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Aphid adaptation in a changing environment through their bacterial endosymbionts: an overview, including a new major cereal pest (*Rhopalosiphum maidis* (Fitch) scenario

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Abstract

Aphids (Hemiptera: Aphididae) are small, phloem-feeding insects that exhibit remarkable adaptability and resilience to various environmental conditions, including heat stress. Recent research has shed light on the role of bacterial symbionts in influencing the heat tolerance of aphids. Additionally, an intriguing avenue of investigation has explored how aphids can acquire bacterial symbionts through a unique mechanism involving soil nematodes. In this paper, we provide an in-depth overview of the interplay between heat stress, bacterial symbionts, and soil nematodes in the context of aphid biology. In reviewing the existing literature and collating available knowledge, we highlight the mechanisms by which bacterial symbionts contribute to aphid heat stress tolerance and examine the symbiont acquisition process facilitated by soil nematodes. Furthermore, we discuss the implications of these symbiotic associations in relation to the ecology, evolution, and agricultural management of a major globally expanding pest aphid, the corn leaf aphid, *Rhopalosiphum maidis* (Fitch). Overall, it may be concluded that both primary and secondary bacterial endosymbionts play a significant role in aphid biology with evolutionary consequences. These include adaptations through bacterial symbionts in terms of longevity and fecundity, heat shock tolerance, and resistance to fungal pathogens and primary hymenopterous wasp parasitoids.

Keywords Aphids · Heat stress · Bacterial symbionts · Soil nematodes · Symbiosis · Adaptation · Heat tolerance · Entomopathogenic nematodes · *Buchnera aphidicola* · Corn leaf aphids

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1 Introduction

Aphids are an ancient group of insects which, due especially to the human prevalence of growing a plethora of crops – agricultural, horticultural and forestry – over wide areas of the Earth's surface, have flourished and have, as a consequence, and aided by their rapid asexual mode of reproduction, become global pests causing billions of US dollars of yield loss annually (Skvarla et al. 2017). Many such pest species are now resistant to a wide range of synthetic pesticides, and as such, are causing increasing problems of control (Loxdale et al. 2020). As the world warms due to climate change, one aspect which may be exploitable in terms of their control is heat stress. Hence, it is of importance to know how they cope with this and how exactly it affects their biology, especially including fecundity (Dunbar et al. 2007). In this same light, it is also valuable to know the factors that possibly enhance or ameliorate these effects.

In the present article, we overview the knowledge concerning aphid heat stress and how this is influenced by endosymbiotic bacteria as well as pathogenic nematodes. Our syntheses is descriptive and not a meta-analysis as such involving statistical analyses of the various factors involved in combatting the success of aphids as important crop pests. Rather, having highlighted the factors and their interactions, we concentrate on one well-studied pest aphid in particular, the economically important and globally expanding cornleaf aphid, *Rhopalosiphum maidis* (Fitch). In this way, we hope to show that knowledge of such interactions between insect host and its constraining abiotic and biotic factors can prove efficacious in aphid control.

2 Aphids: biology and ecological significance

Aphids (Hemiptera: Aphididae) are small, soft-bodied insects that are widely distributed and ecologically significant, being commonly found in both natural as well as agro-ecosystems. They have a complex life cycle that often involves both sexual and asexual reproduction, the latter allowing rapid population growth under favorable conditions (Dixon, 1985). The biology of aphids is characterized by several unique adaptations that contribute to their ecological success. One key feature is their piercing-sucking mouthparts, which they use to extract phloem sap from plant tissues. This specialized feeding behaviour enables them to tap into the nutrient-rich phloem sap, which serves as their primary source of energy and nutrients (Loxdale and Balog 2018).

These insects exhibit a high degree of reproductive plasticity. Many species reproduce asexually via parthenogenesis, allowing a single aphid to establish a colony of largely genetically identical individuals barring mutations of one sort or another (Loxdale and Lushai 2003). This reproductive strategy, combined with their rapid development and short generation time, contributes to their ability to rapidly colonize new plant hosts and regions and exploit available resources (Loxdale and Balog 2018). Aphids heterogony (the alternation of parthenogenetic and sexual generations) can also be viewed in terms of adaptation, in some species sexual alternation can be influenced by several factors, like photoperiods, and temperature. Studies on Pea aphid, *Acyrthosiphon pisum* Harris, have revealed intraspecific reproductive polymorphism, where 'cold-resistant cyclically parthenogenetic lineages' alternate with sexual and asexual generations and 'cold-sensitive obligately parthenogenetic lineages', these producing only asexual females but still a few males (Defendini et al. 2023).

The ecological significance of aphids stems from their interactions with plants, other organisms, and ecosystem processes. They are known as phloem-feeding herbivores (plant parasites) and can cause significant damage to crops and ornamental plants by depleting plant sap and transmitting plant viruses (Stevens and Lacomme 2017). Their feeding activities can lead to stunted growth, leaf curling, and the development of honeydew, a sugary excretion that promotes the growth of sooty mould. As such, they are major pests of agriculture, horticulture and forestry and each year, great efforts and wealth are expended in attempts to combat them globally, either using synthetic pesticdes or one or more biological control agents, including fungal pathogens, insects predators and hymenopterous wasp parasitoids (Van Emden and Harrington 2007, 2017).

Beyond their impact as pests, aphids play a crucial role in various ecological processes. They serve as a food source for many predators, including ladybugs, lacewings, parasitoid wasps and small birds such as warblers and tits, thus contributing to the overall diversity and stability of natural ecosystems (Emden and Harrington 2007). Moreover, aphids interact with symbiotic microorganisms, such as bacteria and fungi, which can influence their physiology, behaviour, and interactions with the environment (Moran and Jarvik 2010). Aphids also engage in mutualistic relationships with ants (Stadler and Dixon 2008). Ants protect aphids from natural enemies and predators, while aphids provide ants with honeydew as a food source. Such mutualistic interaction is known as trophobiosis and has significant implications for nutrient cycling and ecosystem dynamics. Furthermore, aphids have been recognized as model organisms for studying various biological phenomena, including reproductive strategies, developmental plasticity, host plant specialization, and the evolution of symbiotic associations. Their relative amenability to laboratory studies makes them valuable research subjects for understanding broader ecological and evolutionary principles.

