12 Bacterial–Insect Symbiosis in a Context of Climate Change: Implications for Parasitoidism and Biological Control

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Abstract

Insects host a wide range of bacteria, some of which are heritable and have major impacts on their evolutionary ecology, with consequences for host–parasitoid relationships. Climate change is expected to have a significant impact on host–parasitoid and host–symbiont relationships, but these two axes are rarely considered together. We address this issue by focusing primarily on aphids, aphid parasitoids and the diversity of their heritable symbionts. We outline the diversity of bacterial symbionts that coevolve with crop pests and parasitoid wasps and discuss the influence of temperature on bacteria–insect symbiosis. Along the way, we discuss various hypotheses and predictions on how increasing temperature in a context of climate change, by influencing endosymbionts, may affect host–parasitoid relationships and biological control programmes. This critical synthesis suggests new avenues to delve into and should serve as a roadmap for further exploration of the complexity of the host–microbiota–parasitoid network in a context of global warming.

12.1 Setting the Scene: Insects are a Food Resource for Parasitoids and Symbiotic Bacteria

Insects represent the most diverse group of animals on the planet and are the food source for many species (Scudder, 2017). In food webs, insects are also the target of a multitude of natural enemies, either as prey or as hosts. Parasitoidism is a type of biological relationship, particularly common in insects, that has been exploited in crop pest control programmes. A parasitoid is an organism that lives on or in another organism (the host) and eventually causes the death of the host in which it develops (Blaimer *et al.*, 2023). Parasitoidism has contributed to the diversification of the Hymenoptera order, and today forms the basis of many biological control strategies against insect pests in various agricultural systems (Waage and Hassell, 1982).

Insects also interact closely with diverse micro-organisms (bacteria, fungi, viruses, etc.) that form their microbiota and find resources in insects to proliferate (Engel and Moran, 2013). The bacterial dimension of the insect microbiota

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© CAB International 2025. *Biological Control Systems and Climate Change*
(eds Joan van Baaren *et al.*)
DOI: 10.1079/9781800625099.0012

has received increasing attention in recent years, as it has been shown to play an important role in the evolutionary ecology of these invertebrates, affecting host fitness and phenotypes in a variety of ways (Zientz *et al.*, 2004; Feldhaar, 2011; Engel and Moran, 2013; Sudakaran *et al.*, 2017). The nature of relationships between insects and prokaryotes can evolve along the parasitism–mutualism continuum as a function of genetic and ecological parameters (Drew *et al.*, 2021). Insect-associated bacteria can colonize diverse parts of the host, including the surface (ectosymbionts), the digestive tract (gut symbionts) and the host body cavity (endosymbionts) where they can sometimes live intracellularly in specialized cells called bacteriocytes (Baumann, 2005; Engel and Moran, 2013; Ganesan *et al.*, 2023). While some insect symbionts are transient associates, others can hardly live outside their host, which provides them with a habitat with all the resources they need to thrive. These bacteria, which maintain a highly intimate relationship with the host, are faithfully transmitted vertically from one generation to the next (Frago *et al.*, 2020).

Depending on the degree of dependence insects have evolved with heritable symbionts, the latter are usually classified as obligate or facultative symbionts. Obligate symbionts are pervasive in insect taxa that feed on a diet poor in certain nutrients (e.g. blood, plant sap and wood). These taxa generally include species that are agronomically important as crop pests. Without these nutritional symbionts, these insects can hardly develop and reproduce. In many cases, obligate symbioses appeared tens of millions of years ago, and have fostered the diversification of insects, enabling them to exploit otherwise inaccessible ecological niches (Fisher *et al.*, 2017; Sudakaran *et al.*, 2017; Cornwallis, *et al.*, 2023). Insects are also hosts to facultative symbionts, which are heritable associates that are not essential to their host's survival but can affect the insect's adaptive phenotype by producing beneficial or detrimental effects, and/or by selfishly manipulating host reproduction (Feldhaar, 2011; Kaur *et al.*, 2021).

