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The influence of genetic variation on pre-oviposition processes for host-parasitoid co-evolution

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Abstract

1. Despite the importance of parasitoid wasps as biological control agents and the vast literature available on different aspects of their natural history and ecology, it is only recently that an interest in integrating genetics into aphid-parasitoid studies has emerged.
2. Some studies have been completed on the effect of genetic variation on aphid parasitism outcomes, especially after the description of aphid physiological resistance to parasitoids and its role in their co-evolution. The interaction between aphids and parasitoids goes beyond the physiological conflict between the parasitoid egg and the aphid internal defences. A series of aphid and parasitoid attributes, that can be influenced by biotic and abiotic factors, precedes that last step in the oviposition process.
3. The understanding of how genetic variation can play a crucial role in influencing the pre-egg-laying stages of the aphid-parasitoid interaction remains relatively unexplored.
4. Here, we review currently available information on this topic. We contextualise the aphid-parasitoid co-evolution process exemplified by the post-oviposition approach. Knowledge gaps are also discussed and the significance of fulfilling them is addressed.
5. An ecology-evolutionary perspective on aphid-parasitoid research is advocated, by incorporating genetic variation into the study of aphid-parasitoid co-evolution. This will increase the understanding of the adaptation and evolution of both organism's characteristics in response to each other and abiotic pressures, and also the implications for pest management.

KEYWORDS

Aphid, Co-evolution, Genetic variation, Interaction, Parasitism, Resistance

INTRODUCTION

Interspecific interactions are among the most important processes that determine the structure and dynamics of communities in the

animal kingdom (Antonovics, 1992; Johnson & Stinchcombe, 2007). Parasitoidism is an interspecific interaction mostly reported in insects that combines aspects of both predation and parasitism (Neuhauser et al., 2003). Trophic interactions can be affected by many abiotic and

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biotic factors, including reciprocal selective pressures between counterparts (Whitham et al., 2003). The close and dependent host-parasitoid interaction usually results in physiological and gene expression changes in both organisms, which means that genetic diversity within the interacting species plays an important role in determining the outcome. In this review, we argue that pre-egg-laying processes in aphid-parasitoid interactions are an important yet underappreciated part of the interplay. Specifically, we explore how these processes are influenced by genetic variation in the interacting organisms and therefore affect the outcome of parasitism and aphid-parasitoid co-evolution.

The use of parasitoids to control herbivore pests is a fundamental pillar of biological control (Heimpel & Mills, 2017). Many ecological, behavioural and physiological aspects of herbivore-parasitoid interactions have been studied in detail (Haverkamp & Smid, 2020; Henry, 2008; Rezaei et al., 2019; Wellings, 1993); however, a synthesis of the role of host and parasitoid genetic variation in shaping these interactions has been relatively unexplored. In addition, as it has been recently highlighted by Sentis et al. (2022), the study of biological control, including interactions between insect host and parasitoid, needs to integrate an evolutionary perspective as a basic feature of research (Sentis et al., 2022). Aphids and their hymenopteran parasitoids have a dynamic relationship shaped by strong selective pressures from both sides. These pressures include behavioural and physiological parasitoid defence mechanisms in aphids. These physical deterrence traits, and other characteristics that affect aphid abundance or availability, influence life history processes and population dynamics of their natural enemies. Rapid evolutionary responses to each other in both aphids and aphid parasitoids have been identified in recent years (Käch et al., 2018), indicating that genetic variation should not be underestimated as a driver of aphid-parasitoid interactions with important implications for aphid biological control efficiency.

The aphid-parasitoid interaction is a complex and fascinating process. Studies of the importance of genetic variation in aphids and their parasitoids often focus on the last step of the aphid-parasitoid interaction, otherwise known as host suitability. Host suitability refers to the fact that parasitoid oviposition is no assurance for parasitoid development, because intrinsic and extrinsic characteristics of both aphids and parasitoids can come into play to determine whether egg development occurs. However, the importance of understanding that the resistance of hosts to pathogens and parasites (including parasitoids) is a progression of multiple steps (i.e., stepwise infection process) that can all impact the evolutionary ecology of any antagonistic interaction has been highlighted since at least 7 years ago (Hall et al., 2017). In this context, all steps regulating the infection process, regardless of their mechanism (i.e., physiological, mechanical, etc.), are key as each step is linked to genetic and environmental variation (Hill, 2012). That means that a single step (i.e., physiological resistance) is not necessarily representative of the total capacity of a host to mitigate antagonist attack, and that all steps could impact the host–antagonist co-evolution (Hall et al., 2017). Translating this into the aphid-parasitoid interaction will mean that the different stages of the interaction, including pre-oviposition steps, should be integrated

into resistance studies to truly understand the factors affecting the outcome. Nevertheless, the crucial effect of genetic variation on pre-oviposition processes (i.e., host acceptability) has scarcely been mentioned in the literature. Here, we outline the important steps of host-parasitoid interactions linked to their co-evolution for aphids and their hymenopteran parasitoids (Figure 1) as a basis for considering how genetic variation in underpinning traits of each organism might affect interaction outcomes.

APHID-PARASITOID CO-EVOLUTION: A POST-OVIPOSITION ILLUSTRATION

Successful aphid parasitoid development is always fatal to the aphid host, and a successful defence by the aphid always results in a negative outcome for the individual parasitoid offspring. As aphid-parasitoid interactions strongly influence survival and development of both counterparts and, therefore, population persistence, the outcome of the interaction affects the evolutionary success of the species (Sentis et al., 2022). In the host-parasitoid interaction, each antagonist must adapt to the other species and so both are subject to selection pressures arising from ecological processes and evolutionary changes in one another. This can trigger a co-evolutionary process whereby selection pressures imposed by parasitoids generate host adaptations that reduce mortality, which in turn lead to parasitoid counter-adaptations to overcome host defences (Papkou et al., 2021). The existence and maintenance of genetic diversity in these interacting populations will lead to aphid-parasitoid coevolution by promoting characteristics that favour continuous and rapid adaptation to the selection pressures (Ebert & Fields, 2020; Papkou et al., 2016). This dynamic antagonistic co-evolution (i.e., continual reciprocal selection for adaptation and counter-adaptation between two interacting species) of hosts and parasitoids will happen by balancing selection (i.e., genotype frequencies fluctuate over time), which enables high levels of polymorphism to persist for both aphid resistance and parasitoid virulence strategies (Wade, 2007). However, this system consists not just of aphids and parasitoids, but also aphid bacterial endosymbionts as key players (Béréños et al., 2011; Smith et al., 2021).