In conclusion, aphids are ecologically significant insects with a very interesting biology, more especially their reproductive strategies. Their feeding habits, reproductive plasticity, and interactions with plants, predators, and symbiotic microorganisms contribute to their ecological importance. Understanding the biology and ecological significance of these animals is essential for effective pest management, conserving biodiversity, and unraveling fundamental ecological and evolutionary processes.

2.1 Heat stress in aphids: challenges and adaptations

Heat stress is a significant environmental challenge that impacts on the physiology, behaviour and the survival of living organisms, including aphids (Khurshid et al. 2022). Poikilothermic insects like aphids are particularly susceptible to the adverse effects of high temperatures. As temperature rises, they face numerous challenges that can disrupt their normal functioning and threaten their survival. One of the primary challenges posed by heat stress is the disruption of aphid metabolism. High temperatures can accelerate metabolic processes, leading to increased energy demands and altered nutrient requirements. Since aphids primarily feed on plant sap, which is low in essential nutrients such as amino acids, heat stress can exacerbate these nutritional limitations, potentially impairing their growth, development, and reproductive success. In addition, heat stress can induce cellular damage in aphids. High temperatures cause protein denaturation, oxidative stress, and disruption of cellular membranes. Such cellular damage.negatively impacts upon aphid physiology, compromising key functions such as feeding, reproduction, and immune responses. Moreover, it triggers the production of reactive oxygen species (ROS), which may further exacerbate oxidative damage within aphid cells (Dunbar et al. 2007).

To cope with heat stress, aphids have developed various physiological and behavioral adaptations. One critical adaptation is their ability to regulate body temperature through behavioural thermoregulation (Reyes et al. 2019). Trionnaire et al. (2012), who studied the transcriptional cycle of pea aphid, *A. pisum*, under long and short daylength conditions (i.e. summer and autumn) revealed that heat shock-associated proteins were downregulated in the autumn (Trionnaire et al. 2012).

Aphids can actively move around their host plants to seek cooler microclimates or adjust their position on plant leaves to reduce exposure to direct sunlight. These behaviours allow the insects to mitigate the impact of heat stress and maintain body temperature within a tolerable range. In addiution, aphids possess inherent mechanisms to combat the cellular damages caused by heat stress. Heat shock proteins (HSPs) play a vital role in protecting cells from the detrimental effects of high temperatures. These molecular chaperones maintain proper protein folding, prevent protein aggregation, and facilitate cellular repair. Under heat stress conditions, aphids upregulate the production of HSPs to enhance their cellular stress tolerance and improve overall survival (Dunbar et al. 2007; Sanchez-Mahecha et al. 2022).

Bacterial symbionts also contribute to the heat stress tolerance shown by aphids. The primary symbiont of aphids, *Buchnera aphidicola*, has been found to assist in the production of heat shock proteins (Majeed et al. 2022). These symbiotic bacteria play a crucial role in supplying essential nutrients, particularly essential amino acids, which are limited in the aphids' plant sap diet (Douglas 2015; Zhu et al. 2021). By providing such nutrients and supporting the production of HSPs, symbionts enhance the insects' heat stress resilience.

The adaptability of aphids to heat stress is not uniform across species or populations. Variations in thermal tolerance and plasticity have been observed, indicating genetic and environmental influences. Genetic variation among aphids, as well as the specific strains of symbiotic bacteria they harbour, can contribute to differences in heat stress tolerance and adaptive capacity (Burke et al. 2009; Ja et al., 2010).

Understanding the challenges posed by heat stress and the adaptations of aphids provides valuable insights into their ecological dynamics and responses to climate change. With rising global temperatures, studying the mechanisms underlying aphid heat stress resilience will help better predict their population dynamics, geographical distributions, and potential impacts on agricultural systems. Furthermore, exploring the interplay between heat stress and symbiotic associations may well reveal novel strategies for managing aphid populations, thereby mitigating crop losses in a changing climate.

2.2 Symbiotic associations in aphids: overview and importance

Symbiotic associations play a crucial role in the biology and ecological success of aphids and include bacteria, fungi, and yeasts. The bacterial symbionts reside within specialized cells called bacteriocytes or mycetocytes located adjacent to the ovarioles (Braendle et al. 2003), and forming intimate associations that have significant implications for aphid biology, ecology, and evolution (Douglas 1998, 2003).

One of the most studied and indispensable symbiotic relationships in aphids is that formed with the primary bacterium, *Buchnera aphidicola*. *Buchnera* symbionts have a mutualistic association with aphids and are vertically transmitted from mother aphids to their offspring (Shih et al. 2023). These bacteria have coevolved with aphids over tens of millions of years, resulting in an obligate and highly integrated relationship (Dale and Moran 2006). The symbionts provide aphids with essential nutrients, particularly amino acids, which are limited in the aphids' plant sap diet. In return, the aphids supply their *Buchnera* symbionts with carbohydrates produced through phloem feeding. This symbiotic exchange of nutrients has allowed aphids to exploit nutrient-poor plant sap and thrive in diverse ecological scenarios (Cui et al. 2017).

The presence of *Buchnera* symbionts influences various aspects of aphid biology. Thus for example, studies have shown that these symbionts contribute to aphid growth, development, and reproduction (Montllor et al. 2002; Gómez-Valero et al. 2004; Zhang et al. 2019). They are primarily involved in the synthesis of essential amino acids that aphids cannot obtain from their diet, or symnethsise themselves, thus fulfilling their nutritional requirements. Additionally, these symbiotic bacteria modulate aphid reproduction by providing nutrients required for oocyte development and supporting the production of viviparous offspring (Le Trionnaire et al. 2008; Serrato-Salas and Gendrin 2022).