Interestingly, the last two decades have seen a growing awareness of the influence of insect microbiota on host–parasitoid interactions. This is particularly relevant for sap-feeding insects, which can carry a diversity of heritable bacterial symbionts that can confer direct protective effects on their hosts, induce behavioural changes and indirectly influence ecological dynamics (Oliver *et al.*, 2003; Dion *et al.*, 2011; McLean *et al.*, 2016). Although receiving more limited attention, the evolutionary ecology of parasitoids targeting sap-feeding pests may also be influenced by the heritable symbionts with which they are associated, in particular the widespread reproductive manipulator *Wolbachia pipientis* (Dicke *et al.*, 2020). Several studies have highlighted the importance of taking the microbial axis into account in parasitoidism-based pest control (Douglas, 2007; Berasategui *et al.*, 2016; Vorburger, 2018). However, all these interactions are influenced by temperature, and are being challenged by the thermal constraints imposed by global warming. In this context, it is therefore essential to understand how thermal stress influences prey–predator and parasitoid–host relationships through bacterial symbiosis.

A variety of studies have examined the impact of temperature on parasitoidism (Hance *et al.*, 2007; van Baaren *et al.*, 2010; Furlong and Zalucki, 2017). Also, numerous studies have investigated the influence of temperature on microbial symbiosis and its consequences for insect development and the expression of certain phenotypes (Fan and Wernegreen, 2013; Corbin *et al.*, 2017; Hussain *et al.*, 2017; Renoz *et al.*, 2019). However, few studies have focused on the effects of temperature on the host–microbiota–parasitoid network. The aim of this chapter is to examine how temperature, through its influence on heritable symbiosis, can impact parasitoidism. We address this issue in the context of heat stress and global warming, highlighting gaps to offer a fresh perspective on these aspects in the context of biological control. Biological control using parasitoids and predators is a vast field of study. The same is true of the insect microbiota, which comprises an incredible diversity of micro-organisms associated with a variety of effects. For this reason, this chapter deliberately overlooks predators, concentrating instead on parasitoidism, particularly that involving parasitic wasps. It also focuses on the bacterial component of the insect microbiota, in particular heritable symbionts that have evolved intimate relationships with insects, especially sap-feeding insect taxa that include important crop pests. Through this framework, we aim to provide the community with a source of guidance for addressing the diversity of biological systems relevant to biological control in a warming climate.

First, we will examine the nutritional dependence of many insect pests on ancestral symbionts and discuss how their heat sensitivity can impact host–parasitoid relationships. We will then take a closer look at the case of facultative symbiosis, with aphids as study models. Indeed, some heritable facultative symbionts can interfere with interspecific interactions, including parasitoidism, and this influence tends to be temperature dependent. Finally, we will look at the diversity of parasitoid microbiota, a rather neglected area. The prevalent symbiont *W. pipientis* will serve as a case study to understand how an increase in temperature can affect the course of biological control by influencing the interaction between the bacterium and its parasitoid host.

12.2 Many Insect Pests Depend on Degenerate and Heat-sensitive Symbionts

Host quality shapes the life-history traits of parasitoids and is modulated by many factors, including host symbionts (Heimpel *et al.*, 1996; Attia *et al.*, 2022). In the following paragraphs, we examine how symbionts can influence host quality in a context of climate change and increasing extreme heat events. Many insect crop pests have their biology inextricably linked to the presence of heritable symbiotic bacteria in their tissues and cells, which can have a variety of effects on the host (Moran *et al.*, 2008; Łukasik and Kolasa, 2024). Sap-feeding insects have generally evolved a dependence on nutritional endosymbionts that provide them with nutrients essential for their development that are insufficiently present in their diet (e.g. amino acids and vitamins) (Fig. 12.1) (Zientz *et al.*, 2004). Obligate symbionts are pervasive in hemipterans such as aphids, adelgids, psyllids, cicadas, leafhoppers, planthoppers and

