

## Viewpoints

# Why do entomologists and plant pathologists approach trophic relationships so differently? Identifying biological distinctions to foster synthesis

### Summary

Plant interactions with herbivores and pathogens are among the most widespread ecological relationships, and show many congruent properties. Despite these similarities, general models describing how plant defenses function in ecosystems, and the prioritization of responses to emerging challenges such as climate change, invasive species and habitat alteration, often differ markedly between entomologists and plant pathologists. We posit that some fundamental distinctions between how insects and pathogens interact with plants underlie these differences. We propose a conceptual framework to help incorporate these distinctions into robust models and research priorities. The most salient distinctions include features of host-searching behavior, evasion of plant defenses, plant tolerance to utilization, and sources of insect and microbial population regulation. Collectively, these features lead to relatively more diffuse and environmentally mediated plant–insect interactions, and more intimate and genetically driven plant–pathogen interactions. Specific features of insect vs pathogen life histories can also yield different patterns of spatiotemporal dynamics. These differences can become increasingly pronounced when scaling from controlled laboratory to open ecological systems. Integrating these differences alongside similarities can foster improved models and research approaches to plant defense, trophic interactions, coevolutionary dynamics, food security and resource management, and provide guidance as traditional departments increase collaborations, or merge into larger units.

### Introduction

Plant–insect and plant–pathogen interactions have many convergent features. Both involve exploitation of a diverse array of autotrophs by a diverse array of heterotrophs, involve selective pressures generating complex adaptations and counter-adaptations, and can negatively affect human well-being and, in the case of alien invasive species or altered relationships induced by climate

change, ecosystem integrity. In recent years, our understanding of these commonalities between plant–herbivore and plant–pathogen interactions has been strengthened by improved characterization of biochemical pathways, eliciting agents and modes of inheritance (Felton *et al.*, 1999; Thaler *et al.*, 2010; Barrett & Heil, 2012; Karban, 2015; Erb, 2018). However, despite these commonalities, entomologists and plant pathologists often use markedly different models for how these relationships function in natural and man-made ecosystems, and assign divergent response priorities to pest-related challenges driven by climate change, global transport and land use alterations (McManus, 2018; Showalter *et al.*, 2018). Although disciplinary biases are frequently suspected and are surely contributors, we suggest that variable theoretical interpretations and management response strategies reflect some under-appreciated yet fundamentally different facets of the dynamics, ecology and evolution of trophic interactions in open systems. Understanding these differences can contribute to our comprehension of ecosystem processes, our understanding of integrated plant–herbivore–pathogen relationships (Eyles *et al.*, 2007; Busby *et al.*, 2015; Lamit *et al.*, 2015), and to more synthetic solutions to emerging challenges to food security and environmental quality.

We propose that differing perspectives, and their emergent research and management priorities, may arise from some intrinsic biological differences between plant–insect and plant–pathogen interactions. All-encompassing theories have a deservedly strong appeal, and their emphases on similarities have high inherent value. However, it is also worthwhile to identify important biological differences, especially as trophic interactions are being increasingly subjected to anthropogenic change. Identifying key distinctions can provide opportunities to better integrate and synergize understanding, optimize management approaches and investigate insect–pathogen vector systems.

We posit that differences between herbivore and pathogen life history, ecology and evolution foster four important distinctions in their relationships with plants, illustrated in Fig. 1(a): (1) capacity to link behavioral choice with directed movement, that is the spatial scale of oriented host choice; (2) relative ability to evade detection; (3) plant fitness costs, and the extent to which they relate to numerical abundance of the exploiter; and (4) extent of top-down population regulation. We recognize that *all distinctions are actually gradients*, and *there are exceptions and overlap to all generalizations*. Some exceptions are idiosyncratic, while others are more categorical. Categorical exceptions can be taxonomic, such as aphids and other sap-feeding insects that sometimes function much like pathogens. They can also be ecological, such as when the longevity of trees may enable opportunistic pathogens to have strategies that overlap with those of insects (e.g. high dependence on environmental stress, and ability to select over time what herbivores select over space). Rather than repeatedly delineate such exceptions, we acknowledge them up front, and strive to provide a birds-eye view

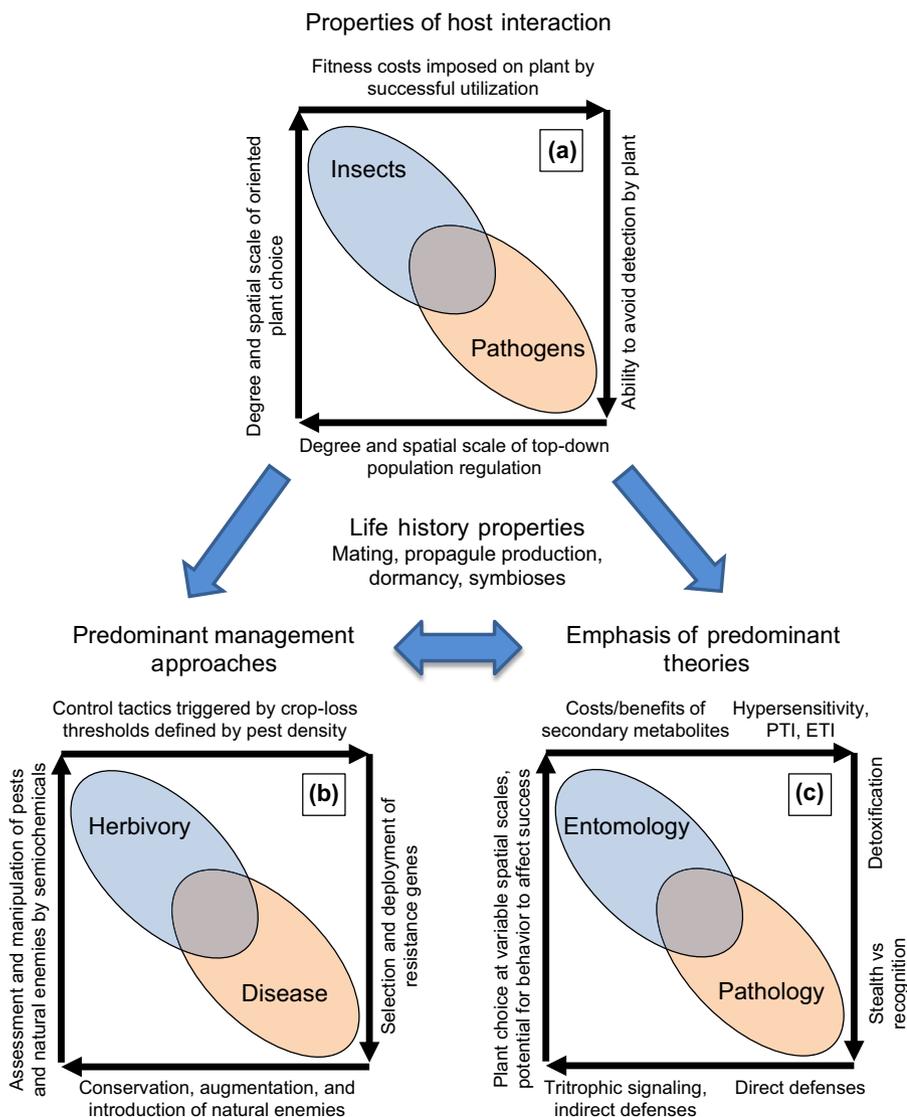
that may help us better interpret the landscape of plant–exploiter relationships within the open systems in which they interact.

We first identify four important features that differ in the *relative degree* to which insects and pathogens interact with plants, and discuss their ecological implications. We then extend this analysis to identify emergent implications and applications to prevailing theories of plant defense (Fig. 1b) and management (Fig. 1c). Finally, we propose a research agenda that fosters synthesis when delineating new hypotheses, devising ecological and evolutionary models, and addressing trophic alterations arising from anthropogenic change.