Aphid-parasitoid interactions can show highly dynamic co-evolution through negative frequency dependence (i.e., Red Queen dynamics) (Vorburger & Perlman, 2018). This type of co-evolutionary cycling maintains genetic diversity because rare genotypes are favoured while common genotypes are not, due to reciprocal continuous selection (Ebert & Fields, 2020). Three determinant characteristics are thought to underpin this co-evolutionary process: (a) genetic diversity available for selection in all important fitness traits, (b) genetic specificity and (c) inherent costs (Vorburger, 2014). Most of the research to date has focused on the role of genetic variation in the aphid and parasitoid for physiological processes occurring after the parasitoid has successfully oviposited egg(s) in the host (Lommen et al., 2017). The first part of this review summarises current knowledge of the post-oviposition stage and the three determinant characteristics of the aphid-parasitoid interaction; this forms the context for

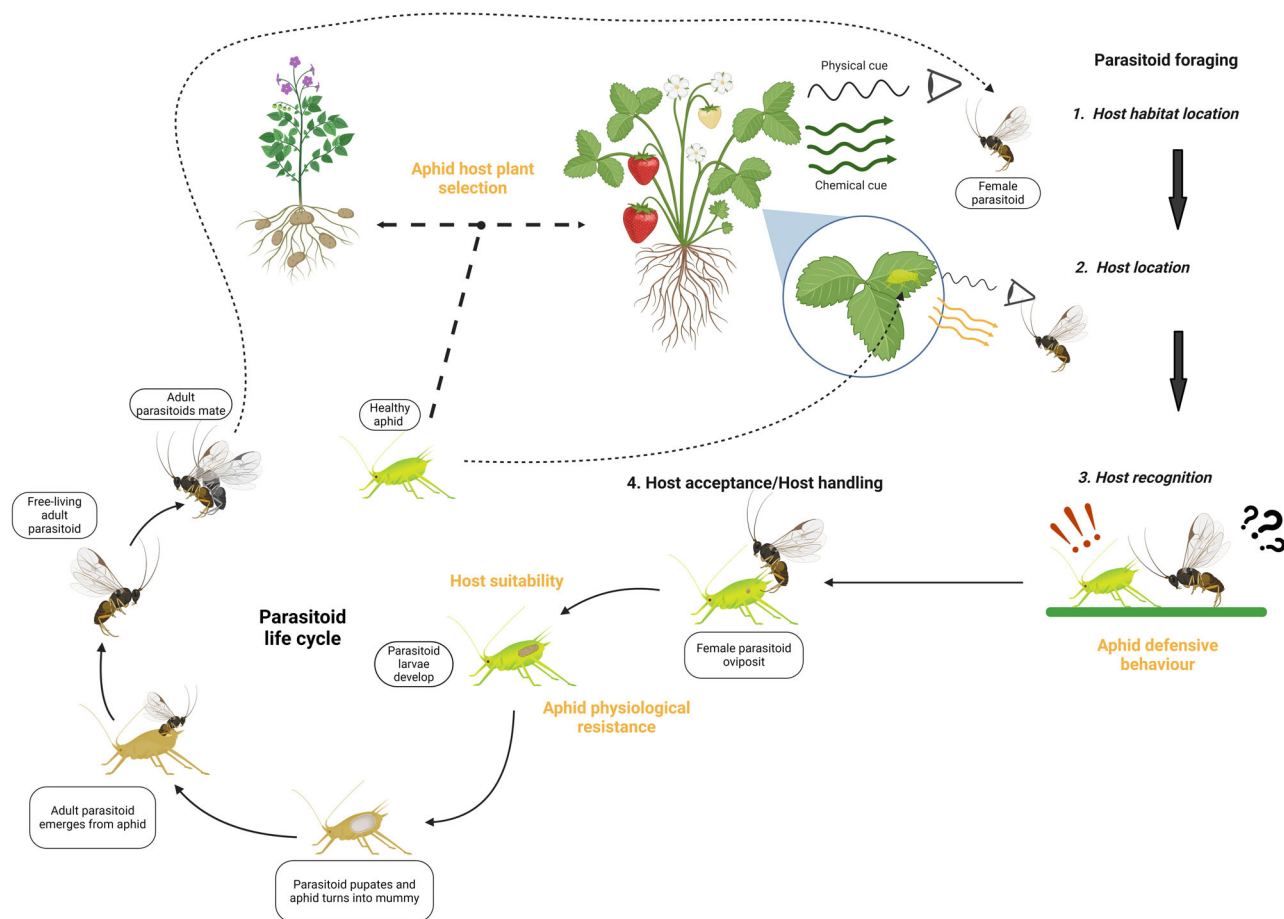


FIGURE 1 Graphical summary of the aphid-parasitoid interaction. The life cycle of a successful parasitoid of aphids is contextualised here in terms of the steps influencing this outcome, including pre-egg laying parasitoid behaviours (numbered 1–4 in black), aphid ecology and behaviour (in orange), and aphid physiological resistance (in orange). Created with [BioRender.com](https://www.biorender.com).

the second part of the review, which examines pre-oviposition steps that underpin the co-evolutionary dynamics.

Genetic variation in aphid and parasitoid characteristics

For a co-evolutionary process to happen it is necessary that populations of interacting counterparts exhibit genetic variation in relevant fitness traits (Kraaijeveld & Godfray, 2009). Many studies have reported differential aphid susceptibility to parasitism, differential virulence of parasitoids, and the role of genetic diversity in determining the outcome of parasitism (e.g., Ferrari et al., 2001; Henter, 1995).

The aphid holobiont

The insect immune response to endoparasitoids is usually cellular encapsulation, in which melanin accumulates around the foreign object to prevent its development (Schmitz et al., 2012). Nevertheless, the aphid immune response has only rarely been documented (Poirié &

Coustau, 2011; Sun et al., 2024). Some evidence has been found for parasitoid egg encapsulation in aphids (Le Ralec et al., 2010). The formation of melanotic capsules around proxies for parasitoid eggs, in addition to upregulated genes linked to immune cell aggregation in aphids responding to parasitoidism support this idea (McLean & Parker, 2020). To our knowledge, it is still not fully understood how the aphid immune system responds to parasitoids, and therefore, there are no reports of how widespread the encapsulation response is, nor whether aphids show genetic variation in this trait.