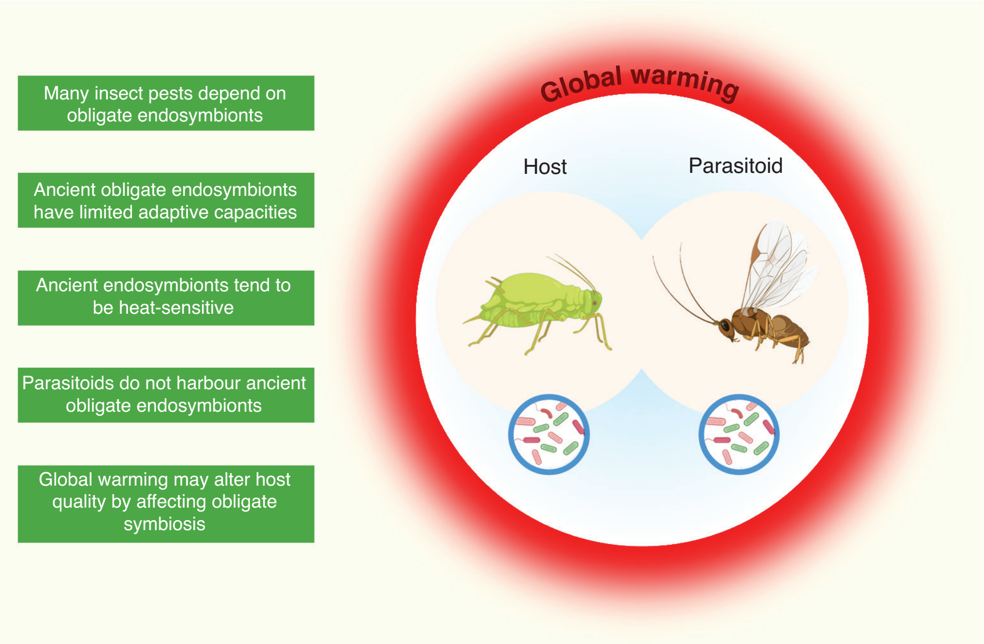


Fig. 12.1. Global warming may modify host quality by affecting ancient obligate symbioses, leading to altered host–parasitoid relationships.

treehoppers (Sudakaran *et al.*, 2017). All these taxa are associated, with one – sometimes several – nutritional symbionts that they often acquired tens of millions of years ago.

A typical feature of these ancient associations is that obligate symbionts are internalized within specific cells that insects have evolved: the bacteriocytes. These cells perform several functions: they mediate metabolic exchanges between the host and its bacterial partners, promote the transmission of symbionts from mother to offspring and regulate symbiont populations according to the host's nutritional needs over its lifetime (Koga *et al.*, 2012; Simonet *et al.*, 2018; Whittle *et al.*, 2021). However, this confined and stable intracellular lifestyle exposes symbionts to reductive genome evolution because it severely limits genetic exchange between nutritional symbionts and other bacteria, promotes asexuality and causes Muller's ratchet. This, coupled with severe population bottlenecks during vertical transmission and the relaxation of purifying selection on genes no longer needed in the context of interdependent association, leads to the emergence of bacterial associates that resemble organelles (Bennett and Moran, 2015). Consequently, after tens of millions of years of reductive evolution, insect host species find themselves dependent on nutritional symbionts with tiny genomes (with a loss of sometimes more than 95% of the original genetic repertoire) and extremely limited adaptive capacities. For example, *Buchnera aphidicola*, the obligate symbiont of aphids, was acquired over 100 million years ago and has a genome size of between 0.4 and 0.6 Mb (Moran *et al.*, 1993; Chong *et al.*, 2019). This is very small compared with 'conventional' free-living bacteria such as *Escherichia coli*, whose genome size is between 4.5 and 5.5 Mb. Some insect symbionts have genomes as small as 0.2 Mb (e.g.*Nardonella* found in some weevil species), encoding fewer than 200 genes, and so have genomes even smaller than some organellar genomes (Anbutsu *et al.*, 2017). Due to their limited adaptive capacities and low tolerance to environmental variation, it has been postulated that these organelle-like symbionts represent an Achilles heel for their host species (Wernegreen, 2012; Bennett and Moran, 2015; Renoz *et al.*, 2019). In the context of global warming, the functioning of the symbiosis could be significantly altered, with consequences for the biology of the host and its quality for higher trophic levels.