## Major differences in how insects and pathogens interact with plants

Behavior, and the spatial scale of active choice among host individuals

Insects and phytopathogens differ markedly in their abilities to actively and iteratively choose among individuals within host plant



**Fig. 1** Conceptual diagram illustrating relative distinctions between plant interactions with insect herbivores and microbial pathogens, and corresponding differences in management and conceptual frameworks surrounding these agents. (a) Basic biological differences, and overlap, in properties of plant–insect and plant–pathogen interactions; overlap varies with feeding guild, taxonomic group and system specificities. These interact with general features of insect and microbial life histories to produce relative differences in management approaches and theoretical frameworks most commonly employed by disciplinary specialists. (b) Relative extents to which various insect and phytopathogen pest control strategies are employed and have achieved practical success in agriculture and forestry. These derive from the four corresponding (positioned along the same axes) biological and ecological differences in (a). General patterns, their exceptions and degrees of overlap vary with plant production system, landscape context, geographic region and socioeconomic factors. Relationships also vary between native vs exotic pests, and with changing climate. (Note: pesticides and transgenic resistance are omitted here because they do not derive directly from trophic interactions.) (c) Influence of intrinsic biological differences between plant–insect and plant–pathogen interactions (a) on corresponding (positioned along the same axes) major theories of plant exploitation and defense. Various conceptual frameworks have achieved different degrees of emphasis by, and utility for, entomologists and plant pathologists. PTI, PAMP-triggered immunity; ETI, effector triggered immunity.

made by insect vectors (and, conversely, some phytopathogens can influence vector behavior (Ingwell *et al.*, 2012; Mauck *et al.*, 2018)). Pathogen chemoreceptors (Matilla & Krell, 2017) function on a much smaller scale, for example in motile propagules of certain fungi and oomycota and flagellate bacteria in soil (Bowers & Parke, 1993; Turrà & Di Pietro, 2015). Chemotropisms direct motile propagules toward a nearby host, but do not enable active choice among widely distributed individuals of plant populations. Infection may likewise progress or be interrupted at multiple stages, but pathogens (with some exceptions as in rhizomorph-producing, foraging fungi such as *Armillaria* spp.) typically lack the ability to resume searching if colonization fails.

A consequence of directed behavior is that individual insects can actively choose not only particular plant genotypes, but also plants experiencing a particular physiological circumstance, age or habitat (Janz *et al.*, 2005; Knolhoff & Heckel, 2014). For example, individuals of various insect species specifically search for individuals within the host species range that are under drought stress or are well hydrated (Carr *et al.*, 1998; Kolb *et al.*, 2016), are previously damaged by abiotic or biotic agents, or, conversely, host individuals that are undamaged (Roininen *et al.*, 1997; Powell *et al.*, 2012; Uesugi *et al.*, 2016), or are of a particular age category (Kearsley & Whitham, 1989). Furthermore, insects may prefer plants that, by chance, are located on a site that provides higher nutritional quality or, conversely, may avoid plants that harbor predators (Stamp & Bowers, 2000) or are near other plant species that emit volatile repellents (Barbosa *et al.*, 2009). In this regard, those species of insect herbivores that exploit weakened plants resemble predators that cue in on a particular prey condition, such as wolves that preferentially attack mammals enfeebled by any of a broad range of physiological stresses, injuries or age. In such species (e.g. bark beetles, wood borers) preference for a particular host condition may override preference for a particular host species or genotype. Pathogens are constrained by more passive dispersal and smaller-scale host-selection mechanisms, so they have less opportunity to actively direct their attack to particular environmentally induced or ontogenetically determined plant phenotypes. Hence, while pathogens may benefit from particular environmental factors, they are largely regulated by specific plant–genotype combinations. Such broad distinctions always break down to some extent. For example, susceptibility to biotrophic pathogens, such as many viruses, phytoplasmas and rust fungi, is often well explained by various forms of gene-for-gene models (Dangl & Jones, 2001; Sacristan & Garcia-Arenal, 2008), whereas necrotrophic pathogens rely more heavily on environmental mediators (Ghelardini *et al.*, 2016), accomplishing in time via dormancy what motile insects achieve in space.

In general, the capacity for more-directed host-selection behavior can increase the environment's role in insect–relative to pathogen–plant interactions. Actively searching for plants that are in a particular physiological condition due to many different abiotic and biotic environments adds substantial stochasticity to the reciprocal selective pressures between insects and plants. This is especially likely in heterogeneous environments such as natural ecosystems, compared to highly managed, homogenized, agroecosystems. The environment is a crucial component of all disease

triangles (i.e. plant, pathogen, environment), but these relationships rarely entail pathogens *actively searching* for plants experiencing a particular circumstance. Hence, each encounter tends to be terminal (i.e. resulting in either pathogen success or failure), without new attempts on other plants. An analogous manner in which some fungi resemble insects is through latency, whereby pathogens reside in a host for lengthy periods (endophytic state), and then express virulence when the host experiences an exogenous or endogenous stress (Ghelardini *et al.*, 2016), that is pathogens incapable of actively seeking hosts in a particular condition can use dormancy as a strategy to wait until their current host is in the appropriate condition.

### Stealth and subterfuge: circumventing the elaborate defense systems of plants

Plants have highly sophisticated mechanisms for detecting the presence and activities of their attackers (e.g. Erb *et al.*, 2012; Zipfel, 2014; Karban, 2015). Cues include plant cell fragments indicative of injury (DAMPs: damage-associated molecular patterns), microbial surface compounds (MAMPs, PAMPs: microbe- or pathogen-associated molecular patterns), salivary, ovipositional or fungal secretions, and others (Jones & Dangl, 2006; Zipfel, 2014). Recognition induces a cascade of plant response syndromes, such as PAMP-triggered immunity (PTI) followed by effector-triggered immunity (ETI), and cross-talk between salicylate and jasmonate signaling pathways (Kunkel & Brooks, 2002). A key challenge to plant exploiters is that cues that betray their presence include signals that are both conserved across large taxonomic phyla and important for other functions (e.g. MAMPs, insect chitin), and are specific to particular exploiting agents (Sacristan & Garcia-Arenal, 2008).

Many pathogens successfully exploit plants through stealth and subterfuge, that is by using mechanisms by which they avoid, circumvent, or silence plant detection systems (Toth & Birch, 2005; Göhre & Robatzek, 2008; Csorba *et al.*, 2015; Stringlis *et al.*, 2018). Whether, or how quickly, a plant detects the microorganism and hence mounts effective defenses is often a key determinant of the interaction's outcome. For example, in incompatible (unsuccessful colonization) interactions, effectors are recognized by products of host resistance genes, triggering effective ETI responses, whereas virulent (compatible) genotypes suppress or evade ETI via molecular countermeasures that often use effectors to inhibit PAMP perception (Toruno *et al.*, 2016).

Insects have fewer opportunities than pathogens to hide their actions. Their means of feeding on or entering plants often entail injuring plant tissues with sclerotized legs, mouthparts and ovipositors. These injuries elicit cascading responses culminating in order-of-magnitude increases and compositional alterations to allelochemicals, or various forms of programmed cell death such as hypersensitive encapsulation or abscission (Coll *et al.*, 2011; Kim *et al.*, 2011). The difficulty of avoiding detection can be compounded by insects' requisite associations with microbial symbionts, which plants sometimes exploit to detect herbivores (Franceschi *et al.*, 2005; Karban, 2015). As free-living organisms, insects are also covered with multiple transient microorganisms, each of which could potentially trigger detection. Interestingly, the

insects most adept at avoiding detection are sucking species, which exhibit a number of microbe-like life history features (low directed locomotion during certain life stages, specialized stylets), intimate relationships with plants and substantial fit to coevolutionary models originally conceived for pathogens (Kaloshian, 2004; Showalter *et al.*, 2018). Additionally, some mandibulate insects use specialized symbionts to mask their feeding (Chung *et al.*, 2013). Overall, however, coevolutionary adaptations between plants and pathogens more commonly take the form of heightened plant detection ability vs increasingly complex microbial stealth and subterfuge (Stringlis *et al.*, 2018), whereas plant–herbivore coevolution often takes the form of new plant toxins vs corresponding detoxification pathways (Berenbaum, 1983; Berenbaum & Zangerl, 2008; Becerra, 2015).

