), this includes "cruisers" like *H. bacteriophora* (Grunseich, Thompson, Hay, et al., 2020). Here we tested whether foraging *H. bacteriophora* IJs respond to olfactory cues from conspecific or heterospecific EPN-infected cadavers. Previous studies of *Steinernema* sp. have yielded contrasting results, suggesting that some but not all EPN species use cadaver cues to avoid interspecific competition (Y. Fu et al., 2020; Grewal et al., 1997). We predicted that foraging *H. bacteriophora* would avoid olfactory cues from other EPN species to bypass competition. However, we instead found they were attracted to heterospecific cues and did not respond to cues from conspecifics when these were presented with attractive *C. sativus* root volatiles. This suggests that either heterospecific cadaver odours alone or synergistically combined cadaver and root volatiles could indicate prey availability to *H. bacteriophora* and that this response overrides avoidance of interspecific competition. It is also possible that *H. bacteriophora* is a superior competitor against the *Steinernema* sp. used in this study. Previous reports indicate that *H. bacteriophora* cannot reproduce as scavengers in freeze-killed *G. mellonella* (Blanco-Pérez et al., 2019), but that their performance is positively affected by co-infection with *S. carpocapsae* and *S. feltiae* (Neumann & Shields, 2006), lending further support to this idea. Co-existence between different EPN species may be possible, particularly if prey resources are abundant and predators can separate into different spatial niches, for example along vertical gradients (Kaya & Koppenhöfer, 1996; Ram, Gruner, McLaughlin, Preisser, & Strong, 2008).

Cascading consequences of herbivore responses to predator olfactory cues

A growing number of studies have documented trophic cascades, where the effects of predators propagate downward through food webs to affect multiple trophic levels (Denno, Gruner, & Kaplan, 2008; Ripple et al., 2016). These predator-induced trophic cascades can be triggered through direct consumption of prey, as well as indirect non-consumptive effects (NCEs), where predators alter prey behaviour, morphology, and/or physiology, with cascading effects on organisms at lower trophic levels (Griffin & Thaler, 2006; Schmitz, Hambäck, & Beckerman, 2000; Wirsing et al., 2021). Here, we report evidence of NCEs in a belowground multitrophic system, where olfactory cues from active-hunting EPNs alter the foraging behaviour of their cucumber beetle prey. Herbivory by *A. vittatum* larvae reduces growth and survival of cucumber seedlings, indicating that EPNs can indirectly influence plant performance both through *A. vittatum* mortality and by repelling foraging larvae (Grunseich, Thompson, Hay, et al., 2020). These findings suggest that some plants may benefit from higher investment in indirect defenses, like herbivore-induced volatiles, that recruit natural enemies, as they can provide multifaceted protection against herbivores. Repelling herbivores to neighbouring plants may also give these plants a boost against their competitors. This highlights the need for future studies examining how EPN-induced NCEs contribute to trophic cascades in soil environments.

CHAPTER V

CONCLUSIONS

This research examined the foraging-behavior of EPNs (*H. bacteriophora*) and a root-feeding herbivore (*A. vittatum* larvae) and how they navigated their environment while avoiding predation risk and competition. This work highlights the critical functions of volatiles in mediating multitrophic ecological interactions. My findings indicate that herbivores and their natural enemies detect and respond to olfactory cues from both EPN-infected cadavers and herbivore-induced plant volatiles to locate food resources and avoid predation risk and competition.

In the third chapter, I found that roots of *C. sativus* plants produce HIPVs for indirect defense against *A. vittatum* larvae by recruiting EPNs natural enemies, while *A. vittatum* use HIPVs to avoid antagonistic interactions with natural enemies and competition with conspecifics. I also found that after sustained herbivory for 7 days, larvae attenuated volatile induction, which reduced predation risk but increased the potential for competition with conspecifics. This work sheds light on the temporal dynamics of belowground chemically mediated interactions across trophic levels, revealing that olfactory cues and their ecological functions can shift over relevant time scales and are context dependent.

In the fourth chapter, I found that insect cadavers infected with different species of EPNs with different hunting modes, produce distinct blends of olfactory cues and that these cues differentially influence the behavior of an insect herbivore and competing EPNs. I Found that *A. vittatum* larvae avoided volatile cues produced by the active-foraging species, *H. bacteriophora*, but did not respond to cues from either of the more sedentary *Steinernema* species. My findings also indicated that the *H. bacteriophora* IJs were attracted to cues from insects infected with heterospecific nematodes, potentially signaling prey availability and not competition for resources.

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