The thermosensitivity of obligate insect symbionts has been highlighted and discussed by studies which, in most cases, have used aphids as models (Dunbar *et al.*, 2007; Burke *et al.*, 2010a; b; Fan and Wernegreen, 2013; Moran and Yun, 2015; Hussain *et al.*, 2017; Shan *et al.*, 2017; Zhang *et al.*, 2019; Heyworth *et al.*, 2020). For example, pea aphids *Acyrthosiphon pisum* (Hemiptera: Aphididae) exposed for a few hours at temperatures up to 38°C have a reduced density of the bacteriocyte-associated symbiont *B. aphidicola*, which can even be completely lost by being lysed (Burke *et al.*, 2010a). However, heat stress experiments conducted on different aphid species have shown that *Buchnera*'s heat tolerance depends on the strain's genotype (Zhang *et al.*, 2019). For example, the cotton aphid *Aphis gossypii* (Hemiptera: Aphididae) and its associate *Buchnera* are little affected by the heat stress applied, while the black bean aphid *Aphis fabae* (Hemiptera: Aphididae) and its associate *Buchnera* are very sensitive, with a significant reduction in aphid fitness and *Buchnera* symbiont numbers. These differences in heat tolerance are not yet well understood. However, previous studies in *A. pisum* have shown that *Buchnera* strains characterized by a mutation in the *ibpA* gene, which encodes for a heat shock protein, are more sensitive to heat than *Buchnera* strains that do not have this mutation (Dunbar *et al.*, 2007; Burke *et al.*, 2010b). In the context of the reductive evolution experienced by obligate symbionts, gene loss is virtually irreversible. Dependence on the obligate symbiont could therefore impose rigidity on the thermal adaptation of host aphids and eventually lead to the displacement of heat-sensitive aphid populations to cooler regions. This could affect the distribution and seasonal ecology of parasitoids, whose life cycle is closely linked to that of their host. However, while symbiont genotype is a key factor explaining symbiont heat tolerance and thermotolerance of hosts, it is also possible that specific host-level mechanisms are at work, for example, perhaps at the level of bacteriocytes, the cells in which nutritional symbionts are confined and which regulate their populations via various cellular and molecular processes (Shigenobu and Stern, 2013; Simonet *et al.*, 2018; Whittle *et al.*, 2021). The study by Shan *et al.* (2017) suggests that bacteriocytes are also thermosensitive, as heat stress tends to severely impact their proliferation and morphology. The genetic variability of obligate symbionts linked to their thermosensitivity, and the compensatory mechanisms deployed by the host to deal with it, are issues that should be addressed in future research.

The thermosensitivity of obligate symbiosis is not limited to aphids; experiments conducted on *Bemisia tabaci* (Hemiptera: Aleyrodidae) show that continuous exposure to heat stress at 35°C almost completely depletes the nutritional symbionts *Portiera* and *Hamiltonella* and inhibits bacteriocyte proliferation (Shan *et al.*, 2017). In most studies, insects are exposed to acute heat stress but even if the frequency of such stresses increases with global warming, this is only one of the many types of heat stress that insects can experience in nature. However, a study that examined the impact of a slight and prolonged increase in temperature on the phytophagous green stink bug *Nezara viridula* (Hemiptera: Pentatomidae) shows that the obligate gut symbiont is severely affected, impairing the insect's normal development (Kikuchi *et al.*, 2016). This study suggests that even a slight increase in temperature can have a dramatic effect on nutritional symbiosis and then on insect development. This study confirms that heat-sensitive symbionts, whether residing in bacteriocytes or in specific crypts of the digestive tract, can be the Achilles heel of insect hosts under climate change conditions, impairing their quality as a food source for other organisms.

Data on the thermosensitivity of obligate symbioses is still limited and comes mainly from aphids living in temperate regions. Further studies are therefore needed to determine whether this high thermosensitivity of obligate symbiosis can be generalized to most symbiotic systems (e.g. insects evolving in tropical regions). However, in the light of current knowledge, we can expect heat stress, by destabilizing the nutritional mutualisms born of millions of years of coevolution, to affect the health of insect hosts in the wild. While it is certain that this will affect higher trophic levels, the exact consequences for parasitoids are difficult to predict. However, as their life cycle is intimately linked to that of the hosts they parasitize, we can assume that, depending on the thermal tolerance of the host's nutritional symbionts, climate change will modify the physiology and feeding habits of parasitoid insects. The quality and geographical distribution of hosts may change, with important consequences for interspecific interactions such as host–parasitoid and prey–predator interactions. Today, these aspects remain little studied, even though they are relevant to agriculture and the orientation of biological control methods based on parasitoidism.

Finally, it is important to note that unlike many of their phytophagous hosts, parasitoid wasps do not harbour ancient obligate symbionts with highly reduced genomes (Dicke *et al.*, 2020). However, the parasitic wasp *Asobara tabida* (Hymenoptera: Braconidae) seems to have evolved a dependence on *Wolbachia* for the proper conduct of oogenesis (Dedeine *et al.*, 2001). It is not known whether this mutualism extends to other parasitoid species, or how temperature sensitive it is. These are aspects that merit further study. Many viruses also form specific obligate mutualistic associations with parasitoids (Dicke *et al.*, 2020), but this aspect is not covered in this review.