It is accepted that variability in aphid susceptibility to parasitoid egg development exists, although the specific internal mechanism has yet to be fully understood. Nevertheless, aphid genotypes have been shown to vary in their susceptibility to parasitoids, in multiple aphid-parasitoid systems (Clarke et al., 2017; Ferrari et al., 2001; Hufbauer & Via, 1999; Von Burg et al., 2008; Vorburger et al., 2009). It is also recognised that while aphid genetic background conferred distinct responses to parasitism, the infection of some aphid species with secondary (facultative) bacterial endosymbionts was also part of the resistance mechanism (Oliver et al., 2003) (Figure 2).

A reduction in parasitism frequencies in aphid clones infected by certain endosymbiotic bacteria compared with non-infected clones has

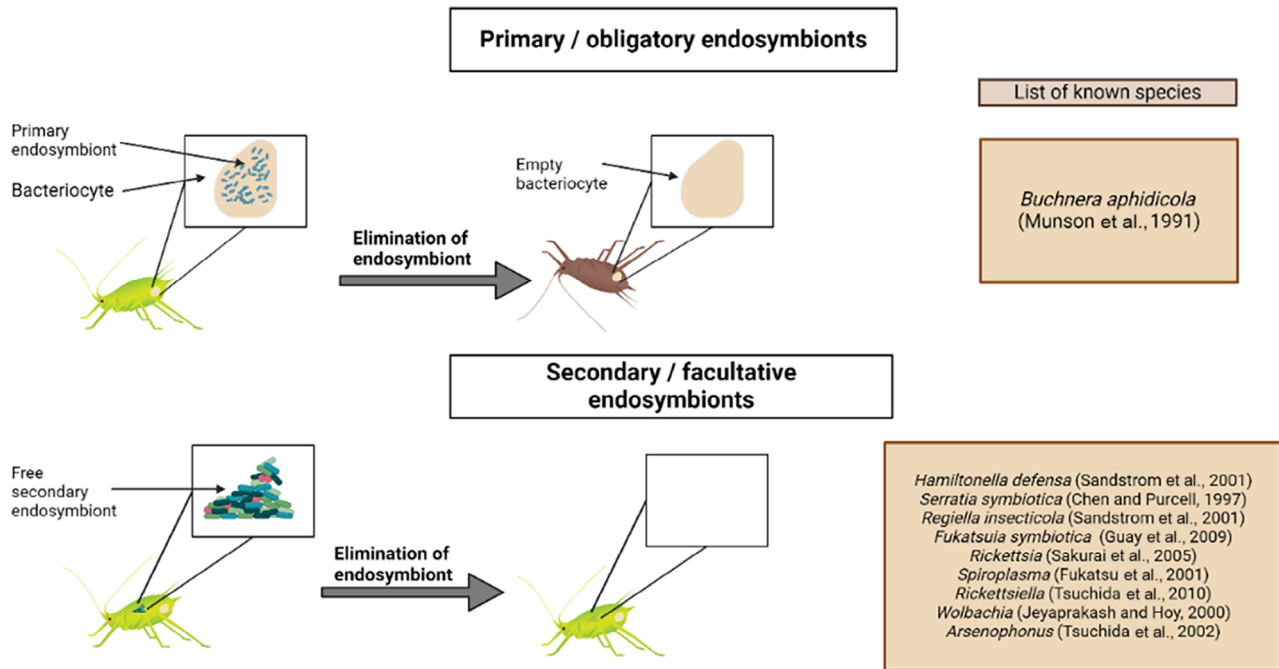


FIGURE 2 Aphid endosymbionts characterised to date. Including location within the aphid, effects of endosymbiont elimination and species described to date. Created with [BioRender.com](https://www.biorender.com).

been described for multiple aphid-parasitoid systems. Secondary endosymbionts linked to this characteristic include *Hamiltonella defensa* (PABS or T-type) (Bensadia et al., 2006; Oliver et al., 2003), *Serratia symbiotica* (PASS or R-type) and *Fukatsua symbiotica* (PAXS or X-type) (Guo et al., 2017). These results suggest that aphid parasitoids must overcome two types of anti-parasitism defences: those innately encoded by the aphid and those conferred by secondary endosymbionts.

Genetic variation in secondary endosymbionts also plays an important role in the variability of aphid parasitoid susceptibility. It has been shown that different isolates of the same bacteria can confer varying levels of aphid susceptibility to parasitoids (Oliver et al., 2005). In addition, in *H. defensa*, the presence and genetic type of APSE bacteriophage (also called haplotype) are essential for the bacteria to confer parasitoid resistance (Chevignon et al., 2018; Oliver & Higashi, 2019). This association of genetic variation in secondary endosymbionts (including APSEs in *H. defensa*) with variation in aphid susceptibility to parasitoids has been described, to date, in two aphid-parasitoid systems (Hansen et al., 2012; Rouchet & Vorburger, 2014; Vorburger et al., 2010). Nevertheless, information about genetic diversity within secondary endosymbionts other than *H. defensa* and *S. symbiotica* (Figure 2) in relation to their protective role are still not available, therefore their potential to differentially influence parasitism of their host remains to be determined.

Parasitoid potential for counteradaptation

The ability of a parasitoid to overcome host defences, including host physiological resistance, is termed virulence (Hufbauer, 2001).

Nonetheless, studies on virulence variation focused on Aphidiinae parasitoids are few.

Parasitoid virulence is linked to the physiological and molecular strategies used to overcome host defences (Drezen et al., 2017). Genetic diversity in virulence traits has been considered in only a few species of aphid parasitoid despite the potential impact on biological control and integrated pest management programmes (Hufbauer, 2001, 2002). For example, high levels of genetic diversity for virulence have been demonstrated for *Lysiphlebus fabarum* (Marshall) (Hafer-Hahmann & Vorburger, 2020; Käch et al., 2018; Sandrock et al., 2010; Vorburger & Rouchet, 2016). In general, virulence factors, such as secreted proteins or viral particles (polydnaviruses or virus-like-particles) produced by the ovaries or venom glands of a female parasitoid, that alter the ability of a host to respond to a parasitoid are indispensable for the counteradaptation processes of the parasitoid itself (Poirié et al., 2009). Intraspecific variability in virulence factors has been described in different parasitoid species (Dennis et al., 2017; Dennis et al., 2019). The evolution of variability in the composition and quantities of venom proteins in parasitoid wasps has been associated with the evolution of resistance mechanisms in their aphid hosts (Cavigliasso et al., 2019; Colinet, Deleury, et al., 2013; Colinet, Mathé-Hubert, et al., 2013; Mathé-Hubert et al., 2019; Ulrich et al., 2021).