Differences in the degree to which pathogens or insects can utilize stealth have important ramifications for ecology and evolution. General theories of plant defense against insects are primarily based on concentrations or unique features of allelochemicals (Feeny, 1976; Berenbaum, 1983; Coley *et al.*, 1985; Herms & Mattson, 1992). These compounds are bioactive against insects, but may be costly to biosynthesize and store, thus imposing tradeoffs among various plant functions. Although these models of antiherbivore defense vary in emphasis, they are typically founded on an arms race between plant production of novel and more rapidly mobilized compounds, and anatomical structures that in many cases store, transport or exude them (Becerra *et al.*, 2001), vs more effective pathways of detoxification, excretion and sequestration (Heckel, 2014), as well as active behavior countering host toxin delivery (Dussourd, 2017), by insects. By contrast, the major theories of plant defense against pathogens place less emphasis on the quantities and quality of antimicrobial compounds, and more strongly emphasize mechanisms of plant recognition and pathogen evasion that govern the rapidity of genetic and physiological responses (Jones & Dangl, 2006). Differences in the relative importance of allelochemical concentrations in determining outcomes are further supported by genetic manipulation experiments. Systems in which pathogen success is correlated with allelochemicals have sometimes remained unaltered after production of those compounds was reduced or suppressed, suggesting an associative more than causal relationship (Glazebrook *et al.*, 1997). By contrast, when genetic manipulations alter compounds affecting herbivory, the resultant changes in insect performance are often consistent with causal relationships (Steppuhn & Baldwin, 2007). The greater importance of total quantities of allelochemicals in intraspecific differences in host susceptibility to insects than to pathogens may add to the role of environmental mediation. That is, absolute concentrations are often strongly influenced by environmental factors, particularly in heterogeneous natural ecosystems (Herms & Mattson, 1992; Raffa *et al.*, 2008), even in systems where chemical composition (compounds present and their relative proportions) is under strong genetic control (Latta *et al.*, 2003; Zhang *et al.*, 2016).

#### Plant tolerance: consequences of successful plant utilization

Plants have variable abilities to tolerate (sustain) a given amount of herbivory or infection without a corresponding reduction in fitness

(Strauss & Agrawal, 1999). Tolerance is sometimes related to intrinsic growth rate, but can be conferred by a number of general and specific plant physiological processes (Rosenthal & Kotanen, 1994). In some cases tolerance arises from herbivore-imposed selection, but can also be a by-product of other selective forces, such as drought (Rosenthal & Kotanen, 1994). Both interspecific and intraspecific genotypic variation in tolerance is well documented. Tolerance and resistance can be inversely related, but there are many exceptions (Leimu & Koricheva, 2006).

Although often quite dramatic, herbivory does not always reduce plant fitness (Rosenthal & Kotanen, 1994). Plants often experience remarkably high levels of leaf removal before being killed or even experiencing sublethal effects, such as reduced growth or increased sensitivity to other biotic and abiotic stressors (Mauricio & Rausher, 1997; Poveda *et al.*, 2012). Particular densities of insects are required to exert damage beyond a plant's tolerance limits. Tolerance varies greatly with feeding guild, often being lower to subcortical and root feeders than to folivores, and being lowest to species that vector pathogens, create infection courts or inject toxins that induce abnormal cell growth (Showalter *et al.*, 2018). Pathogens, by contrast, cause disease, a continual source of cellular and tissue injury. Plant fitness and yield losses usually greatly exceed what could be attributed solely to substrate removal. It is more difficult to separate tolerance from resistance with pathogens, in that both can involve delayed containment. Evolutionary trajectories can also proceed from reduced virulence to nondamaging symbioses as with some endophytes (Delays *et al.*, 2013), or the reverse as with host jumps that commonly occur with invasive pathogens.

A consequence of underlying differences in tolerance is a much greater opportunity for plant fitness to be increased by the activity of density-dependent predators, parasitoids and entomopathogens of herbivores (Krause & Raffa, 1996). Tolerance can provide a critical delay between a herbivore's initial feeding and its populations increasing enough to threaten plant fitness, allowing natural enemy populations time to increase and regulate the herbivore. When available, this linkage may provide a stronger basis for active incorporation of natural enemies into plant defense syndromes, such as when herbivore-injured plants emit volatiles that attract parasitoids and predators, sometimes with specific volatiles responding to specific herbivores (Turlings & Erb, 2018).

#### Top-down population control

High proportions of phytophagous insect populations are killed by a diverse array of predators, parasitoids and pathogens that kill them (Vidal & Murphy, 2018). These 'natural enemies' range from highly generalist (e.g. birds, spiders) to highly specialized (e.g. viruses) enemies, and also range from operating largely independently of plant properties to being highly linked behaviorally and developmentally to specific host plant features. Parasitoids and predators possess acute chemical, visual and auditory sensitivities, plus strong learning capacities, to locate even cryptic prey (Turlings & Erb, 2018). Evidence of high mortality and population regulation by natural enemies is substantiated by life tables, field and laboratory experiments, simulation models, *post hoc* analyses of

population trends, case studies of accidental pest introductions, and planned biological control (Hajek & Leger, 1994; Rosenheim, 1998; Páez *et al.*, 2017; Vidal & Murphy, 2018). In addition to killing herbivores, natural enemies provide substantial reductions in plant consumption by causing herbivores to hide, flee or feed on suboptimal tissues (Buchanan *et al.*, 2017), and likewise, in addition to killing herbivores, plant toxins increase herbivore exposure to lethal natural enemies by delaying their growth (Shikano *et al.*, 2018).

Pathogens must also contend with natural enemies (Handelsman & Stabb, 1996), such as *Trichoderma* spp. that parasitize fungi. However, there is much less compelling evidence than with insects of region-wide, density-dependent numerical population control by natural enemies (Parratt & Laine, 2018), especially in natural ecosystems. More commonly, 'beneficial' microbes provide specific barriers at the plant surface, especially when augmented by targeted agronomic tactics (Finkel *et al.*, 2017; Lombardi *et al.*, 2018). Some natural enemies of pathogens show sophisticated host-orienting mechanisms, but these typically function at a more microsite scale than the long-distance directed locomotion of predators and parasitoids attacking insects.

The large extent to which natural enemies impact herbivores can make the reciprocal selective pressures between plants and herbivores more 'diffuse', in the sense of being strongly mediated by multiple external drivers (e.g. Thompson, 1994) in addition to the interactions between plant and insect *per se*. This in turn has ecological and evolutionary consequences. For example, the relative impacts of natural enemies appear to vary among feeding guilds, with externally feeding species often subjected to greater top-down pressures, and internal feeders subjected to greater bottom-up pressures (Vidal & Murphy, 2018). By comparison, the substantially lower top-down numerical regulation of pathogens (Parratt & Laine, 2018; Vega, 2018) than of herbivores places even greater relative selective pressures on the host–pathogen interaction *per se*. This biological distinction fosters disciplinary differences. Entomologists typically classify various species of herbivores by the degree to which their populations are primarily regulated by bottom-up, top-down or lateral (competition) forces (Denno *et al.*, 1995). Such a top-tier classification scheme is not particularly common or useful for plant pathologists. This distinction also influences plant defense theory. For example, entomologists classify plant defenses as direct, that is provided by the plant itself, or indirect, where defense arises from recruitment of natural enemies (Turlings & Erb, 2018), a framework uncommon among plant pathologists.

### Life history features of insects and pathogens leading to scalar differences in their interactions with plants

Each of the above features of trophic interactions is further influenced by some important life history differences between insects and microorganisms (Fig. 1, center). Microorganisms often have shorter generation times and produce more propagules than insects, traits that can accelerate adaptation. Furthermore, pathogens often undergo genetic and epigenetic changes within a single plant, thereby augmenting their ability to overcome defenses

(Dubey & Jeon, 2017). Some piercing–sucking arthropods undergo genetic changes over several generations on host plants (Edmunds & Alstad, 1978), but most insects disperse, a behavior driven by the need to locate mates, escape natural enemy buildup, avoid competitors, and abandon plants that are reaching new ontogenetic stages or deteriorating.

Obligate sexual reproduction, as in the case of many phytophagous insect species, confers many benefits, but the need to locate mates may also render populations more susceptible to Allee effects (Berec *et al.*, 2018). Variable mating success can yield a mosaic of herbivore densities in space and time, adding stochasticity to and in some cases reducing their selective pressures on plants. On the other hand, pathogens have flexible reproductive systems and various resting structures that enable local persistence during long periods of unsuitable environments or unavailable hosts (Agrios, 2005). Pathogen resting stages may remain viable for many years to decades. One consequence is that mechanisms used by plants to avoid herbivory, such as escape in time via phenological asynchrony, rapid development or seed predator satiation (Feeny, 1976), are less reliable against pathogens. Insects also have mechanisms for enduring extreme conditions, but diapause and aestivation tend to be timed to annual climatic cycles. When insects are confronted with an absence of suitable hosts, they typically disperse, so local abundance commonly undergoes booms and busts.

Insect metamorphosis can result in different stages of the same organism imposing different selective pressures on plants. For example, many insects are herbivores during immature stages, but predators, decomposers or pollinators as adults. Some fungi, such as latent pathogens, endophytes and mycorrhizal fungi, can plastically change lifestyles from commensal or mutualistic to pathogenic (Yun *et al.*, 1997). Again, a key difference is in scales of space vs time. When insects shift from herbivory to other lifestyles, the feedbacks are commonly to different plant individuals, species or communities, and are relatively rapid. With pathogens, directional switches commonly exert feedbacks on the same host, often after lengthy latent intervals.