Besides *Buchnera* symbionts, aphids also harbour one or more secondary or facultative symbionts, including species from the genera *Hamiltonella, Regiella*, and *Rickettsia*, among others (Guo et al., 2017). These facultative symbionts reside in sheath cells within the haemolymph related to the bacteriome or in the bacteriocytes themselves, where they displace *Buchnera*, are not required for survival and reproduction, and are transmitted mainly maternally or occasionally horiziontally within and between species (Oliver et al., 2010). As such, they can have diverse effects on aphid biology and ecology. Hence, some facultative symbionts enhance aphid resistance to natural enemies, such as parasitoid wasps (Hymenoptera: Braconidae) and arthropod predators, thereby providing protection against biological threats (Guo et al., 2017; Oliver et al. 2003; Frago et al. 2017). They can also influence aphid interactions with plant hosts, altering feeding behavior, host plant range, and susceptibility to plant defenses (Liu et al. 2023).

The presence of facultative symbionts may result in phenotypic variation among aphid populations, as different symbiont combinations confer different fitness advantages or trade-offs. This variation has significant implications for aphid adaptation, population dynamics, and ecological interactions within communities. Importantly, such symbiotic associations in aphids have broader ecological and evolutionary implications. Since aphids, as phloem feeders, excrete large amounts of honeydew, a sugary substance rich in carbohydrates, this serves as a nutrient resource for a range of organisms, including ants, bees, wasps, butterflies, and fungi. This trophic interaction facilitates nutrient cycling and influences the structure and dynamics of ecological communities.

By exploring the intricacies of these symbiotic relationships, our understanding of aphid biology is enhanced, more especially their interactions with the environment, and the broader implications for ecosystem functioning.

3 Aphid heat stress tolerance and bacterial symbionts

3.1 *Buchnera aphidicola*: a key symbiont influencing aphid heat tolerance

The close symbiotic relationship between *Buchnera* and aphids coevolved over millions of years, has resulted in a highly integrated and obligate association. As aforementioned, because aphids are poikilothermic organisms, they are particularly vulnerable to high temperatures. In this light, *Buchnera* symbionts have been found to contribute to the heat tolerance of their aphid hosts. Several mechanisms have been identified that help aphids cope with such stress.

One of the key contributions of *Buchnera* to aphid heat tolerance is its involvement in nutrient provisioning. Since *Buchnera* supply essential amino acids to aphids, which are limited in their plant sap diet, and hence are crucial for various physiological processes including protein synthesis, energy metabolism, and cellular repair during heat stress, the demand for amino acids increases due to accelerated metabolic processes and protein turnover. The continuous supply of amino acids provided by *Buchnera* enables aphids to maintain crucial cellular functions and mitigate the negative effects of heat stress. Additionally, *Buchnera* assist in the production of HSPs in aphids (Moran 2021). These in turn help in maintaining proper protein folding, preventing protein aggregation, and repairing damaged cellular components caused by high temperatures. The presence of *Buchnera* symbionts thus enhances the aphids' capacity to cope with heat stress at the cellular level.

The genetic variation among *Buchnera* strains has also been found to influence the heat tolerance of aphids, resulting in variations in heat stress resilience among different aphid populations (Zhang et al. 2011; Tougeron and Iltis 2022). Understanding the specific strains of *Buchnera* present in aphids and their genetic characteristics can provide insights into the differential heat tolerance observed among aphid populations.

The influence of *Buchnera* on aphid heat tolerance highlights the importance of symbiotic associations in the adaptation and resilience of aphids to changing environmental conditions. The provision of essential nutrients and the facilitation of heat stress response mechanisms by *Buchnera* contribute to the overall survival and fitness of aphids under such conditions. Further research on the molecular mechanisms underlying the interactions between *Buchnera* and aphids will unbdoubtedly provide valuable insights into the mechanisms of heat stress tolerance per se as well as the broader implications for aphid ecology, evolution, and agricultural management.

3.2 Role of heat shock proteins (HSPs) in aphid heat stress response

During heat stress, aphids experience cellular damage due to the denaturation of proteins, oxidative stress, and disruption of cellular membranes. In response to these stressors, aphids upregulate the expression of HSPs to protect cellular structures and maintain essential cellular functions. The induction of HSPs is triggered by the activation of heat shock transcription factors (HSFs), which bind to specific DNA sequences known as heat shock elements (HSEs) in the promoter regions of HSP genes. The expression of HSPs in aphids is not only induced by high temperatures but also regulated by other environmental factors and physiological conditions. For example, HSP expression is known to be influenced by the presence of symbiotic bacteria such as *Buchnera* and indeed have been shown to contribute to the production of HSPs in aphids, enhancing their heat stress tolerance (Kang et al. 2017). This in turn helps the insects to cope with cellular damage caused by heat stress and ensures their survival under challenging conditions.

The protective role of HSPs goes beyond protein folding and maintenance of cellular integrity. HSPs are involved in various cellular processes, including antioxidant defense, immune responses, and signal transduction pathways (Hu et al. 2022). They contribute to the activation of stress response cascades and help modulate the expression of other stress-related genes, thereby improving the overall stress tolerance of aphids. The upregulation of HSPs in aphids can have implications for their interaction with other organisms and the broader ecological context (Porras et al. 2020). Thus, HSPs have been shown to influence aphid resistance against pathogens, parasites, and arthropod predators. They can enhance immune responses, limit pathogen proliferation, and protect aphids from the detrimental effects of hymenopterous parasitoid wasps (Hu et al. 2022). In these various ways, induction of HSPs contributes to the survival and fitness of aphids under the influence of both abiotic and biotic stressors. This being so, understanding the regulation and functions of HSPs in aphids not only enhances our knowledge of thermal tolerance but also contributes to the broader understanding of stress responses in other organisms.