12.3 Insect Pests Host Facultative Symbionts Associated with Important Ecological Traits

12.3.1 The diversity of facultative symbionts and their effects: Aphids in the spotlight

Many insect species, whether associated with obligate symbionts or not, are infected by heritable facultative symbionts that are not necessary for host development but which can affect the insect's adaptive phenotype in different ways (Oliver *et al.*, 2010; Feldhaar, 2011; Kaur *et al.*, 2021). These bacteria can produce beneficial or detrimental effects, the expression of which is conditioned by the genotype of both partners and by the ecological context, including the thermal environment (Fig. 12.2). Facultative symbionts also include bacteria that selfishly manipulate insect reproduction to propagate within populations (e.g. *Wolbachia* symbionts). As these bacteria have been acquired more recently than obligate symbionts, they have

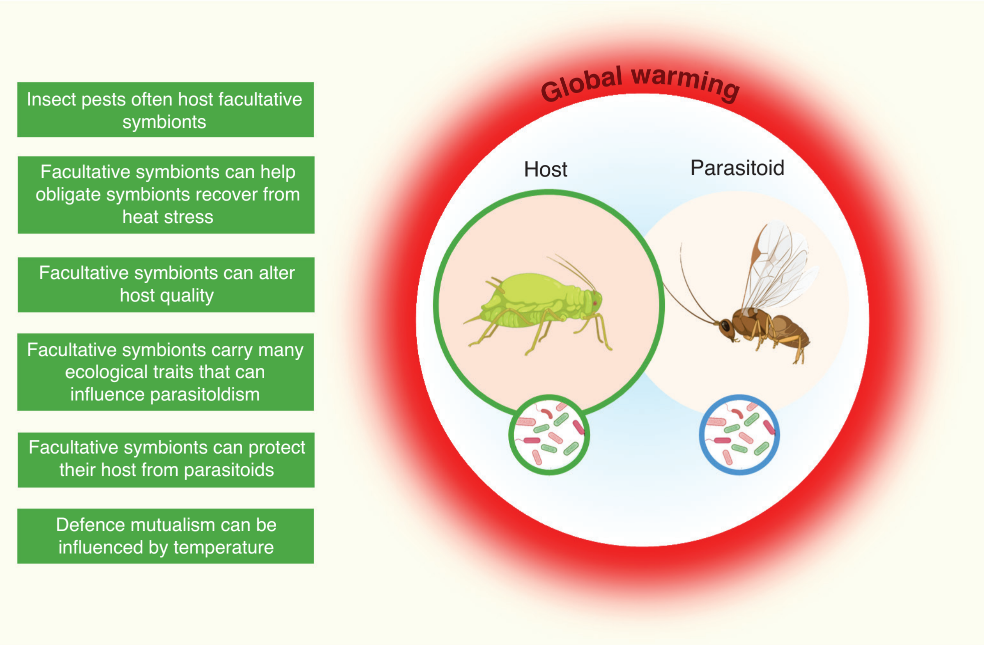


Fig. 12.2. Facultative symbiosis is an important dimension to consider in the evolutionary ecology of insect pests in a context of global warming.

less reduced genomes, can infect a wider range of tissues and cells (bacteriocytes, sheath cells, hemolymph, digestive tract, etc.) and can occasionally circulate in the environment and infect new hosts.

Facultative symbiosis has evolved in many insect species but aphids are historical models for its study as they can host a dozen or so facultative symbionts associated with diverse properties (Oliver *et al*., 2010). For example, *Spiroplasma* bacteria can manipulate aphid reproduction (Simon *et al*., 2011), *Rickettsiella viridis* can modify the body colour of infected insects (Tsuchida *et al*., 2010) and *Regiella* and *Arsenophonus* symbionts can play a nutritional role by influencing aphid adaptability to host plants (Tsuchida *et al*., 2004; Wagner *et al*., 2015; Tian *et al*., 2023; Renoz, 2024). *Serratia symbiotica* and other facultative symbionts species are known to induce protection against acute thermal stress (Burke *et al*., 2010a). Finally, certain facultative symbionts confer protection to aphids against pathogenic fungi and/or parasitoids (Oliver *et al*., 2003; Scarborough *et al*., 2005; Vorburger *et al*., 2010; Ballinger and Perlman, 2019). Although faithfully transmitted vertically, facultative symbionts can also undergo horizontal transmission, so that the important ecological traits with which they are associated can be passed on within insect populations or even acquired by other taxa (Oliver *et al*., 2010).