Parasitoid counteradaptation to aphid resistance is difficult to measure directly in the field, but a series of laboratory-based experimental evolution assays has recently highlighted the adaptive potential of parasitoids (Ulrich et al., 2021). For example, individuals of *A. ervi* exposed to *A. pisum* aphids infected with a highly protective strain of *H. defensa* increased in virulence over 10 generations (Dion,

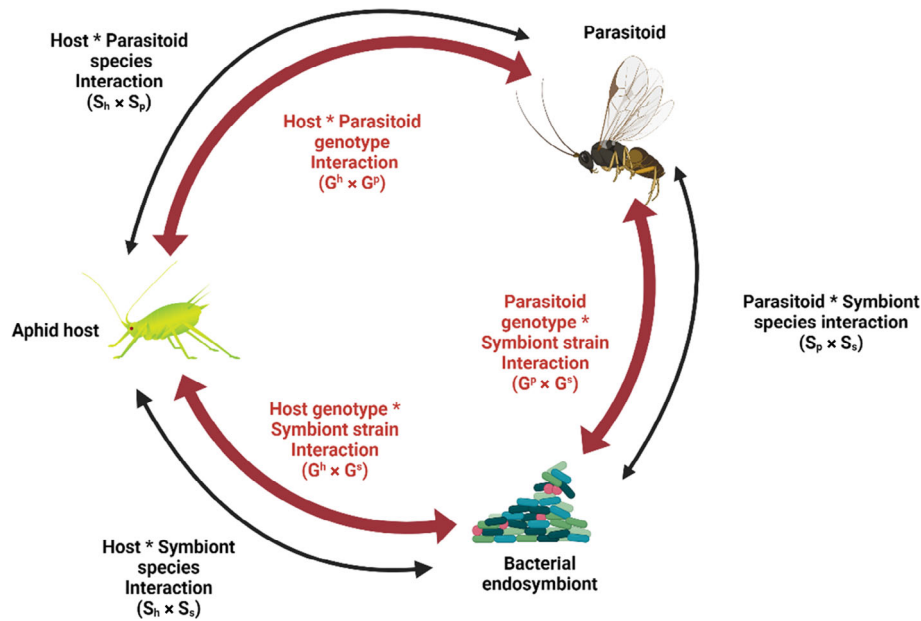


FIGURE 3 Illustrations of the 3-way genetic interactions between aphid hosts, aphid facultative symbionts and parasitoid wasps at two different levels: species (black arrow) and sub-species (red arrow). G^h , Host genotype; G^p , parasitoid genotype; G^s , symbiont genotype; S_h , Host species; S_p , Parasitoid species; S_s , symbiont species. Created with BioRender.com.

Zélé, et al., 2011). Similarly, when *L. fabarum* was exposed to *A. fabae* infected with *H. defensa*, enrichment of transcripts for venom and virus-like-particles encoding genes was recorded (Dennis et al., 2017; Rouchet & Vorburger, 2014).

Genetic specificity in the aphid-parasitoid interaction

Genetic specificity can be determined by traits expressed by interacting species or by genotypic variants within each species. Several examples of parasitoid species-specific resistance by aphids, mediated by facultative symbionts, have been described to date, as for example, the case of the cowpea aphid (*Aphis craccivora* Koch) in which *H. defensa* confer almost complete resistance to parasitism by *Binodoxys communis* (Gahan) and *Binodoxys koreanus* Starý, but had no effect on parasitism levels by *Lysiphlebus orientalis* Starý & Rakhshani and *A. colemani* (Asplen et al., 2014). In addition, the protection provided by a strain of secondary endosymbiont can depend on aphid species, as for example a strain of *H. defensa* conferring protection in *A. pisum* against *A. ervi* but not in the English grain aphid (*Sitobion avenae* Fabricius) (Łukasik et al., 2013). Genotype-by-genotype (GxG) interactions or genetic specificity (Gerardo & Parker, 2014; Parker et al., 2017) describes how genetic diversity within populations of interacting species can influence the outcome of their interactions (Tétard-Jones et al., 2007) (Figure 3).

Strong GxG interactions between parasitoids and aphid endosymbionts, and their role in inducing frequency-dependent selection, have previously been described (Cayetano et al., 2015; Gimmi & Vorburger, 2021; McLean & Godfray, 2015; Rouchet & Vorburger, 2014; Schmid et al., 2012). A lack of significant GxG

interactions between aphid genotype and parasitoid genotype in some systems (Cayetano et al., 2015; Martinez et al., 2018; Sandrock et al., 2010) suggests that GxG interactions between aphids and parasitoids are less common than GxG interactions between aphid endosymbionts and parasitoids. This indicates that endosymbionts might be driving the interaction between the aphid holobiont and their natural enemies, in accordance with the finding that the protection conferred by endosymbionts is stronger than that encoded in the aphid genome (Vorburger et al., 2009). In addition, aphid genotype-endosymbiont strain interactions can also affect the fitness of parasitism-resistant aphids following a parasitoid attack, as demonstrated by variable effects of *H. defensa* strains on *A. pisum* genotypic variation in longevity and reproduction when it survives attack by *A. ervi* (Martinez et al., 2018).

Inherent costs

An important aspect of aphid-endosymbiont interactions is that hosting endosymbionts usually comes with a fitness cost to the aphid host, including physiological (i.e., reduced life span and fecundity) (Vorburger & Gouskov, 2011) and ecological (i.e., increasing susceptibility to predators, restricted plant-host range) costs (Dion, Polin, et al., 2011; Zytynska et al., 2021). These costs might explain why these symbionts have variable frequencies in their host populations (i.e., do not go into fixation). This can be key to aphid-parasitoid balancing selection (Vorburger, 2021): defensive symbionts have been shown to be even more costly when parasitoid pressure is reduced, to the extent of being the cause of colony decay (Sanders et al., 2016; Vorburger, 2014). Genetic variation between endosymbiont strains