3.3 Genetic variation in *Buchnera aphidicola* and its impact on heat stress resilience

The genetic variation in *Buchnera* arises from several factors, including genetic drift, recombination, and selection pressures. These processes can lead to the emergence of distinct lineages or strains within *Buchnera* populations. Different *Buchnera* strains may exhibit variations in their genomic composition, gene content, and functional attributes, which in turn can impact the heat stress resilience of their aphid hosts (Dunbar et al. 2007; Shih et al. 2023).

Importantly, the impact of genetic variation in *Buchnera* on aphid heat stress resilience is not uniform across aphid species or populations. Different aphid species may have distinct associations with specific *Buchnera* strains (Moran 2021) and the performance of aphids under heat stress can be influenced by the specific combination of aphid host and *Buchnera* strain (Tougeron et al. 2023). Furthermore, environmental factors, such as the prevailing ambient temperature, can also interact with the genetic variation in *Buchnera* and affect the heat stress resilience of therse insects.

4 Symbiont acquisition through soil nematodes

4.1 Entomopathogenic nematodes: biology and host-seeking behavior

Entomopathogenic nematodes (EPNs) are a group of microscopic roundworms that parasitise and kill insects, including various pest species (Dillman et al. 2012; Tomar et al. 2022). Such nematodes belong to the families *Heterorhabditidae* and *Steinernematidae* and have evolved a highly specialized lifestyle involving infecting and reproducing within their insect hosts.

EPNs exhibit a complex biology and life cycle that allows them to seek out and infect suitable insect hosts. They rely on a symbiotic relationship with bacteria from the genera *Photorhabdus* (in Heterorhabditidae) or *Xenorhabdus* (in Steinernematidae), which are harboured in their gut and released into the host upon infection. The nematodes and bacteria work in tandem to overcome the host's defenses and establish an infection (Awori 2022).

It has alos been found that EPNs have a distinct host-seeking behavior that enables them to locate and infect their insect hosts. When present in the soil, the infective juvenile (IJ) stage actively seeks out potential hosts. This behavior is facilitated by chemical cues released by insects, such as carbon dioxide, heat, and volatile organic compounds. The IJs respond to these cues and move towards potential hosts, often using a 'cruising' strategy where they move in a sinuous pattern in search of them. The nematodes are also attracted to host-associated vibrations, excretions, and volatile compounds, aiding in their host location (Lok 2016).

On encountering a suitable insect host, the IJ penetrates the host through orifices including the mouth and spiracles. The bacteria associated with EPNs are then released into the host's body cavity, where they rapidly multiply, producing toxins and degrading enzymes that contribute to host mortality (Dillman et al. 2012). The nematodes feed on the bacteria and the host tissues, completing their life cycle within the host. Once the host is depleted, new nematode generations develop and emerge as IJs to seek out further hosts.

The biology and host-seeking behavior of EPNs have important implications for their potential use in biological control strategies. EPNs have been successfully utilized as biological agents for controlling various insect pests in agricultural, horticultural, and forestry settings (Van Der Linden et al. 2022). Their ability to actively seek out and infect hosts makes them promising candidates for integrated pest management (IPM) programmes, particularly against soil-dwelling insect pests. Here, understanding the biology and host-seeking behavior of EPNs is important for optimizing their efficacy in biological control. Factors such as environmental conditions, nematode species, and host preferences can influence the success of EPNs as biocontrol agents. Current research aims to further elucidate the mechanisms behind their host-seeking behavior, including the role of chemical cues, sensory systems, and the interactions between nematodes and their associated bacteria (Gang and Hallem 2016; Castelletto et al. 2020).

In summary, entomopathogenic nematodes exhibit a fascinating biology and host-seeking behavior that allows them to locate and infect insect hosts. Their symbiotic relationship with bacteria and their ability to actively search for hosts make them valuable tools for the biological control of insect pests.

4.2 Mechanisms of symbiont acquisition via nematode infection

The acquisition of symbiotic bacteria by aphids through nematode infection represents a unique mechanism of symbiont transmission. This process involves the interplay between aphids, entomopathogenic nematodes, and symbiotic bacteria, offering insights into the complex dynamics of symbiosis as well as horizontal gene transfer (HGT).

The symbiotic bacteria transmitted by EPNs differ from the primary symbiont *Buchnera aphidicola*, which is vertically transmitted from mother aphid to offspring. Instead, the symbiotic bacteria acquired through nematode infection are considered facultative or secondary symbionts. The specific mechanisms by which the symbiotic bacteria are acquired and maintained in aphids following nematode infection are not yet fully understood (Nikoh et al. 2010; Sajnaga and Kazimierczak 2020; Qin et al. 2021). However, several hypotheses have been proposed. These include: (1). *Nematode-mediated transfer*: It is thought that the nematodes themselves serve as carriers of the symbiotic bacteria (Ledón-Rettig et al. 2018). The bacteria are present within the nematode's digestive tract and are released into the aphid during nematode infection. The bacteria then establish symbiotic associations within the aphid bacteriocytes (Singh et al. 2021) (2). *Transmission through nematode excretions*: Another possibility is that the symbiotic bacteria are present in the excretions or secretions of the nematodes. As the nematodes move within the aphid's body or during their egress from the aphid, these bacterial cells are released and establish symbiotic associations within aphid cells; and (3*). Horizontal gene transfer*: The acquisition of symbiotic bacteria through nematode infection provides an opportunity between different aphid lineages. HGT can occur when the symbiotic bacteria release genetic material (such as plasmids or transposons) that are taken up by aphid cells, potentially influencing aphid biology and adaptation (Tagu et al. 2010; Drew et al. 2021).