It is important to note that while *Wolbachia* (Alphaproteobacteria) is widely distributed in many insect taxa (e.g. Hymenoptera and Diptera), the symbiont seems rarer in aphids and other sap-feeding insects, and its effects on these insects remain puzzling (Augustinos *et al*., 2011). On the other hand, it is widespread in other insects targeted by biological control with parasitoids, such as certain *Drosophila* species (Diptera: Drosophilidae). In these insects, *Wolbachia* can have a wide range of effects. While some strains are pathogenic, others are nutritional mutualists (Min and Benzer, 1997; Brownlie *et al*., 2009). Some strains protect hosts against pathogenic viruses and parasites (Bruner-Montero and Jiggins, 2023; Perlmutter *et al*., 2023). *Wolbachia* can also modify the behaviour of *Drosophila* hosts (Bi and Wang, 2020). In the context of *Drosophila*–parasitoid relationships, *Wolbachia* can interfere with parasitoidism by interacting with parasitoid viruses. For example, Martinez *et al.* (2012) showed that *Wolbachia* hosted by *Drosophila* flies could either modify the oviposition preferences of the parasitoid *Leptopilina boulardi* (Hymenoptera: Figitidae), depending on the presence of LbFV virus in the latter, or help the host fly escape parasitism from LbFV-infected parasitoids by increasing the rate of encapsulation, a typical defence mechanism against parasitoid eggs. Our study deliberately focuses on sap-feeding insect hosts but given that the effects of *Wolbachia* on aphids remain unknown, the interaction between *Drosophila* and *Wolbachia* is a source of inspiration to fill this gap.

12.3.2 Facultative symbionts are also heat sensitive (but maybe less than obligate symbionts!)

In general, facultative symbionts appear to be less sensitive to heat stress than obligate symbionts. For example, exposure of *B. tabaci* to heat stress severely affects the populations of obligate symbionts, whereas facultative symbionts show an ability to resist more effectively (Shan *et al.*, 2014; 2017). This could be explained by the fact that, although these heritable symbionts possess many of the same genomic features as obligate mutualists (e.g. in terms of genome reduction), these are generally less pronounced, and they retain a generally complete wall and membrane (Wernegreen, 2012). However, a number of studies also show that high temperatures can deplete populations of facultative symbionts and reduce the efficiency of their vertical transmission (Anbutsu *et al.*, 2008; Burke *et al.*, 2010a; Corbin *et al.*, 2017; Liu *et al.*, 2019). For example, temperatures above 30°C suppress *Wolbachia* infection in the spider mite *Tetranychus urticae* (Arachnida: Tetranychidae) (van Opijnen and Breeuwer, 1999). The aphid symbiont *R. viridis* can be readily transmitted horizontally by plants, but not at temperatures above 25°C (Gu *et al.*, 2023). This is important because horizontal transmission drives inter- and intraspecific transfer of facultative symbionts and the important ecological traits they are associated with. All this suggests that the increased frequency of heat stress due to climate change could have an impact on the persistence and dynamics of facultative symbioses in natural insect populations, and on how the associated traits are transmitted and expressed (Martins *et al.*, 2023).

12.3.3 Facultative symbionts can help obligate symbionts recover from heat stress

Facultative symbionts can be a game changer when it comes to insect resistance to extreme thermal events. Indeed, some facultative symbionts have the ability to protect their hosts from the deleterious effects of high temperatures, thereby increasing their thermal tolerance. For example, certain strains of *S. symbiotica* increase the survival and reproduction of aphids exposed to heat shock (Burke *et al.*, 2010a). Furthermore, the heat protection delivered by *S. symbiotica* tends to be resilient to repeated thermal stress (Tougeron *et al.*, 2023). Subsequent studies have shown that these protective effects extend to other facultative symbionts (e.g. *Regiella*, *Hamiltonella* or *Fukatsuia*) (Russell and Moran, 2006; Heyworth *et al.*, 2020). However, while a recent meta-analysis shows that facultative symbionts tend to improve or maintain aphid fitness under heat stress, these protective effects could vary greatly depending on the strain, as some symbiont strains tend to exacerbate host thermosensitivity (Russell and Moran, 2006).

The mechanisms behind this heat protection are largely unknown, but one clearly observed trend is that the presence of certain facultative symbionts attenuates the collapse of *Buchnera* cell density under heat stress, while the density of facultative symbionts falls rapidly but recovers after the stress episode (Burke *et al.*, 2010a; Heyworth *et al.*, 2020). A study conducted on *S. symbiotica* in the pea aphid *A. pisum* suggests that it is the metabolites released after cell lysis of the facultative symbionts that help protect the integrity of the obligate symbiosis with *B. aphidicola* (Burke *et al.*, 2010a). More recently, it has been shown that *S. symbiotica* can complement the *Buchnera* DNA repair system to form a complete system that would preserve the integrity of the *Buchnera* genome and thus improve the thermostability of the nutritional symbiosis (Ling *et al*., 2024). It is not known whether this mechanism extends to other facultative symbionts. However, in the field, this increase in heat tolerance provided by facultative symbionts could result in greater prevalence in populations evolving in warm areas (Montllor *et al*., 2002).