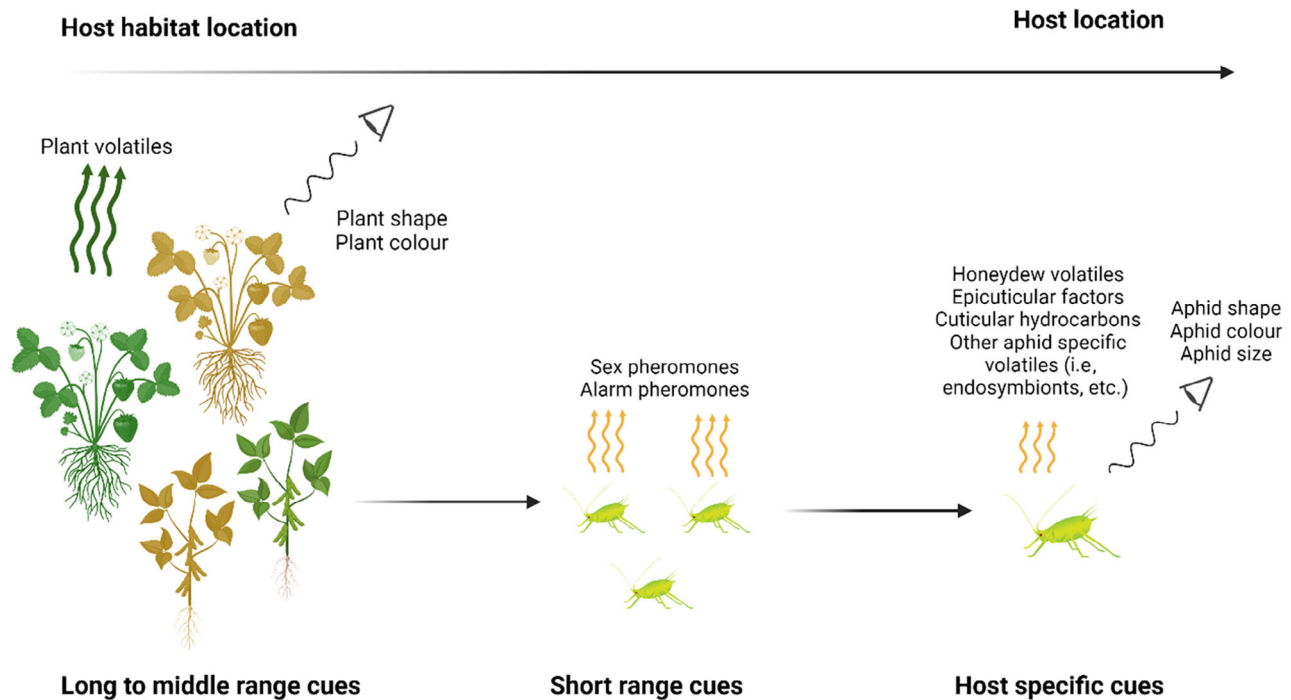


FIGURE 4 Main cues used by female aphid parasitoids when searching and assessing hosts. Chemical (in orange) and visual (in green) cues used by parasitoids to locate hosts at different levels of host searching. Created with [BioRender.com](https://www.biorender.com).

leads to differential effects on their host phenotype and fitness. Fitness costs associated with intrinsic resistance to parasitoids in aphids have been less explored, but less susceptible lines of *A. pisum* not linked with endosymbionts had a lower fecundity than their more susceptible counterparts (Gwynn et al., 2005). These costs can be experienced innately (e.g. Leybourne, Valentine, et al., 2020) or induced following attack (e.g. Vorburget et al., 2008), but information is scarce. On the other hand, new adaptative developments in parasitoid wasp virulence to counter aphid resistance can have mixed effects on parasitoid fitness. For example, increased virulence can improve progeny survival, but also lead to reduced parasitoid size in *L. fabarum*, which has previously been linked to reduced female fecundity, emergence and development (Dion, Polin, et al., 2011; Rouchet & Vorburget, 2014; Schmid et al., 2012).

WHAT WE KNOW ABOUT THE ROLE OF INTRA-SPECIFIC VARIATION IN THE PRE-EGG LAYING STAGE OF APHID-PARASITOID INTERACTIONS

Parasitoid host selection involves a series of steps in which the female parasitoid must locate and select suitable hosts driven by chemical and physical cues originating from the aphid host and its wider environment (Andow & Prokrym, 1990; Vinson, 1976). The use of these cues by female parasitoids is determined by the physiological sensors that are encoded in each wasp genome and its prior experience. The internal processing of those cues results in a series of behavioural

responses by the female parasitoid, which directly impact the host selection process (Andow & Prokrym, 1990; Rehman & Powell, 2010) (Figure 4). In addition, physiological and behavioural responses of aphids to abiotic and biotic factors such as plant hosts and natural enemies can also vary intra-specifically, which can greatly influence the outcome of aphid-parasitoid interactions (Mooney, 2011). The potential for a population to undergo any adaptative changes is linked to their standing genetic variation involved in each interacting step (Hall et al., 2017; Sentis et al., 2022). However, aphid and parasitoid genetic variation in traits affecting pre-oviposition processes of the aphid-parasitoid interaction has rarely been explored. In the next section, we discuss how genetic diversity can influence the outcome of the steps before parasitoid oviposition and why it is important to explore this variation further.

Aphids and host plant choice

Just as parasitoids assess and select their aphid hosts, the herbivore host also makes decisions about their host plants. These decisions affect the herbivore-parasitoid interaction, particularly because herbivore fitness will greatly depend on the nutrition provided by the plant (Powell et al., 2006; Slater et al., 2019) and herbivore host quality (i.e., size) can be used as a proxy by female parasitoids for host acceptance (Holmes et al., 2023; Rehman & Powell, 2010). Aphids undergo a host plant selection process that includes several successive events in which plant physiochemical cues are key (Jaouannet et al., 2014). Aphid acceptance of host plants is a complex process, which can be

influenced by aphid genetics and there is evidence of aphid intraspecific variation in host plant choice and habitat use (Ferrari et al., 2006). One well-known example is the case of *A. pisum*, in which different genotypes (or biotypes) have been found to be adapted to specific host plants in different genera (Birkle & Douglas, 1999). In this case, each genotype has been shown to have a reduced fitness when it is transferred to another host plant (Peccoud et al., 2009).