Most, if not all, insect herbivores rely on microbial symbionts to utilize plants (Douglas, 2015). These microorganisms provide essential functions, such as nutrient acquisition, overcoming plant defenses, protection from natural enemies and pheromone signaling. Insect–symbiont systems reflect pronounced coevolution, and use a wide variety of mechanisms to maintain these linkages, making almost all relationships with plants at least tripartite. Phytopathogens sometimes show symbioses with other microbes (Partida-Martinez & Hertweck, 2005), but these appear to be relatively uncommon, possess a narrower range of functions and are less essential than with insects, again resulting in more bipartite relationships.

### Toward integration: implications and applications

We identify the above distinctions not to over-emphasize differences or dissuade assimilating approaches, but rather to highlight opportunities for integration, application and directed research. We provide some brief examples below, which are not intended to

be comprehensive, but rather to suggest linkages between the above disparities and subsequent recommendations for future research.

### Food security, sustainability and natural resource protection

The intrinsic differences between plant–insect and plant–pathogen interactions discussed above are manifested in the predominant approaches taken to agronomic and forest protection against pests, which are depicted in Fig. 1(b). We suggest that recognizing these historical discrepancies in emphasis between entomologists and plant pathologists as outcomes of the intrinsic differences of the two groups of plant consumers, illustrated in the corresponding axes of Fig. 1(a), offers opportunities for fruitful integrative approaches.

Differing levels of directed movement toward host plants have at least four management implications. First, chemical attractants are widely used to quantitatively sample herbivore and natural enemy populations for integrated pest management of insects. Plant pathologists usually lack these opportunities (except at very fine spatial scales), and often must rely on passive sampling methods. Second, insect behavior provides an additional opportunity for control, with semiochemicals being deployed to interfere with host and mate finding (Cook *et al.*, 2007). Third, behavioral components of plant–insect interactions have long been exploited in breeding programs, whereby resistance is based on low attraction to visual or chemical plant cues (e.g. Silva *et al.*, 2014). Crops are also being developed for higher attraction to natural enemies (Turlings & Erb, 2018). Such approaches are less possible and are much less common in pathogen management. Fourth, the dimension of behavior provides opportunities to mitigate insect biotype evolution against genetically modified organisms and traditionally bred resistant plants. Biotype prevention is particularly effective when intermixed resistant and susceptible plants can be behaviorally perceived by insects, so directed movement to preferred susceptible plants (refugia) reduces selection to overcome resistance (Tabashnik *et al.*, 2013). Plant pathologists lack this advantage in designing biotype-management strategies.

Processes of stealth and recognition form an essential component of gene-for-gene and associated models, which arguably comprise the most successful paradigm for breeding crop protection from pathogens (Dodds & Thrall, 2009). Historically, gene-for-gene models have achieved more practical success against pathogens than insects, with some notable exceptions involving herbivores that have highly intimate host associations or that vector phytopathogens (Hill *et al.*, 2006). However, several recent trends suggest the applicability of these models can be broadened in some cases, or their limits can be better delineated in others. For example, microbial symbionts can suppress elicitation of plant defense pathways by gall-forming, leaf mining and externally chewing insects (Chung *et al.*, 2013; Giron *et al.*, 2016), opening avenues for better understanding other modalities of herbivore stealth. Likewise, so-called ‘minor’ resistance genes (associated with polygenic, or quantitative, resistance) are becoming more widely valued for their utility in preventing both pathogen and insect biotype evolution (Gonzalez *et al.*, 2012). Such genes may prove particularly valuable in heterogeneous ecosystems such as forests, and against invasive pathogens for which major resistance genes

may be lacking in naïve populations. Third, emerging genome-for-genome models that emphasize dynamic host–pathogen interactions based on genetic diversity and developmental immunity may prove to be more robust and better able to incorporate a wide array of independent and interacting selective forces than traditional approaches (Krasileva *et al.*, 2011).

Differing tolerances likewise have important implications for agriculture and forest protection. First, insect pest management can afford to rely more heavily on biological, cultural and semiochemical controls, and on delaying pesticide applications until populations reach economic thresholds. Second, plant tolerance can provide a specific target for breeding, such as with injury and yield loss to European corn borer infestations (Panouillé *et al.*, 1998). Tolerance has the added benefit of not imposing selective pressures on the herbivore while safeguarding yield, thus de-escalating the genetic arms race between insects and plants (Páez *et al.*, 2017; Peterson *et al.*, 2017). Third, understanding where tolerance is least prominent against insects provides strong guidance to programs aimed at biological control of invasive weeds, especially in the selection prioritization of potential agents. Implementing tolerance is substantially more difficult in managing, and breeding against, pathogens. In addition to causing progressive disease, pathogens often render plants susceptible to other agents, reduce aesthetic value and produce hazardous toxins. Hence, a much higher degree of suppression is often required against pathogens than insects.

The high degree of top-down regulation of herbivores has allowed biological control to become a cornerstone of integrated pest management. It is widely recognized as a *top-level* equivalent to chemical, cultural and host-resistance controls, because of its self-perpetuating nature and low environmental impact. It is also the basis of ‘insecticide windows’, whereby sprays are targeted to periods when natural enemies are relatively absent or in nonvulnerable stages. Cultural manipulations are likewise designed to limit impacts on natural enemies. Classical biological control, the deliberate introduction of natural enemies, has likewise succeeded in reducing insect populations to tolerable levels in many agricultural and natural ecosystems (Hajek & Leger, 1994; MacQuarrie *et al.*, 2016; Heimpel & Mills, 2017; Páez *et al.*, 2017). By comparison, biological control can be a valuable asset to protecting plants from pathogens in agroecosystems, but does not rise to the same levels as host resistance or antimicrobial pesticides (Vega, 2018). The most effective natural enemies of pathogens are often microbial competitors in the phytobiome, but plant infection by competing agents often does not confer acceptable crop protection. When natural enemies do provide crop protection from pathogens, it is usually at a finer spatial scale than with insects (e.g. protection of individual plants by endophytes), rather than spatiotemporal dynamics of populations at ecosystem levels (Handelsman & Stabb, 1996; Daguerre *et al.*, 2015).

Despite these distinctions, commonalities in management approaches against insects, pathogens and vector complexes can provide practical, cost-effective benefits to both agriculture and sustainable utilization of natural resources. Much of the information gained about each system is broadly applicable and transferable, so areas where different degrees of emphasis have arisen merit exploration as sources of novel approaches. Understanding

relative differences, however, can help to identify areas where priorities of limited resources may be misallocated, and hence opportunities lost, if these commonalities are over-extended, especially when scaling from molecular to field levels, and from biochemistry to epidemiology (Showalter *et al.*, 2018).

### Interpreting insect–pathogen vector systems

Insect–pathogen vector systems present both some of the most challenging problems to agriculture and forestry, and impose some of the strongest selective pressures in nature. Although each insect–pathogen complex has unique features, there is value to approaching vector systems as hybrids of the features shown in Fig. 1 rather than as simple combinations of herbivores and pathogens. An example is provided by bark beetle–microbial complexes. The moderately phytopathogenic fungi vectored by these herbivores appear to aid beetle attack by exhausting or detoxifying tree defenses. However, the fungi lose opportunities for stealth by being linked to such tissue-damaging insects, and incur predation by beetle-vectored mites. They also gain directed entry via insect choice into those trees that are physiologically predisposed to infection, benefit from the beetles' pheromone-mediated aggregation behavior that greatly increases propagule pressure, and gain protection from antagonistic fungi by the beetles' symbiotic bacteria (Hammerbacher *et al.*, 2013).

Viewing insect–pathogen complexes as hybrids may also provide improved management opportunities. For example, practices that add environmental heterogeneity or multidirectional selection pressures on the symbiosis may help to accentuate differences between the insect's and microbe's optimal strategies. Variation in the degrees of herbivore–symbiont associations that arise from geographic region, population phase and host species may provide opportunities for enhancing these distinctions. In other cases, abilities to detect invasive pathogens may be improved by exploiting herbivore behavior, such as using host volatiles and pheromones to identify vector presence and hence probable new infection sites. For example, pheromone-based trapping of beetle vectors of the thousand canker disease fungus (*Geosmithia morbida*) of walnut has facilitated rapid detection and sanitation of this otherwise cryptic pathogen (Blood *et al.*, 2018).