Elucidating the mechanisms of symbiont acquisition through nematode infection (spatial contact between a soil-dwelling and a leaf-dwelling species) provides valuable insights into the diversity and dynamics of symbiotic associations in aphids; however to date very few results have been published in this topic. The ability of aphids to acquire symbiotic bacteria from the environment through such unconventional means contributes to their adaptability and capacity to form novel symbiotic relationships.

4.3 Symbiotic bacteria associated with aphids through nematode transmission

Symbiotic bacteria associated with aphids through nematode transmission represent a unique form of symbiosis that involves the interplay between three players – the aphids, entomopathogenic nematodes, and bacterial endosymbionts. This mechanism of symbiont acquisition provides insights into the diverse microbial interactions within aphid populations and the potential for HGT.

The acquisition of symbiotic bacteria through nematode transmission involves a series of events:

(1*). Nematode infection*: EPNs infect aphids by entering their body through natural openings or by penetrating the cuticle. Upon infection, the nematodes release their associated bacteria into the aphid's haemocoel, the open body cavity; (2*). Bacterial establishment*: The bacteria released by the nematodes establish themselves within the bacteriocytes. These provide a protected environment for the symbiotic bacteria to reside and proliferate; (3). *Symbiotic associations*: The symbiotic bacteria interact with the aphid host, potentially influencing various aspects of aphid biology and ecology. As mentioned earlier, different bacterial species or strains can confer different benefits or exert varying effects on aphid fitness, heat tolerance, resistance to natural enemies, or host plant utilization. The specific effects of these acquired symbiotic bacteria can vary depending on the bacterial species, aphid host, and environmental conditions. Some symbiotic bacteria, such as *Hamiltonella defensa*, provide aphids with protection against natural enemies, including hymenopterous parasitoid wasps, whilst others like *Rickettsia*, may influence aphid reproduction or heat stress tolerance (Sajnaga and Kazimierczak 2020).

In summary, the acquisition of symbiotic bacteria through nematode transmission provides a mechanism for HGT within aphid populations. Symbiotic bacteria can carry genetic elements, such as plasmids or transposons, that can be transferred to the aphid host. HGT potentially influences aphid biology, adaptation, and the evolution of symbiotic associations.

5 Aphids resistance against parasitic wasps and fungal pathogens

Exposure of the Indian grain aphid, *Sitobion miscanthi* (Takahashi) to the ladybird *Harmonia axyridis* (Pallas) (Coleoptera: *Coccinelida*), without direct contact between predator and prey, influences the aphid's population dynamics more as a result of exposure duration and less to the presence of the facultative symbiont *Regiella insecticola*, suggesting a potential evolutionary model for aphids (Luo et al. 2022). Short-term exposure (4 h), causes aphid populations to increase, but aphids lacking the facultative *R. insecticola* symbiont show lower longevity and fecundity. Long-term exposure (24 h), causes aphid population reduction (Luo et al. 2022). Interestingly, in the case of direct exposure of the aphid to the predator, the presence of the facultative symbiont increased prey protection against the predator (Luo et al. 2022). In addition, the presence of the facultative symbiotic bacteria *H. defensa* and *R. insecticola* in the English grain aphid, *Sitobion avenae* (F.) has been found to delay the infection process with pathogenic fungal species *Beauveria bassiana* and *Metarhizium bruneum*, but does not influence fungal growth on the host after its death and thereby significantly reduces mortality. Their absence results in decreased fecundity of aphids infected with both these pathogens (Ali et al. 2022).

The primary wasp parasitoid *Aphidius ervi* Haliday (Braconidae) is less effective on its host the Pea aphid, *A. pisum* in the presence of the predator, the green lacewing, *Chrysoperla carnea* (Stephens) (Neuroptera: *Chrysopidae*) if facultative symbionts are present. As a conseqiuence, such symbionts are found to be directly involved in symbiont – aphid – parasitoid/predator interaction (Purkiss et al. 2022). In contrast, the presence of the facultative symbiont *R.insecticola* in the body of *A. pisum* does not provide protection against the pathogenic fungus *Batkoa apiculate* (Inchauregui et al. 2023).

Under field conditions, the resistance conferred by the presence of *H. defensa* in the Black Bean aphid, *Aphis fabae* Scopoli against primary wasp parasitoids fluctuates, depending on the temperature regime to which the previous generation of aphids were subjected. The symbiont here provides the aphids with a higher tolerance to heat, but at the same time, the aphid's defence capacity against parasitoids under such stress conditions may decrease (Gimmi et al. 2023).

Under controlled laboratory conditions, the success of *A. ervi* in attacking *A.pisum* is influenced by the presence of facultative symbiontic bacteria. Thus in the presence of protobacterium type – R, a 22.5% reduction in parasitization rate was observed, whereas in the presence of protobacterium type – T, a 41.5% reduction occurred, whilst protobacterium type - U did not seemingly influence the parasitization rate compared to the control, as the parasitoid laid eggs in an undifferentiated manner in both uninoculated and facultative symbiont-inoculated aphid nymphs (Oliver et al. 2003).

It has been also been shown, also under laboratory conditions, that the presence of *R.insecticola* in the body of *A. fabae* results in a significant reduction in the percentage of parasitism of nymphs by the primary wasp parasitoid *Aphidius colemani* (Dalman) (Braconidae) compared with the control in which aphids lacked the bacterium (Vorburger et al. 2010).

Under conditions of superparasitism, the presence of the facultative symbionts *H.defensa* and type - X revealed that parasitism of *A. pisum* by *A. ervi* was significantly reduced (Donald et al. 2016). In a further demonstration of the effects of faculatative symbnionts on aphid fitness, according to (Postic et al. 2020), the parasitism rate by *A. ervi* was high in the Geranium aphid, *Acyrthosiphon malvae* (Mosley) (37.7%) and Potato aphid, *Macrosiphon euphorbiae* Thomas (27.7%) and low in the Yellow Rose aphid, *Rhodobium porosum* (Sanderson) (6.7%). The presence of *H. defensa*, either alone or together with *R.insecticola*, revealed a significant reduction in the rate of parasitism by

A. ervi attacking *A. malvae*, whilst in *M. euphorbiae* and *R. porosum*, the rate of parasitism did not vary significantly. Furthermore, the natural presence of *H.defensa* in *A.malvae* clones was found to result in higher resistance to parasitism by *A. ervi* (Postic et al. 2020). Lastly, the defensive capacity of aphid species harbouring *H. defensa* and *R. insecticola*, respectively, to attack by *A. ervi* was seen to be variable, with the parasitoid adapting to aphid resistance (Postic et al. 2020).