It has been shown that aphids exhibit intra-specific variation in an array of important adaptive traits that influence host plant choice. For example, variation in genes associated with salivary effector proteins has recently been described (Botha, 2021; Singh et al., 2021). There is limited information on how this influences aphid interactions with their natural enemies. An experiment exposing *A. fabae* and *M. persicae* cultured on sugar beet and fava bean crops to three parasitoid species (*Aphidius colemani* Viereck, *Lysiphlebus testaceipes* (Cresson) and *L. fabarum*) showed that herbivore host plants played a significant role in parasitoid host acceptance and host suitability, as both species of aphid were preferred by the parasitoids when feeding on fava bean plants, which was linked with apparent differences in the plant volatiles produced (Albittar et al., 2016). Further, host plant genotype can influence parasitism frequency of aphids, as shown for *Macrosiphum euphorbiae* Thomas attacked by *A. ervi* on different plant species and genotypes of the genus *Solanum* (Karley et al., 2017) and *Rhopalosiphum padi* (L.) attacked by *A. colemani* on quack-grass (*Elytrigia repens* (L.)) (Schädler et al., 2010). This could be linked to differences between plant species in the released volatile organic compounds (VOCs) when infested by the same aphid species (Staudt et al., 2010). As VOCs are used as chemical cues by parasitoid wasps in the host search process (Rehman & Powell, 2010), then aphid plant-choice can have an impact on parasitoid performance by influencing host location and acceptance (Frago et al., 2017; Leybourne et al., 2019; Mehrparvar et al., 2019). However, the effect of host plant choice on aphid-parasitoid interactions is not only limited to differential emission of chemical cues but also to plant-mediated effects on aphid fitness (Schillewaert et al., 2017). These can impact aphid quality as a host and therefore affect host acceptance by parasitoids (Kansman et al., 2021). For example, certain host plant species can be detrimental for aphid fitness of some clones of *S. avenae* and *A. pisum* (Gao et al., 2014; Slater et al., 2019). Even though polyphagous aphid species can survive on a wide range of host plant species, variation in host plant quality within and between plant species affects aphid fitness (Karley et al., 2008; Von Burg et al., 2008; Vorburger et al., 2008), leading to changes in aphid quality that have an impact on their acceptance by, and suitability for, aphid parasitoids. It has been reported that *Praon volucre* (Haliday) prefers aphids feeding on the same host plant genotype from which they have developed and emerged (Rehman, 1999). Also, for *Aphelinus mali* (Haldeman) attacking *Eriosoma lanigerum* (Hausmann), parasitoid size and sex ratios varied significantly between host plant species (Peñalver-Cruz et al., 2022). Nevertheless, the magnitude of any consequences of aphid host plant choice on parasitoid host selection will depend on the cost to the parasitoid of changing its host preferences, which can be linked to parasitoid genetic variation (Samková et al., 2021).

Parasitoid foraging

Parasitoid foraging, also referred to as host searching, is a complex process that involves multiple steps: (1) host habitat location, (2) host location and (3) host recognition. Each one of these steps can also be influenced by other members of trophic (plants) and non-trophic levels (endosymbionts) (Bennett et al., 2016; Mehrparvar et al., 2019). Parasitoid foraging involves landscape, visual, tactile and chemical cues, although chemical stimuli appear to play a major role (Lewis et al., 1990). In addition to host plant effects on pre-oviposition behaviour (described above), it has been shown that the presence of certain secondary endosymbionts, such as *S. symbiotica*, can affect parasitoid foraging, especially host location. For example, *A. ervi* females prefer to move towards uninfected aphids and spend more time in patches with uninfected aphid hosts (Attia et al., 2022). This could be due to the fact that aphids with different secondary endosymbionts and different strains of the same secondary endosymbionts show significant differences in the composition of cuticular hydrocarbon profiles, which can be used by parasitoids to locate and recognise their host (Awater-Salendo et al., 2020; Hertaeg et al., 2021). It has also been described that endosymbionts can modulate volatile chemical cues emitted by aphid hosts or emanate their own (Frago & Zytynska, 2023). This might also suggest that aphids with a different infection status produce a different odour. Also, endosymbiont infection has been linked to changes in indirect host cues used by the parasitoids to locate their hosts, such as frass or honeydew; and reduction of the emission of plant herbivore induce volatiles (Frago & Zytynska, 2023). While few studies investigating the role of different strains of secondary endosymbionts on parasitoid foraging have been reported, this is an area of research that should be explored further.

Innate intraspecific variation in parasitoid foraging behaviour has been described for parasitoids attacking hosts other than aphids (Cronin & Strong, 1996; Gallot et al., 2023; Guerrieri et al., 1999; Vet, 2001), however, no information is available for aphid parasitoids. The need for research and information regarding intra-specific variability in parasitoid host searching and particularly in genetic variation associated with the different pre-oviposition steps and cues has long been considered essential (Lewis et al., 1990), but with little progress to date. It should be noted that described differences in parasitoid foraging behaviour have previously been associated with intraspecific variation in the ability to learn new odour cues (Bhagavan et al., 1994; Haverkamp & Smid, 2020) or to retain the learned information (Liefing et al., 2020). However, it is difficult to differentiate the role of genetics and conditioning during parasitoid development, as the latter has also been linked with host preference and differences in parasitoid foraging behaviours (Du et al., 1997; Kruidhof et al., 2019; Vos & Vet, 2004).

Aphid defensive behaviour

Aphids have a repertoire of behavioural defences against natural enemy attack that include dropping from the plant, release of cornicle

secretions, emission of alarm pheromones, walking away, body twitching and leg kicking (Wu et al., 2010). There is evidence for clonal differences in the frequency of dropping as an escape response exhibited by *A. pisum* clones when challenged with natural enemies or in response to the alarm pheromone *E*- β -farnesene (Badji et al., 2021; Kunert et al., 2010; Schuett et al., 2011). It has also been described that clonal lines of different colours (green or red), which are usually linked to different genetic backgrounds and/or endosymbiont infection status (Tsuchida et al., 2010), in the pea aphid differed considerably in their propensity to show dropping as a defensive behaviour to artificial stimuli, nevertheless, there was no difference when aphids were attacked by a predator (Braendle & Weisser, 2001). However, no clonal variation has been detected for other *A. pisum* defensive behaviours in response to parasitoid contact (Muratori et al., 2014). Phenotypic plasticity in responses to natural enemies is common in many herbivore species. In aphids, a frequent response to increasing predator and parasitoid abundance is the asexual production of winged (alate) forms. Clonal differences in the proportion of winged individuals formed when exposed to ladybirds have been described for *A. pisum*, but no information is available for aphids challenged by parasitoids (Sentis et al., 2019). Although efforts have been made to understand the role of intraspecific genetic variation in aphid defensive behaviours, research has focused on *A. pisum* as a model organism, and further research is required to study these behaviours in other aphid species.