There is no longer any doubt that many facultative symbionts are associated with protective effects against heat stress. However, the other aspects of these bacterial associates should not be overlooked: despite their advantages in specific ecological contexts, facultative symbionts are often moderate pathogens that impose costs on their host's fitness (Zytynska *et al*., 2021; Clavé *et al*., 2022). For example, aphids infected with *S. symbiotica* have a reduced survival rate, reproduce less and are smaller (Perreau *et al*., 2021; Attia *et al*., 2022; Tougeron *et al*., 2023). The costs associated with facultative symbionts may explain why, in some cases, their presence exacerbates the host's thermosensitivity (Russell and Moran, 2006). Thus, the extreme versatility of facultative symbionts on the parasitism–mutualism evolutionary continuum makes it difficult to predict the impact of these bacteria on host–parasitoid relationships in a warming climate. One hypothesis is that an increase in the prevalence of facultative symbionts with heat-protective effects in a warming climate could lead to lower-quality hosts and hinder parasitoid development, with overall impacts on their populations and their effectiveness in pest regulation. This is supported experimentally by the study of Attia *et al*. (2022), which showed that a *S. symbiotica* strain with heat-protective effects alters the quality of aphid hosts, which in turn influences the foraging behaviour and life-history traits of the parasitoid *Aphidius ervi* (Hymenoptera: Braconidae).

12.3.4 Defensive mutualism under heat stress

As discussed above, facultative heritable symbionts can provide aphids with a whole range of advantages. One of the most notable is defensive mutualism: some facultative symbionts effectively protect their host from fungal pathogens or parasitoids (Oliver *et al*., 2003; Scarborough *et al*., 2005; Oliver *et al*., 2014; Ballinger and Perlman, 2019; McLean *et al*., 2020). Defensive mutualism has been reported in aphids but also in other insect groups (e.g. *Drosophila* flies) (Vorburger, 2022).

In aphids, the ability of the facultative symbiont *H. defensa* to protect these insects from parasitoids has received significant attention. This protection is due to a phage called APSE, which infects the symbiont and produces toxins that prevent the development of parasitoids in the host, with the level of protection depending on the phage variant (Oliver *et al*., 2009). The thermal sensitivity of the defensive symbiosis involving *Hamiltonella* has been examined in a few studies. There is experimental evidence that heat stress can undermine the protection provided by *H. defensa* against parasitoids (Bensadia *et al*., 2006; Guay *et al*., 2009; Cayetano and Vorburger, 2013). In their study, Bensadia *et al*. (2006) hypothesized that the resistance provided by *H. defensa* to the pea aphid *A. pisum* against *A. ervi* might be temperature dependent and tested this on several resistant and non-resistant aphid clonal lines under controlled conditions. Three clones showing complete immunity to *A. ervi* at 20°C and containing *H. defensa* lost resistance to the parasitoids at 25°C and especially at 30°C, a temperature normally reached during the agricultural season. These differences were not related to host acceptance but were clearly related to the development of the first parasitoid larvae. The authors concluded that the temperature-dependent susceptibility of the resistant clones could be explained by a strong inhibitory effect of temperature on the physiological immunity of pea aphids.

The results of the Bensadia *et al*. (2006) study were later confirmed by that of Guay *et al*. (2009) conducted on other *A. pisum* clones. In addition, they showed that clones coinfected with *H. defensa* and *Fukatsuia symbiotica* (previously named PAXS) (Patel *et al*., 2019)) remained resistant to *A. ervi* at high temperature compared with clones containing *H. defensa* alone. In this study, the effect of the *F. symbiotica* symbiont alone was not investigated (Guay *et al*., 2009). Heyworth and Ferrari (2015) also showed that the aphid endosymbiont *F. symbiotica* (again formerly 'X-type' or PAXS symbiont) improves both tolerance to thermal shock and resistance to natural enemies, particularly against the parasitoid *A. ervi* and the fungal pathogen *Pandora neoaphidis*, but the authors did not test the combined effect of high temperature and natural enemies. Heyworth and Ferrari (2016) examined the effect of *F. symbiotica* alone on protection against parasitoids under conditions of heat stress. They found that under a benign temperature regime, aphids carrying *F. symbiotica* tend to be better protected against the parasitoid than cured aphids. However, when aphids underwent heat shock before being parasitized, aphids carrying *F. symbiotica* were more susceptible than cured aphids. All these studies revealed that symbionts other than *H. defensa* can play an important role in host–parasitoid interaction under heat stress, and that the thermosensitivity of the defensive symbiosis may depend on a combination of symbionts within the same host.