6 Fitness benefits of aphids under different environmental conditions influenced by bacterial symbionts

Symbiotic relationships are found widely in nature and have played a crucial role in the evolution of life on Earth (Zientz et al. 2001). Insects represent the largest and most diverse group of animals globally, with nearly half of all insect species believed to host bacterial endosymbionts (Bourtzis and Miller 2006). In the majority of cases, these bacterial endosymbionts are vertically transmitted from one generation to the next (Russell and Moran 2006). Bacterial endosymbionts found in insects can be classified into two groups: (1) obligate or primary symbionts, and (2) facultative or secondary symbionts. Nearly all aphid species carry the primary endosymbiont *Buchnera aphidicola.*

Bacterial secondary symbionts are known to facultatively colonize their hosts. They are not permanent residents but occur more occasionally within the host's body. Unlike *B. aphidicola*, which are confined to bacteriocytes, these symbionts can be found living freely in the haemolymph, the bacteriome, or other tissues of their aphid hosts (Oliver et al. 2010; Dion et al. 2011).

To date, few studies have been performed to explore how aphids can adapt to different environmental condition via their symbionts. One previous study focused on the role of *Buchnera* in the fitness parameters of aphid hosts, such as their survival, maturation time, and fecundity (Csorba et al. 2022). This study specifically examined the effects of heat exposure on aphids and their symbionts. Different aphid species showed varying levels of adaptation to heat exposure. Here, it was observed that the presence and composition of symbionts played a significant role in determining the aphid host's fitness under heat stress (Zhang et al. 2019). The symbionts, particularly *Buchnera*, were observed to influence the survival, maturation time, and fecundity of the aphids. In the case of the Black Bean aphid, *A. fabae*, heat treatment resulted in high mortality due to the suppression of the obligate *Buchnera* population, which had direct effects on the host's development as well as reducing its fecundity.

In the Blue Alfalfa aphid, *Acyrthosiphon kondoi* Shinji and the Pea aphid, *A. pisum*, heat exposure has been found to cause a rapid decrease in *Buchnera* symbiont abundance (Zhang et al. 2019). Additionally, the heat-exposed aphids showed reduced survivorship, slower development, and decreased fecundity. Overall, this research highlighted the vulnerability of these aphid species to heat exposure, as this leads to a decline in *Buchnera* symbiont abundance and negatively impacts their development and reproduction (Zhang et al. 2019a, b).

Other research (Wegierek et al. 2017; Xu et al. 2021) has revealed that aphids in the tribe *Cerataphidini* (subfamily Hormaphidinae) have the ability to acquire new symbiotic species or replace existing ones when the current symbiont is no longer providing necessary functions. In this particular case, *Cerataphidini* aphids have an extracellular fungal symbiont that lives in their body cavities (Wegierek et al. 2017). It seems that aphids living in warm climates may be more likely to acquire novel symbionts that are more heat-tolerant than their current symbiont, *Buchnera*. This adaptation could help the insects thrive in their changed environment (Yorimoto et al. 2022).

Yorimoto, (2022) reviewed the recent advances in genome analysis of aphid symbionts and highlighted the dynamic evolution of the hologenome, whislt even more recently, Shih et al. (2023) summarized the available information on plant–aphid interactions and argued for new research to be directed specifically in the subject area (Yorimoto et al. 2022; Shih et al. 2023). Previous studies found that the symbiont flora of aphids does not appear to be significantly affected by the host plant or geographical location. They also found that two Peach-potato aphid, *Myzus persicae* (Sulzer) samples from the Sonchus-leaf Crepidiastrum, *Crepidiastrum sonchifolium* (Family Asteraceae) harboured a high abundance of *Rickettsia* symbionts, suggesting that this particular symbiont may have a positive effect/s on the aphid populations feeding on this plant. Lastly, it has been demonstrated in *A. pisum* that *Rickettsia* confers resistance against entomopathogens (Łukasik et al. 2013).

In research conducted by Liu et al. (2023), the bacterial community of the Bamboo Woolly aphid, *Psudoregma bambucicola* (Takahashi) was assessed. These authors found low diversity of symbionts, with three species dominating, i.e. *Buchnera*, *Pectobacterium* and *Wolbachia*. *Pectobacterium*'s ability to support *P. bambucicola* in feeding on hard bamboo stems suggests that a symbiotic relationship exists between the two organisms. Genetic distance analysis further supports the view that *Pectobacterium* present in *P. bambucicola* may represent a newly discovered species of aphid endosymbiont (Liu et al. 2023).

Wolbachia is known to be associated with the transition of reproduction modes in certain organisms, and it could potentially be playing a similar role in *P. bambucicola*. Alternatively, it might have a nutritional role here (Liu et al. 2021). *Wolbachia* is indeed one of the most common secondary symbionts found in insects, including aphids. In many arthropods, it is associated with various effects on their hosts. In some aphid species, the presence of *Wolbachia* is correlated with the prevalence of asexual lineages, indicating a potential role in influencing reproductive mode (De Clerck et al. 2014).