The presence of post-oviposition parasitoid resistance traits, whether conferred by facultative endosymbionts, such as *H. defensa*, or encoded by the aphid genome can affect pre-ovipositional behavioural defences against natural enemies. Changes in defensive behaviours might be adaptative to reduce costly defensive actions (i.e., dropping, running, etc.) when they are less needed (i.e., in physiologically resistant lines). For example, a clonal line of *A. pisum* infected with *H. defensa* displayed reduced dropping frequency in response to a female *Aphidius ervi* (Dion, Polin, et al., 2011). By contrast, a recent study of resistant and susceptible lines of *A. pisum* (encoded by *H. defensa* and *M. euphorbiae* (encoded by aphid genotype) showing that resistant lines were more likely to exhibit defensive behaviours than their parasitism-susceptible counterparts when disturbed by predators (ladybird or lacewing larvae) (Humphreys et al., 2022). It is possible these defensive strategies have been co-selected in environments of high natural enemy pressure (parasitoids and predators), although further research work is needed to fully understand the causes; aphid clonal differences were also observed in their post-dropping behaviour (Humphreys et al., 2021a, 2021b, 2022).

Parasitoid host acceptance, handling time and attack rate

Once the female parasitoid has direct contact with a potential aphid host, a series of chemical and physical cues are assessed to trigger behavioural responses that result in host acceptance and oviposition decisions (Rehman & Powell, 2010). Host acceptance can be divided

into two behavioural steps: (1) host handling, which consists of the female wasp pursuing, subduing, ovipositor probing and ovipositor insertion (Wu et al., 2011); and (2) oviposition (successful release of a parasitoid egg inside the host) (Rehman & Powell, 2010). However, in biological control, the term host acceptance is commonly used to encompass both terms without distinction (Barzman & Daane, 2001).

Host acceptance plays a vital role in the success of parasitoid wasps in controlling herbivore populations. One of the most important components of the aphid-parasitoid interaction is the “functional response” (Tazerouni et al., 2019), which describes how a natural enemy responds to changes in the density of its host and depends on two important parameters: handling time and attack rate (Zamani et al., 2006). The handling time is defined as the average time that a female needs to parasitise a single host and the attack rate (or search efficiency) is the number of hosts successfully attacked within a unit of time and at a given host density (Kehoe et al., 2016; Tazerouni et al., 2019). Both parameters are parasitoid-host species specific and strongly linked to parasitism success. Therefore, it has been hypothesised that the outcome of the functional response could be at least partially under genetic control (Wu et al., 2011). If genetic diversity exists in the parasitoid population for the genes encoding functional response attributes, it will have consequences for the outcome of the host-parasitoid interaction (Carlsson et al., 2009; Wu et al., 2011). However, despite the importance of these parameters, research and information on intraspecific variability of parasitoid handling times is scarce (Preedy et al., 2020). Attack rate can directly affect the fitness of all participants (Tazerouni et al., 2019) and directly impacts the ability of a parasitoid to exploit its host species (Kruitwagen et al., 2021). In addition, there is also limited information available on how parasitoid genetic diversity can affect the attack rate of aphids. However, in other host-parasitoid systems, such as parasitoids of flies (i.e., *Drosophila suzukii* (Matsumura)-*Leptopilina heterotoma* (Thomsom); *Musca domestica* L.-*Muscidifurax raptor* Girault and Sanders), intraspecific variation in handling times and attack rates have been described (Antolin, 1989; Kruitwagen et al., 2021; Le Masurier & Waage, 1993). Nevertheless, available information on parasitoid attack rates is often overshadowed by the link between handling time, attack rate and changes in female parasitoid behaviour due to learning, which makes it difficult to determine the role of genetic variability for the individual traits (Wajnberg, 1989). It has also been shown that both traits can be influenced by host plant identity, non-trophic traits such as interspecific parasitoid competition, the physiological state of both participants and the environmental conditions (Heard et al., 2006; Hopper et al., 2013; Ives et al., 1999; Thierry et al., 2019). Research in this area is important as recently published models have highlighted that individual variation in attack rates and handling times in parasitoid species can impact the interaction strength of the host-parasitoid system by affecting parasitoid specificity and thus potentially affecting the stability of food webs and communities (Gibert & Brassil, 2014).

To our knowledge, only one study has investigated the influence of aphid parasitoid genetic variation on host acceptance (Hopper et al., 2019) even though many parasitoid physiological factors are

linked to it. There are, however, more non-aphid examples including *Cotesia glomerata* L. (Hymenoptera: Braconidae), where genetic variation was found among iso-female lines in their acceptance of the host *Pieris brassicae* (L.) (Gu & Dorn, 2000; Hiroyoshi et al., 2017). In addition, for two species of Scelionidae from North America there is evidence of intraspecific variation in host acceptance of the eggs of the brown marmorated stinkbug, *Halyomorpha halys* Stal (Hemiptera: Pentatomidae) (Costi et al., 2020).

Genetic variation has been noted in some host acceptance behaviours. For example, some genotypes of *A. ervi* attacking *A. pisum* tend to superparasitise aphids (i.e., the same aphid host is attacked multiple times by a single parasitoid, resulting in >1 egg per aphid) as a defensive strategy when presented repeatedly with aphids with low levels of susceptibility (Oliver et al., 2012) or parasitoids tend to avoid individuals infected with protective symbionts (Łukasik et al., 2013). Nevertheless, the limited information available on this subject has shown that the ability of parasitoid wasp populations to overcome aphid resistance through mechanisms involving changes in parasitoid gene expression, physiology and behaviour could be linked with parasitoid genetic diversity.

Aphid fitness and quality as a host

Host quality assessment is the last decision step for a parasitoid female about its aphid host. It is usually closely associated with host size and influenced by host age and development stage (Kouamé & Mackauer, 1991). Intraspecific variation has been described for aphids, such as *A. pisum*, in terms of different fitness traits such as development time, adult mass and fecundity (Chong & Moran, 2016). However, there is limited information on how this affects quality assessment by parasitoid wasps. For example, certain parasitic wasps have been shown to lay more eggs on smaller aphids independently of their age, but they attacked all hosts with equal probability independently of their size or age (Kouamé & Mackauer, 1991). It is worth mentioning, however, that a trade-off between aphid size and ease of parasitism (bigger aphids provide more nutrients but are also better at defending themselves from attack) and its influence on attack rates has been also described (Khatri et al., 2016). Nevertheless, differential parasitoid acceptance has been found in *Aphidius rhopalosiphii* Stefani-Perez when it attacks different genotypes of *S. avenae* and *Microlophium carnosum* (Buckton), which could be linked to the parasitoid perceiving differences in host quality between the aphid genotypes (Powell & Wright, 1988). It has also been reported that drought conditions can negatively impact aphid fitness in *R. padi* but no differences were observed in *A. colemani* foraging behaviours or acceptance for that host (Kansman et al., 2021). Unfortunately, no information is available on how genetic variation, in either aphids or parasitoids, can affect the host quality assessment by female wasps.