### Countering biological invasions

Inadvertent movement of phytophagous insects and phytopathogens is one of the most damaging components of global change to environmental quality and human well-being (Pimentel *et al.*, 2005). Differences between the ecology of insects and phytopathogens can help establish response priorities. For example, despite appreciable numbers of successful classical biological control (i.e. the establishment or re-establishment of top-down forces) against insects (Van Driesche *et al.*, 2010; MacQuarrie *et al.*, 2016; Heimpel & Mills, 2017), there have been far fewer against pathogens (Showalter *et al.*, 2018). An exception is mycovirus-induced hypovirulence of the chestnut blight fungus in Europe (Milgroom & Cortesi, 2004). However, establishment in new biomes can alter many of the above generalities, and control

recommendations need to be established accordingly. For example, coevolved defenses limit emerald ash borer to severely stressed hosts in its native China, so sanitation and silviculture can provide effective controls. Due to lack of coevolutionary history, however, North American ashes possess little resistance or tolerance, so tree mortality approaches extirpation levels, and neither silvicultural tactics nor native or introduced natural enemies seem likely to exert adequate protection (Showalter *et al.*, 2018).

Another feature of biological invasions is that relatively benign symbionts of insects can become virulent phytopathogens in the introduced range, such as with Dutch elm disease and laurel wilt of redbay (Showalter *et al.*, 2018). In others, exotic phytopathogens acquire new vectors in their introduced zone, as with pitch canker in California (Hoover *et al.*, 1996). Thus, the ubiquity of herbivore–symbiont relationships necessitates that introduced insects and microbes be viewed as potential invasive insect–microbial complexes (Vasanthakumar *et al.*, 2008), and also that potential hybrid features should be rapidly explored.

### Predicting and responding to impacts of climate change on trophic interactions

Changing temperature and precipitation regimes can dramatically alter plant–consumer interactions by directly benefitting the insect or microbe, weakening host defense or tolerance, and altering tritrophic interactions (McDowell *et al.*, 2008). Climate change can also facilitate geographic range expansions, which potentially allows new host associations. Given the vastness of this subject area, we describe one case study that includes both insect and microbial members, to illustrate some key points as they relate to our synthesis, and the uncertainties caused by a shifting environmental template. This case study illustrates some general overriding principles, such as different patterns among insect behavior, symbiont virulence and tree defense physiology during range expansions, and different feedbacks arising from different levels of scale.

The mountain pine beetle, *Dendroctonus ponderosae*, and its phytopathogenic fungal symbiont, *Grosmannia clavigera*, are native to western North American conifer biomes, and have always undergone intermittent outbreaks. As temperatures have risen, however, landscape-altering population eruptions have become more frequent and larger than historical norms (Raffa *et al.*, 2008). Additionally, populations are expanding into previously climatically unsuitable regions. Predicting their impacts is confounded by differential effects of multiscale processes on beetles and their associated fungi. For example, recent warming has allowed *D. ponderosae* to expand northward, into British Columbia, Canada, in very dramatic fashion. The resulting large-scale outbreaks breached the historical geophysical barrier of the Rocky Mountains. The beetle is now firmly established in Alberta, Canada, and poses an unprecedented threat to the Canadian boreal forest and the Great Lakes Region. The novel host jack pine is at least as, and probably more, susceptible to *G. clavigera* than historical hosts (Erbilgin *et al.*, 2014). Likewise, the novel host red pine is more conducive to brood development. However, more rapid development may expose resulting beetle life stages to higher

winter mortality (Rosenberger *et al.*, 2018), and high temperatures alter the beetle's symbiont complex (Addison *et al.*, 2015). Adding to the complexity, midwestern forests generally have higher populations of competitors and predators (Raffa *et al.*, 2015). Conversely, local natural enemies show weak attraction to *D. ponderosae* pheromones, with which they had no previous contact. Landscape-scale factors, such as a more diverse forest structure, contribute to the possibility that these climate-driven invaders may establish but not undergo outbreaks.

Increasing temperatures have also favored *D. ponderosae* expansion into higher elevation stands, many of which are dominated by semi-naïve whitebark pines (a species already threatened by an invasive fungus) that have weaker defenses elicited by *G. clavigera* than the historical low-elevation host lodgepole pine (Raffa *et al.*, 2015). However, the beetle still preferentially orients to lodgepole pine, again showing how insect behavior and host responses to herbivore symbionts may not necessarily evolve at the same rate. This raises the management possibility of exploiting the current disparity between insect behavior and fungal pathogenicity to help preserve these fragile ecosystems, such as by favoring within-stand species mixtures.

Throughout all phases of this range expansion, then, not only will tree defense physiology be an important determinant, but so too will behavior and learning by both the herbivore and its enemies, relationships of symbionts with both insect vectors and host plants, and landscape-scale processes such as forest structure. Partitioning these various processes can help to address such a complex, otherwise intractable, suite of interactions.

### Understanding disciplinary differences

In light of the relative differences in biological attributes of the systems they study, entomologists tend to view trophic interactions largely, or even primarily, as a question of population dynamics, whereas plant pathologists usually place greatest emphasis directly on the plant–pathogen interaction *per se*. The spatiotemporally more diffuse nature of plant–insect interactions often orients research emphasis toward how multiple environmental inputs interact, such as the impacts of efficient natural enemies, constraints imposed by the need to find mates, competition, limited duration of survival during environmental extremes, host scarcity, and the coupling of host selection with directed locomotion. By contrast, plant pathologists have found success with models that are primarily genetically based, and that incorporate environmental factors largely as conditions under which the pathogen may or may not achieve various life history stages, or as conditions under which host defenses or suitability may be partially altered. These perspectives are reflected in the major paradigms of plant defense that arise from and inform these disciplines (Fig. 1c).

Biological distinctions may in turn influence disciplinary differences. For example, the prospects for reducing pest damage by manipulating higher-level factors are often viewed with more optimism by entomologists, based on successes with cultural controls and natural enemy enhancements that accompany resistance breeding. By contrast, plant pathologists have achieved many of their successes through heritable resistance, and only a

mixed record of successes (e.g. crop rotation) and failures (e.g. alternative host eradication) with higher-level manipulations. Similarly, the prospect of reducing plant disease by controlling vectors is often met with substantial skepticism by plant pathologists, given the relatively few successes in agriculture and even fewer in forests. But the same prospect is met with cautious optimism by entomologists who cannot help but be influenced by medical entomology's contribution to enormous reductions in human disease through vector control. The biological differences that lead to the relative ease of detecting and observing insects vs pathogens may also influence how fundamental system properties, such as host species range, are defined (Schikora *et al.*, 2011; Barrett & Heil, 2012). Likewise, disciplinary differences in how traditional and molecular methods are integrated to delineate species can potentially introduce, respectively, over- and underestimates of herbivore and microbial host ranges that confound comparative studies.

At a yet finer disciplinary scale, the differing emphases on population dynamics vs host–parasite interactions might even influence the stature that various subdisciplines achieve within their broader science. As an example, the greater impacts of top-down and higher-scale population drivers on plant–insect interactions often incline agricultural entomologists to value and incorporate work conducted in forests, due to the latter systems' greater temporal stability, higher heterogeneity, larger spatial scale, lesser genetic effects of centuries-long breeding, and lesser cultural manipulation. By contrast, those same ecosystem attributes may be perceived as detracting from the quality of experimental control of the plant–microbe interface by many basic molecular and agricultural plant pathologists, resulting in lower recognition of and investment in forest pathology research and personnel.

The disciplinary distinctions we describe are not necessarily detrimental to greater ecological and evolutionary understanding or management success. Rather, we propose that understanding how underlying biological differences and historical disciplinary trajectories interact can help to foster integration, synthesis and application. Some examples include ecological interactions among multiple community members (Tack & Dicke, 2013), and tactics to offset opposing plant mechanisms of herbivore vs pathogen resistance, when needed (Fantaye *et al.*, 2015). Likewise, recognizing the conceptual advances of each field offers opportunities for cross-pollination of ideas, but understanding their biological underpinnings can help safeguard against overextension and the formulation of misplaced priorities. Understanding how to best interface commonalities and distinctions can be especially useful and timely as many institutions are merging entomology and plant pathology departments into larger plant protection or plant science units.