Hamiltonella defensa seems to play a protective role in the Pea aphid, *A. pisum* and other aphid species by providing resistance against hymenopterous parasitoid wasps. Hence, the presence of *H. defensa* in these insects enhances their chances of survival by preventing the wasps from laying eggs inside their bodies. This defense mechanism could potentially increase the overall fitness of the Pea aphid and other aphid species populations that harbour the symbiont (Martinez et al. 2016; Brandt et al. 2017). In contrast, it has been found that aphids hosting *H. defensa* alone or in association with PAXS (Pea aphid X symbiont) suffer higher predation by ladybirds than uninfected ones (Polin et al. 2014). Overall, current research demonstrates that when symbionts provide resistance against wasp parasitoids, it actually increases vulnerability to predators.

In related studies, it has been demonstrated that infection with *H. defensa* increases the fitness of *S. miscanthi* by increasing its adult weight, offspring number and a higher rate of wingless morphs (Qian et al. 2018). The result showed that clones of *Hamiltonella*-infected aphids exhibited lower sensitivity to most of the insecticides tested at low concentrations. In addition, levels of the detoxification enzymes acetylcholinesterase, glutathione transferase and carboxylesterase were significantly higher in these clones. The variation in levels of wasp parasitoid resistance conferred by different strains of *H. defensa* on Pea aphids indicates the potential of these symbionts in protection against parasitoids in a range of aphid species. Such diversity could have important implications for the survival and adaptation of the Pea aphid population (Cayetano and Vorburger 2015).

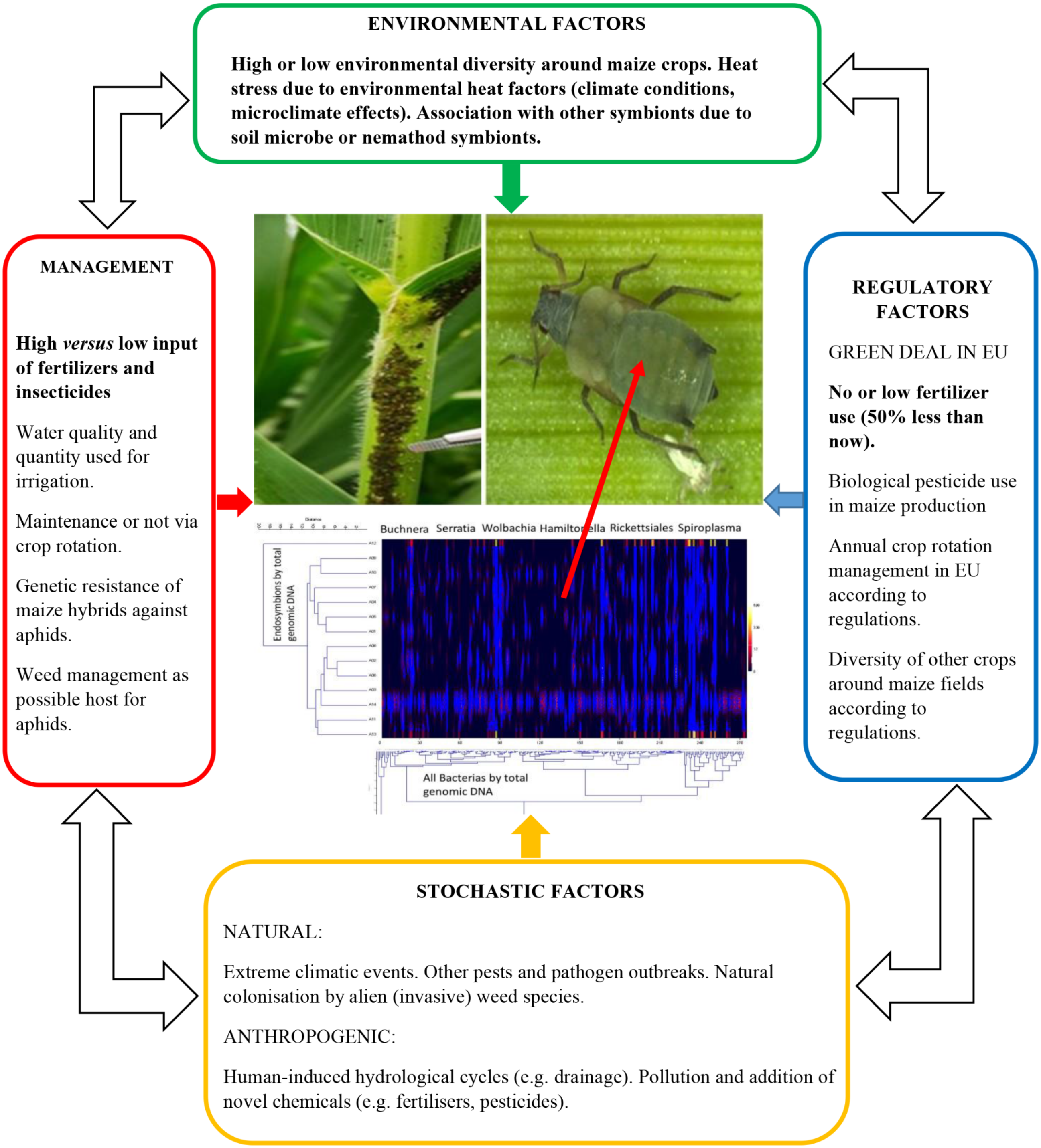
Resistance to infection by the double-stranded (ds) DNA phage, initially known as *A. pisum* secondary endosymbiont (APSE), is commonly observed in *H. defensa*, an organism found not only in aphids but in other hemipterans also (Rollat-Farnier et al. 2015). APSEs are integrated into the main chromosome of *H. defensa*. They are transferred vertically from mother to offspring during the process of maternal transmission (Brandt et al. 2017; Chevignon et al. 2018). Whilst assessing the evolutionary genomics of APSE, it was found that tailed phage lysogenically convert the bacterium *H. defensa* into a heritable protective symbiont. Studies on grain aphids, specifically *S. avenae*, which harbour secondary bacterial symbionts such as *H.defensa* or *R.insecticola*, have demonstrated that they are able to withstand exposure to different pathogenic fungal isolates of *Beauveria bassiana* and *Metarhizium brunneum* (Boyd et al. 2021; Yasir Ali et al. 2022). In fact, bacterial secondary symbionts have been found to have a significant impact on the lifespan and mortality of such aphids when exposed to strains of these fungi. In comparison to aphids without the symbionts, those with them showed considerably longer lifespans and reduced mortality rates when subjected to these fungal strains (Ali et al. 2022).