The role of endosymbiont composition in determining aphid fitness has been widely discussed, and the presence of certain protective secondary endosymbionts, such as *H. defensa* and *S. symbiotica*, can affect host quality and therefore the development and life history

traits of emerging parasitoids (Attia et al., 2022; Leybourne, Bos, et al., 2020). However, no research has been undertaken on the role of endosymbiont strain variation on aphid quality and subsequent parasitoid fitness traits. A study by Schmid et al. (2012), showed that *H. defensa* can produce sublethal effects on *L. fabarum*, leading to smaller adults, but they could not determine if this was mediated by aphid body size (and therefore host quality) or if it was an indirect effect of the presence of the bacteria itself. It should also be noted that aphids have two morphotypes (alate and apterous), which might be perceived by natural enemies as being of different nutritional quality. Studies have found that winged aphids represent a better source of nutrients with higher lipid, protein and sugar content for parasitoids than their wingless counterparts (Sampaio et al., 2008). No differences in parasitoid fitness or female oviposition preference between morphotypes were found, raising questions about the role of host nutritional quality as a decisive factor for parasitoid host acceptance (Pirrotte et al., 2018; Sampaio et al., 2008). However, it should be noted that alate aphids tend to be smaller-bodied than apterous aphids which might contribute to a lack of parasitoid acceptability based on nutritional quality (van Emden & Harrington, 2017). In the case of *M. persicae*, nutritional differences between both morphotypes have also been described but had little impact on oviposition rates for *A. colemani* (Pirrotte et al., 2018).

CONCLUSIONS AND FUTURE DIRECTIONS

Biological control programmes are based on the available knowledge of herbivore-natural enemy interactions. Research in the past 10–20 years has highlighted how genetic variation in aphid and parasitoid traits plays a crucial role in the outcome of the aphid-parasitoid interaction, with significant consequences for biological control efficacy (Leung et al., 2020; Lommen et al., 2017). Of particular interest is the intra-specific variation in aphid physiological responses to the oviposition of a parasitoid egg (i.e., aphid parasitism resistance), the parasitoid counter-adaptation to this process, and the possibility of co-evolution between both characters. Aphids and parasitoids display life history, behavioural and physiological traits that can further shape this interplay. Therefore, throughout this review, we have synthesised (1) the information on physiological resistance of aphids to parasitoids to illustrate how co-evolution in this system works and (2) the limited research on the roles of genetic variation in pre-oviposition steps of host-parasitoid interactions (Table 1). In herbivores, including aphids, information on this intra-specific variability has been described in terms of their quality as parasitoid hosts and in their defensive behaviours. In terms of parasitoids, information is limited on the importance of intra-specific variability for foraging and host acceptance behaviours. In addition, no studies have addressed genotype-by-genotype interactions, and few discuss fitness consequences of genetic variation in pre-oviposition processes, thus restricting our understanding about their evolutionary consequences. Having such limited exploration of genotype-by-genotype interactions in non-physiological related traits and the role of endosymbiont genetic diversity in the

TABLE 1 Summary of the information available on genetic variation associated with traits of the pre-egg-laying stage of the aphid–parasitoid interaction.

Stage of the aphid-parasitoid interaction	Trait	Knowledge gap strength	Apparent impact on the aphid-parasitoid outcome
Host habitat location	Genetic variation in aphid plant host choice	+	+
	Effect on parasitoid foraging		
	Plant volatiles	++	++
Host location	Plant physical traits	+++	+
	Genetic variation in aphid short-range cues	+++	+++
	Effect on parasitoid foraging		
	Sex pheromones	+++	++
	Alarm pheromones	++	+++
Host recognition	Other short-range cues	+++	+++
	Genetic variation in host-specific cues	+++	+++
	Effect on parasitoid foraging		
	Honeydew volatiles	+++	++
	Other specific volatiles	++	+++
Host acceptance/handling	Aphid physical traits	+++	++
	Genetic variation in aphid defensive behaviours	+++	+++
	Genetic variation in aphid fitness and quality as host	++	++
	Effect on parasitoid acceptance		
	Defensive behaviours	+++	+++
	Host quality	+	++
	Effect on parasitoid handling time/attack rate		
Defensive behaviours	+++	+++	
Host quality	++	++	

Note: Strength levels: + (medium), ++ (strong), +++ (very strong). Knowledge gap strength refers to the degree to which information is missing in the current literature. Apparent impact on the aphid-parasitoid outcome refers to the degree to which genetic variation in the trait is likely to affect the outcome of parasitism.

pre-egg-laying interaction between aphid hosts and parasitoids is problematic for the future of biological control. This is because co-evolutionary processes can happen for traits in which both herbivores and parasitoids have genetic variation. Genetic variation potentially exists for pre-oviposition traits of aphid-parasitoid interactions, but this has largely been ignored. Future research should not only focus on the role of intra-specific variability on post-oviposition herbivore parasitoid resistance but also on the earlier steps of the host-parasitoid interaction. This will help to establish a more complete picture of the role of insect genetic variation in shaping host-parasitoid interactions, information that is indispensable for ecological and evolutionary understanding and for the future of the use of parasitoids as biological controllers of insect pests. A combination of the application of molecular tools for a deeper characterisation of the genetic diversity in host and parasitoid populations (including next-generation sequencing and quantitative genetics), complemented by selection experiments should be used for this purpose. In addition, characterisation of the variation on VOCs and cuticular hydrocarbons of aphids, accompanied by assays to understand their effect on parasitoid host

location and acceptance is needed. Finally, it is crucial to include a diverse range of behavioural assays to discern the variation and effects of parasitoid host searching behaviours at different scales, and of aphid defences on the interaction.

AUTHOR CONTRIBUTIONS

Laura Marcela Martinez-Chavez: Conceptualization; writing – original draft; investigation; writing – review and editing. **Joe M. Roberts:** Conceptualization; writing – review and editing; supervision. **Alison J. Karley:** Conceptualization; writing – review and editing; supervision. **Francis O. Wamombe:** Writing – review and editing; supervision. **Tom W. Pope:** Conceptualization; writing – review and editing; supervision.

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The authors declare no conflicts of interest.

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Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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