### Future research directions

Based on the above analysis of contrasts and commonalities between plant–insect and plant–pathogen interactions, and our extension of implications and applications that emerge from these differences, we propose the following future research directions:

(1) Develop integrative ecosystem-scale models of plant defense that incorporate both herbivores and pathogens, but apply

appropriate weighting to: the extent to which active behavioral choice allows focusing on both specific genotypes and particular environmental circumstances; differences in spatiotemporal patterns of abundance and persistence, and their main drivers; the extent to which plant fitness is influenced by exploiter actions extending beyond strict consumption, the numerical abundance of the exploiter, and multiple life history stages of the exploiter; and the extent to which ultimate outcomes of encounters are determined by recognition vs stealth or total allelochemical concentration vs detoxification, and how such differences influence tradeoffs that plants face among competing life history processes.

(2) Place more emphasis on understanding gene-by-environment interactions in both plant–herbivore and plant–pathogen interactions, particularly within the context of the varying degrees of physical, biotic and spatiotemporal heterogeneity that characterize different native and managed ecosystems.

(3) Determine the extent and manner by which insect–microbial vector relationships modify the above models.

(4) Determine the extent to which the above relationships and the relative importance of their various drivers vary along a continuum from highly cultivated to natural ecosystems.

(5) Determine the extent to which the above relationships and the roles of various drivers are influenced by changing climate, and by new host associations arising from range expansions mediated by climate change and human transport.

(6) Evaluate ways in which some historically under-emphasized subdisciplines may have particularly high potential for developing integrative models bridging gaps between traditional plant–insect and plant–pathogen studies.

(7) Evaluate the degree to which these comparisons can be extended to vertebrate herbivores, and overlay our comparisons with additional system features, such as external vs internal development/feeding, diversity of plant tissue affected, longevity of host plant, frequency of disturbance regime, and agronomic vs native ecosystems.

## Conclusions

(1) Despite their commonalities as plant consumers, and the substantial overlap in the defense responses that confront them, insect herbivores and phytopathogens show substantial differences in how they interact with plants. These variations arise from relative differences in the scale at which host selection and directed locomotion are coupled, the degree to which stealth and subterfuge can be employed, the intimacy of their associations, plant tolerance to their activities, the extent to which natural enemies regulate their population dynamics, and life history traits affecting evolution rates, intrinsic growth rates, modalities of reproduction and reliance on symbionts.

(2) Top-level differences between the dynamics of herbivory and disease have important implications for the ecology, evolution, and management of insects and pathogens. Understanding these differences offers opportunities to better manage crop and forest ecosystems, contend with vector systems, and respond to emerging challenges such as invasive species and climate change.

(3) Incorporating key differences between plant–herbivore and plant–pathogen interactions can improve the mechanistic underpinnings of global models and analyses, and provide guidance for future research directions.

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## References

- Addison A, Powell JA, Bentz BJ, Six DL. 2015. Integrating models to investigate critical phenological overlaps in complex ecological interactions: the mountain pine beetle–fungus symbiosis. *Journal of Theoretical Biology* **368**: 55–66.
- Agrios GN. 2005. *Plant pathology*. Burlington, MA, USA: Elsevier Academic Press.
- Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A, Szendrei Z. 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. *Annual Review of Ecology, Evolution, and Systematics* **40**: 1–20.

- Barrett LG, Heil M. 2012. Unifying concepts and mechanisms in the specificity of plant–enemy interactions. *Trends in Plant Science* 17: 282–292.
- Becerra JX. 2015. Macroevolutionary and geographical intensification of chemical defense in plants driven by insect herbivore selection pressure. *Current Opinion in Insect Science* 8: 15–21.
- Becerra JX, Venable DL, Evans PH, Bowers WS. 2001. Interactions between chemical and mechanical defenses in the plant genus *Bursera* and their implications for herbivores. *Integrative and Comparative Biology* 41: 865–876.
- Berec L, Kramer AM, Bernhauerová V, Drake JM. 2018. Density-dependent selection on mate search and evolution of Allee effects. *Journal of Animal Ecology* 87: 24–35.
- Berenbaum M. 1983. Coumarins and caterpillars: a case for coevolution. *Evolution* 37: 163–179.
- Berenbaum MR, Zangerl AR. 2008. Facing the future of plant–insect interaction research: Le retour à la “raison d’être”. *Plant Physiology* 146: 804–811.
- Blood B, Klingeman W, Paschen M, Hadziabdić Đ, Couture J, Ginzler M. 2018. Behavioral responses of *Pityophthorus juglandis* (Coleoptera: Curculionidae: Scolytinae) to volatiles of black walnut and *Geosmithia morbida* (Ascomycota: Hypocreales: Bionectriaceae), the causal agent of Thousand Cankers Disease. *Environmental Entomology* 47: 412–421.
- Bowers JH, Parke JL. 1993. Colonization of pea (*Pisum sativum* L.) taproots by *Pseudomonas fluorescens*: effect of soil temperature and bacterial motility. *Soil Biology and Biochemistry* 25: 1693–1701.
- Bruce TJ, Wadhams LJ, Woodcock CM. 2005. Insect host location: a volatile situation. *Trends in Plant Science* 10: 269–274.
- Buchanan AL, Hermann SL, Lund M, Szendrei Z. 2017. A meta-analysis of non-consumptive predator effects in arthropods: the influence of organismal and environmental characteristics. *Oikos* 126: 1233–1240.
- Busby PE, Lamit LJ, Keith AR, Newcombe G, Gehring CA, Whitham TG, Dirzo R. 2015. Genetics-based interactions among plants, pathogens, and herbivores define arthropod community structure. *Ecology* 96: 1974–1984.
- Carr TG, Roininen H, Price PW. 1998. Oviposition preference and larval performance of *Nematus oligospilus* (Hymenoptera: Tenthredinidae) in relation to host plant vigor. *Environmental Entomology* 27: 615–625.
- Chapman R. 2003. Contact chemoreception in feeding by phytophagous insects. *Annual Review of Entomology* 48: 455–484.
- Chung SH, Rosa C, Scully ED, Peiffer M, Tooker JF, Hoover K, Luthe DS, Felton GW. 2013. Herbivore exploits orally secreted bacteria to suppress plant defenses. *Proceedings of the National Academy of Sciences, USA* 110: 15728–15733.
- Coley PD, Bryant JP, Chapin FS. 1985. Resource availability and plant antiherbivore defense. *Science* 230: 895–899.
- Coll NS, Epple P, Dangel JL. 2011. Programmed cell death in the plant immune system. *Cell Death and Differentiation* 18: 1247–1256.
- Cook SM, Khan ZR, Pickett JA. 2007. The use of push–pull strategies in integrated pest management. *Annual Review of Entomology* 52: 375–400.
- Csörba T, Kontra L, Burgyan J. 2015. Viral silencing suppressors: tools forged to fine-tune host–pathogen coexistence. *Virology* 479: 85–103.
- Daguerrre Y, Siegel K, Edel-Hermann V, Steinberg C. 2015. Fungal proteins and genes associated with biocontrol mechanisms of soil-borne pathogens: a review. *Fungal Biology Reviews* 28: 97–125.
- Dangel JL, Jones JD. 2001. Plant pathogens and integrated defence responses to infection. *Nature* 411: 826–833.
- Delays L, García-Guzmán G, Heil M. 2013. Endophytes versus biotrophic and necrotrophic pathogens—are fungal lifestyles evolutionarily stable traits? *Fungal Diversity* 60: 125–135.
- Denno RF, McClure MS, Ott JR. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual Review of Entomology* 40: 297–331.
- Dodds P, Thrall P. 2009. Recognition events and host–pathogen co-evolution in gene-for-gene resistance to flax rust. *Functional Plant Biology* 36: 395–408.
- Douglas AE. 2015. Multiorganismal insects: diversity and function of resident microorganisms. *Annual Review of Entomology* 60: 17–34.
- Dubey A, Jeon J. 2017. Epigenetic regulation of development and pathogenesis in fungal plant pathogens. *Molecular Plant Pathology* 18: 887–898.
- Dussourd DE. 2017. Behavioral sabotage of plant defenses by insect folivores. *Annual Review of Entomology* 62: 15–34.
- Edmunds GF, Alstad DN. 1978. Coevolution in insect herbivores and conifers. *Science* 199: 941–945.
- Erb M. 2018. Volatiles as inducers and suppressors of plant defense and immunity—origins, specificity, perception and signaling. *Current Opinion in Plant Biology* 44: 117–121.
- Erb M, Meldau S, Howe GA. 2012. Role of phytohormones in insect-specific plant reactions. *Trends in Plant Science* 17: 250–259.
- Erbilgin N, Ma C, Whitehouse C, Shan B, Najjar A, Evenden M. 2014. Chemical similarity between historical and novel host plants promotes range and host expansion of the mountain pine beetle in a naïve host ecosystem. *New Phytologist* 201: 940–950.
- Eyles A, Chorbadian R, Wallis C, Hansen R, Cipollini D, Herms D, Bonello P. 2007. Cross-induction of systemic induced resistance between an insect and a fungal pathogen in Austrian pine over a fertility gradient. *Oecologia* 153: 365–374.
- Fantaye CA, Köpke D, Gershenzon J, Degenhardt J. 2015. Restoring (E)- $\beta$ -caryophyllene production in a non-producing maize line compromises its resistance against the fungus *Colletotrichum graminicola*. *Journal of Chemical Ecology* 41: 213–223.
- Feeny P. 1976. Plant apparency and chemical defense. In: Wallace JW, Mansell RL, eds. *Biochemical interaction between plants and insects*. Boston, MA, USA: Springer, 1–40.
- Felton G, Korth K, Bi J, Wesley S, Huhman D, Mathews M, Murphy J, Lamb C, Dixon R. 1999. Inverse relationship between systemic resistance of plants to microorganisms and to insect herbivory. *Current Biology* 9: 317–320.
- Finkel OM, Castrillo G, Herrera Paredes S, Salas González I, Dangel JL. 2017. Understanding and exploiting plant beneficial microbes. *Current Opinion in Plant Biology* 38: 155–163.
- Franceschi VR, Krokene P, Christiansen E, Krokling T. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist* 167: 353–375.
- Ghelardini L, Pepori AL, Luchi N, Capretti P, Santini A. 2016. Drivers of emerging fungal diseases of forest trees. *Forest Ecology and Management* 381: 235–246.
- Giron D, Huguet E, Stone GN, Body M. 2016. Insect-induced effects on plants and possible effectors used by galling and leaf-mining insects to manipulate their host-plant. *Journal of Insect Physiology* 84: 70–89.
- Glazebrook J, Zook M, Mert F, Kagan I, Rogers EE, Crute IR, Holub EB, Hammerschmidt R, Ausubel FM. 1997. Phytoalexin-deficient mutants of *Arabidopsis* reveal that *PAD4* encodes a regulatory factor and that four *PAD* genes contribute to downy mildew resistance. *Genetics* 146: 381–392.
- Göhre V, Robatzek S. 2008. Breaking the barriers: microbial effector molecules subvert plant immunity. *Annual Review of Phytopathology* 46: 189–215.
- Gonzalez AM, Marcel TC, Niks RE. 2012. Evidence for a minor gene-for-minor gene interaction explaining nonhypersensitive polygenic partial disease resistance. *Phytopathology* 102: 1086–1093.
- Hajek AE, Leger RJS. 1994. Interactions between fungal pathogens and insect hosts. *Annual Review of Entomology* 39: 293–322.
- Hammerbacher A, Schmidt A, Wadke N, Wright LP, Schneider B, Bohlmann J, Brand WA, Fenning TM, Gershenzon J, Paetz C. 2013. A common fungal associate of the spruce bark beetle metabolizes the stilbene defenses of Norway spruce. *Plant Physiology* 162: 1324–1336.
- Handelsman J, Stabb EV. 1996. Biocontrol of soilborne plant pathogens. *Plant Cell* 8: 1855–1869.
- Heckel DG. 2014. Insect detoxification and sequestration strategies. *Annual Plant Reviews* 47: 77–114.
- Heimpel GE, Mills NJ. 2017. *Biological control: ecology and applications*. Cambridge, UK: Cambridge University Press.
- Herms DA, Mattson WJ. 1992. The dilemma of plants: to grow or defend. *Quarterly Review of Biology* 67: 283–335.
- Hill CB, Li Y, Hartman GL. 2006. A single dominant gene for resistance to the soybean aphid in the soybean cultivar Dowling. *Crop Science* 46: 1601–1605.
- Hoover K, Wood DL, Storer AJ, Fox JW, Bros WE. 1996. Transmission of the pitch canker fungus, *Fusarium subglutinans* f. sp. *pini*, to Monterey Pine, *Pinus radiata*, by cone- and twig-infesting beetles. *Canadian Entomologist* 128: 981–994.
- Ingwell LL, Eigenbrode SD, Bosque-Perez NA. 2012. Plant viruses alter insect behavior to enhance their spread. *Scientific Reports* 2: 578.