The promotion of Pea aphid fecundity by *R. insecticola* was observed specifically on white clover, *Trifolium repens* (Tsuchida et al. 2004), but supporting evidence for this finding has not subsequently been obtained in interactions between Pea aphids harbouring either *R. insecticola* or other facultative symbionts and feeding on other plant hosts (McLean et al. 2011). Lastly, previous studies have demonstrated that the endosymbiont *Serratia symbiotica* can colonize multiple tissues within *A. pisum*, including the bacteriocytes, gut, and haemolymph (Skaljac et al. 2018). The colonization of the aphid's mouthparts, particularly the stylets, facilitates the transfer of *S. symbiotica* into its host plant. Probabbly the maintenance of *S. symbiotica* through repeated transmission via plants contributes to its high frequency in aphid populations (Skaljac et al. 2019).

7 Linking corn leaf aphid. *Rhopalosiphum maidis* (Fitch) (Hemiptera: aphididae) adaptation through symbionts and possible influential factors

The corn leaf aphid, *Rhopalosiphum maidis* (Fitch), a major pest of maize, *Zea mays*, in Europe, the USA, China and many other cereal growing countries of the world, has shown a rapid population expansion during the past five years, especially in Europe on maize itrself (Csorba et al. 2022). Besides maize, its hosts include other members of the family Poaceae, i.e. barley, oats, and wheat, and wild grasses. Ii is also a significant vector of pathogenic plant viruses, including barley yellow dwarf virus (BYDV), sweet potato feathery mottle virus (SPFMV), millet red leaf virus (MRLV00), sugarcane mosaic virus (SCMV), and maize dwarf mosaic virus (MDMV). The aphid propagates asexually over much of its range, but in parts of Asia (where it originated), it is known to occasionally reproduce sexually, host alternating between Poaceae (the secondary host) and *Prunus* spp.(the primary overwintering host) on which, after mating, sexual females lay cold hardy eggs (Blackman & Eastop, 2000).

In our previous work, a total of 365 genus-level bacterial taxa were identified related to corn leaf aphid under the



ENVIRONMENTAL FACTORS

High or low environmental diversity around maize crops. Heat stress due to environmental heat factors (climate conditions, microclimate effects). Association with other symbionts due to soil microbe or nemathod symbionts.

MANAGEMENT

High *versus* low input of fertilizers and insecticides

Water quality and quantity used for irrigation.

Maintenance or not via crop rotation.

Genetic resistance of maize hybrids against aphids.

Weed management as possible host for aphids.

REGULATORY FACTORS

GREEN DEAL IN EU

No or low fertilizer use (50% less than now).

Biological pesticide use in maize production

Annual crop rotation management in EU according to regulations.

Diversity of other crops around maize fields according to regulations.

STOCHASTIC FACTORS

NATURAL:

Extreme climatic events. Other pests and pathogen outbreaks. Natural colonisation by alien (invasive) weed species.

ANTHROPOGENIC:

Human-induced hydrological cycles (e.g. drainage). Pollution and addition of novel chemicals (e.g. fertilisers, pesticides).

Fig. 1 The most important factors and associated elements influencing corn leaf aphid adaptations via their bacterial symbionts. Elements marked in bold were assessed and demonstrated from our own researches and data sets

four management systems of maize (Large-scale farming, medium-scale farming, small-scale farming and gardens) (Csorba et al. 2022). An average of 50–53 bacterial taxons per management systems were detected. Considering only the endosymbiotic bacterial taxa, these varied between management systems, with six genera from six phyla being identified, including the following: the obligate symbiont *Buchnera* was present at all sites, but with different frequencies according to the total genomic DNA analyzed. Facultative symbionts *Serratia*, *Wolbachia, Candidatus*

Hamiltonella, Rickettsiales and *Spiroplasma* were also detected under different management systems (Csorba et al. 2022). According to these data and scientific references cited in the publication, a conceptual model was produced and the main topics in various articles considered as relevant factors for model construction. Of four factors reported and chosen for modelling, these were checked separately and each component from these factors added as described in the scientific references, i.e. if one particular element was reported and represented as having a significant effect on corn-leaf aphid adaptation via their symbiont/s, this was incuded as being a significant factor. Similarly, our own data sets obtained were added and marked in bold. Lastly, different factors were marked with different colours and if interactions between factors were detected, these were designated with arrows. The overlaps between factors were again checked using a search mining software (DataSEE). Corrections, if necessary, were made and a final, overall graphical representaion produced (Fig. 1). The model fits within the DPSIR (Driving force–Pressure–State–Impact–Response) framework, thereby facilitating the development of relevant social and economic actions and policy actions. Because certain of the factors considered (especially regulation and stochastic factors) are highly unpredictable, some of the linkages illustrated should be treated as hypothetical, but the high number of fits were found between factors demonstrate that the method used can be considered robust from a scientific point of view.

8 Conclusions

The aformentioned case studies reveal that bacterial endosymbionts, both primary and secondary, play a pivotal role in aphid biology, more especlaly in terms of longevity and hence fecundity, heat shock tolerance, and resistance to fungal pathogens and primary hymenopterous wasp parasitoids, both agents widely used in IPM programmes to control these serious pests of agriculture, horticulture and forestry. In this respect, futher researches are important to tease out which of these infiuences may be most readily exploited to combat aphids, here the model species, corn-leaf aphid, whilst meanwhile reducing the impact of synthetic chemical pesticides in the environment.

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Declarations

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