- Janz N, Bergström A, Sjögren A. 2005. The role of nectar sources for oviposition decisions of the common blue butterfly *Polyommatus icarus*. *Oikos* 109: 535–538.
- Jones JD, Dangl JL. 2006. The plant immune system. *Nature* 444: 323–329.
- Kaloshian I. 2004. Gene-for-gene disease resistance: bridging insect pest and pathogen defense. *Journal of Chemical Ecology* 30: 2419–2438.
- Karban R. 2015. *Plant sensing and communication*. Chicago, IL, USA: University of Chicago Press.
- Kearsley MJC, Whitham TG. 1989. Developmental changes in resistance to herbivory: implications for individuals and populations. *Ecology* 70: 422–434.
- Kim J, Quaghebeur H, Felton GW. 2011. Reiterative and interruptive signaling in induced plant resistance to chewing insects. *Phytochemistry* 72: 1624–1634.
- Knolhoff LM, Heckel DG. 2014. Behavioral assays for studies of host plant choice and adaptation in herbivorous insects. *Annual Review of Entomology* 59: 263–278.
- Kolb TE, Fettig CJ, Ayres MP, Bentz BJ, Hicke JA, Mathiasen R, Stewart JE, Weed AS. 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. *Forest Ecology and Management* 380: 321–334.
- Krasileva KV, Zheng C, Leonelli L, Goritschnig S, Dahlbeck D, Staskawicz BJ. 2011. Global analysis of *Arabidopsis*/Downy Mildew interactions reveals prevalence of incomplete resistance and rapid evolution of pathogen recognition. *PLoS ONE* 6: e28765.
- Krause SC, Raffa KF. 1996. Defoliation tolerance affects the spatial and temporal distributions of larch sawfly and natural enemy populations. *Ecological Entomology* 21: 259–269.
- Kunkel BN, Brooks DM. 2002. Cross talk between signaling pathways in pathogen defense. *Current Opinion in Plant Biology* 5: 325–331.
- Lamit LJ, Busby PE, Lau MK, Compson ZG, Wojtowicz T, Keith AR, Zinkgraf MS, Schweitzer JA, Shuster SM, Gehring CA *et al.* 2015. Tree genotype mediates covariance among communities from microbes to lichens and arthropods. *Journal of Ecology* 103: 840–850.
- Latta RG, Linhart YB, Snyder MA, Lundquist L. 2003. Patterns of variation and correlation in the monoterpene composition of xylem oleoresin within populations of ponderosa pine. *Biochemical Systematics and Ecology* 31: 451–465.
- Leimu R, Koricheva J. 2006. A meta-analysis of tradeoffs between plant tolerance and resistance to herbivores: combining the evidence from ecological and agricultural studies. *Oikos* 112: 1–9.
- Lombardi N, Vitale S, Turrà D, Reverberi M, Fanelli C, Vinale F, Marra R, Ruocco M, Pascale A, d'Errico G *et al.* 2018. Root exudates of stressed plants stimulate and attract *Trichoderma* soil fungi. *Molecular Plant–Microbe Interactions* 31: 982–994.
- MacQuarrie CJK, Lyons DB, Lukas Seehausen M, Smith SM. 2016. A history of biological control in Canadian forests, 1882–2014. *Canadian Entomologist* 148: S239–S269.
- Matilla MA, Krell T. 2017. The effect of bacterial chemotaxis on host infection and pathogenicity. *FEMS Microbiology Reviews* 42: fux052.
- Mauck KE, Chesnais Q, Shapiro LR. 2018. Evolutionary determinants of host and vector manipulation by plant viruses. In: Malmstrom CM, ed. *Advances in virus research*. New York, NY, USA: Academic Press, 189–250.
- Mauck KE, De Moraes CM, Mescher MC. 2016. Effects of pathogens on sensory-mediated interactions between plants and insect vectors. *Current Opinion in Plant Biology* 32: 53–61.
- Mauricio R, Rausher MD. 1997. Experimental manipulation of putative selective agents provides evidence for the role of natural enemies in the evolution of plant defense. *Evolution* 51: 1435–1444.
- McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG *et al.* 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178: 719–739.
- McManus KA, ed. 2018. *29th USDA Interagency Research Forum on Invasive Species*. FHTET-2016-09: US Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team.
- Milgroom MG, Cortesi P. 2004. Biological control of chestnut blight with hypovirulence: a critical analysis. *Annual Review of Phytopathology* 42: 311–338.
- Páez DJ, Dukic V, Dushoff J, Fleming-Davies A, Dwyer G. 2017. Eco-evolutionary theory and insect outbreaks. *American Naturalist* 189: 616–629.
- Panouillé A, Anglade P, Boyat A, Gouesnard B, Vible J-C, Dupin M. 1998. Assessment of 10 years of maize pedigree breeding for European corn borer tolerance and high-yielding combining ability. *Agronomie* 18: 299–308.
- Parratt SR, Laine A-L. 2018. Pathogen dynamics under both bottom-up host resistance and top-down hyperparasite attack. *Journal of Applied Ecology* 55: 2976–2985.
- Partida-Martinez LP, Hertweck C. 2005. Pathogenic fungus harbours endosymbiotic bacteria for toxin production. *Nature* 437: 884.
- Peterson RKD, Varella AC, Higley LG. 2017. Tolerance: the forgotten child of plant resistance. *PeerJ* 5: e3934.
- Pimentel D, Zuniga R, Monison D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273–288.
- Poveda K, Gómez Jiménez MI, Halitschke R, Kessler A. 2012. Overcompensating plants: their expression of resistance traits and effects on herbivore preference and performance. *Entomologia Experimentalis et Applicata* 143: 245–253.
- Powell EN, Townsend PA, Raffa KF. 2012. Wildfire provides refuge from local extinction but is an unlikely driver of outbreaks by mountain pine beetle. *Ecological Monographs* 82: 69–84.
- Raffa KF, Andersson MN, Schlyter F. 2016. Host selection by bark beetles: playing the odds in a high-stakes game. In: Blomquist GJ, Tittiger C, eds. *Advances in insect physiology*. New York, NY, USA: Academic Press, 1–74.
- Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Kolb TE. 2015. Responses of tree-killing bark beetles to a changing climate. In: Bjorkman C, Niemela P, eds. *Climate change and insect pests*. Preston, UK: CAB International, 173–201.
- Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience* 58: 501–517.
- Roininen H, Price PW, Bryant JP. 1997. Response of galling insects to natural browsing by mammals in Alaska. *Oikos* 80: 481–486.
- Rosenberger DW, Venette RC, Aukema BH. 2018. Development of an aggressive bark beetle on novel hosts: implications for outbreaks in an invaded range. *Journal of Applied Ecology* 55: 1526–1537.
- Rosenheim JA. 1998. Higher-order predators and the regulation of insect herbivore populations. *Annual Review of Entomology* 43: 421–447.
- Rosenthal JP, Kotanen PM. 1994. Terrestrial plant tolerance to herbivory. *Trends in Ecology & Evolution* 9: 145–148.
- Sacristan S, Garcia-Arenal F. 2008. The evolution of virulence and pathogenicity in plant pathogen populations. *Molecular Plant Pathology* 9: 369–384.
- Schikora A, Virlogeux-Payant I, Bueso E, Garcia AV, Nilau T, Charrier A, Pelletier S, Menanteau P, Baccarini M, Velge P *et al.* 2011. Conservation of *Salmonella* infection mechanisms in plants and animals. *PLoS ONE* 6: e24112.
- Schoonhoven LM, Van Loon B, van Loon JJ, Dicke M. 2005. *Insect–plant biology*. New York, NY, USA: Oxford University Press.
- Severns PM, Sackett KE, Mundt CC. 2015. Outbreak propagule pressure influences the landscape spread of a wind-dispersed, epidemic-causing, plant pathogen. *Landscape Ecology* 30: 2111–2119.
- Shikano I, McCarthy E, Hayes-Plazolles N, Slavicek JM, Hoover K. 2018. Jasmonic acid-induced plant defenses delay caterpillar developmental resistance to a baculovirus: slow-growth, high-mortality hypothesis in plant–insect–pathogen interactions. *Journal of Invertebrate Pathology* 158: 16–23.
- Showalter DN, Raffa KF, Sniezko RA, Herms DA, Liebhold AM, Smith JA, Bonello P. 2018. Strategic development of tree resistance against forest pathogen and insect invasions in defense-free space. *Frontiers in Ecology and the Environment* 6: 124.
- Silva JPGF, Baldin ELL, Canassa VF, Souza ES, Lourenção AL. 2014. Assessing antixenosis of soybean entries against *Piezodorus guildinii* (Hemiptera: Pentatomidae). *Arthropod–Plant Interactions* 8: 349–359.
- Stamp NE, Bowers MD. 2000. Foraging behaviour of caterpillars given a choice of plant genotypes in the presence of insect predators. *Ecological Entomology* 25: 486–492.
- Stappuhn A, Baldwin IT. 2007. Resistance management in a native plant: nicotine prevents herbivores from compensating for plant protease inhibitors. *Ecology Letters* 10: 499–511.
- Strauss SY, Agrawal AA. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution* 14: 179–185.
- Stringlis IA, Zhang H, Pieterse CM, Bolton MD, de Jonge R. 2018. Microbial small molecules—weapons of plant subversion. *Natural Product Reports* 35: 410–433.

- Tabashnik BE, Brévault T, Carrière Y. 2013. Insect resistance to Bt crops: lessons from the first billion acres. *Nature Biotechnology* 31: 510.
- Tack AJM, Dicke M. 2013. Plant pathogens structure arthropod communities across multiple spatial and temporal scales. *Functional Ecology* 27: 633–645.
- Thaler JS, Agrawal AA, Halitschke R. 2010. Salicylate-mediated interactions between pathogens and herbivores. *Ecology* 91: 1075–1082.
- Thompson JN. 1994. *The coevolutionary process*. Chicago, IL, USA: University of Chicago Press.
- Toruno TY, Stergiopoulos I, Coaker G. 2016. Plant–pathogen effectors: cellular probes interfering with plant defenses in spatial and temporal manners. In: Leach JE, Lindow S, eds. *Annual Review of Phytopathology*, Vol. 54, 419–441.
- Toth IK, Birch PR. 2005. Rotting softly and stealthily. *Current Opinion in Plant Biology* 8: 424–429.
- Turlings TC, Erb M. 2018. Tritrophic interactions mediated by herbivore-induced plant volatiles: mechanisms, ecological relevance, and application potential. *Annual Review of Entomology* 63: 433–452.
- Turrà D, Di Pietro A. 2015. Chemotropic sensing in fungus–plant interactions. *Current Opinion in Plant Biology* 26: 135–140.
- Uesugi A, Morrell K, Poelman EH, Raaijmakers CE, Kessler A. 2016. Modification of plant-induced responses by an insect ecosystem engineer influences the colonization behaviour of subsequent shelter-users. *Journal of Ecology* 104: 1096–1105.
- Van Driesche RG, Carruthers RI, Center T, Hoddle MS, Hough-Goldstein J, Morin L, Smith L, Wagner DL, Blossey B, Brancatini V *et al.* 2010. Classical biological control for the protection of natural ecosystems. *Biological Control* 54: S2–S33.
- Vasanthakumar A, Handelsman J, Schloss PD, Bauer LS, Raffa KF. 2008. Gut microbiota of an invasive subcortical beetle, *Agrilus planipennis* Fairmaire, across various life stages. *Environmental Entomology* 37: 1344–1353, 1310.
- Vega FE. 2018. The use of fungal entomopathogens as endophytes in biological control: a review. *Mycologia* 110: 4–30.
- Vidal MC, Murphy SM. 2018. Bottom-up vs. top-down effects on terrestrial insect herbivores: a meta-analysis. *Ecology Letters* 21: 138–150.
- Webster B, Cardé RT. 2017. Use of habitat odour by host-seeking insects. *Biological Reviews* 92: 1241–1249.
- Yun W, Hall I, Evans L. 1997. Ectomycorrhizal fungi with edible fruiting bodies. I. *Tricholoma matsutake* and related fungi. *Economic Botany* 51: 311–327.
- Zhang S, Jiang J, Luan Q. 2016. Genetic and correlation analysis of oleoresin chemical components in slash pine. *Genetics and Molecular Research* 15.
- Zipfel C. 2014. Plant pattern-recognition receptors. *Trends in Immunology* 35: 345–351.

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