Several field studies have been conducted to examine the influence of heat stress on defensive mutualism. One of these studies showed a negative correlation between *H. defensa* frequencies and mean temperature in various North American localities, confirming the trends reported by the experimental approaches (Doremus *et al.*, 2018). However, Gimmi *et al.* (2023) reported a positive correlation between the presence of *H. defensa* in the aphid *Aphis fabae* and the number of hot days (temperature ≥30°C) in the preceding 8 to 4 weeks, while its frequency dynamics was only weakly correlated with parasitism risk. Quite similar results were reported by Smith *et al.* (2021), who found no relationship between *H. defensa* prevalence and parasitism levels, while showing that temperature was the strongest predictor of endosymbiont presence, with a marked effect of seasonality. These two field studies suggest that rapid seasonal adaptation in multivoltine organisms may be mediated by the multiple effects of heritable bacterial endosymbionts. These somewhat contradictory results between field and experimental studies call for further investigation of the role of *H. defensa* under stressful temperatures and the additional effects associated with the symbiont (e.g. costs, benefits under high temperatures) (Hudson *et al.*, 2024). Although there is evidence that resistance to parasitoid wasps conferred by facultative symbionts is highly temperature dependent, further studies are needed to better assess how rising global temperatures influence defensive mutualisms, what the consequences are for host–parasitoid coevolution, and at what level this may interfere with parasitoid-based pest management strategies.

12.3.5 Other ecological traits carried by facultative symbionts that could influence parasitoidism

Beyond defensive mutualism, facultative symbionts may carry other important ecological traits that can influence parasitoidism. The expression of these effects should undoubtedly be studied from a thermal perspective. For example, the bacterial endosymbiont *R. viridis* can change the body colour of aphids from red to green, which is ecologically important as parasitoid wasps tend to prefer to lay their eggs in green aphids (Losey *et al.*, 1997; Libbrecht *et al.*, 2007). Interestingly, Gu *et al.* (2023) found that this body colour change tends to disappear at higher temperatures. By modulating aphid colour through bacterial symbiosis, temperature could therefore influence the behaviour of parasitoids towards their host.

Facultative symbionts can also influence wing polyphenism. For example, it has been reported that *S. symbiotica* can inhibit the apterization of pea aphids and favour the development of winged forms (Kang *et al.*, 2022). In the context of parasitoidism, this is important because winged forms can disperse to colonize new plants and escape parasitoids. Infected winged aphids can also contribute to parasitoid dispersal (Walton *et al.*, 2011). Winged forms are also reputed to be of lesser quality to parasitoids, although this does not always appear to be true (Pirotte *et al.*, 2018). At the same time, studies have reported that the production of winged forms tends to decrease with increasing temperature (Müller *et al.*, 2001). The combined effect of temperature and the presence of symbionts in wing polyphenism should undoubtedly be the subject of further study.

Facultative symbionts can also influence host behaviour (Hosokawa and Fukatsu, 2020). For example, by analysing the behaviour of aphids in the presence of parasitoids, it was found that aphids infected with *H. defensa* tend to show reduced aggressiveness and escape reactions compared with uninfected aphids (Dion *et al*., 2011). However, this influence on behaviour seems to vary from one symbiont species to another and from one strain to another (Sochard *et al*., 2021). It is therefore conceivable that temperature, by influencing defensive symbiosis, could modify aphid behaviour towards parasitoids.

Finally, as mentioned above, facultative symbionts are often associated with fitness costs for the host. For example, a costly strain of the symbiont *S. symbiotica* hosted by *A. pisum* has an impact on the behavioural response and development of the parasitoid *A. ervi*. Parasitoids tend to choose uninfected hosts and when they develop in infected hosts, they show reduced physical quality, lower emergence rates and a higher proportion of male offspring when developing in infected aphids (Attia *et al*., 2022). This bias in sex ratio is an important consideration in biological control with parasitoids, as it can lead to cascading effects on populations and even at community level (Monticelli *et al*., 2019). If rising temperatures increase the frequency of certain symbionts and this combination degrades host quality for parasitoids, the result could be a skewed sex ratio among parasitoids, favouring males and thus compromising the reproductive fitness of parasitoid populations.

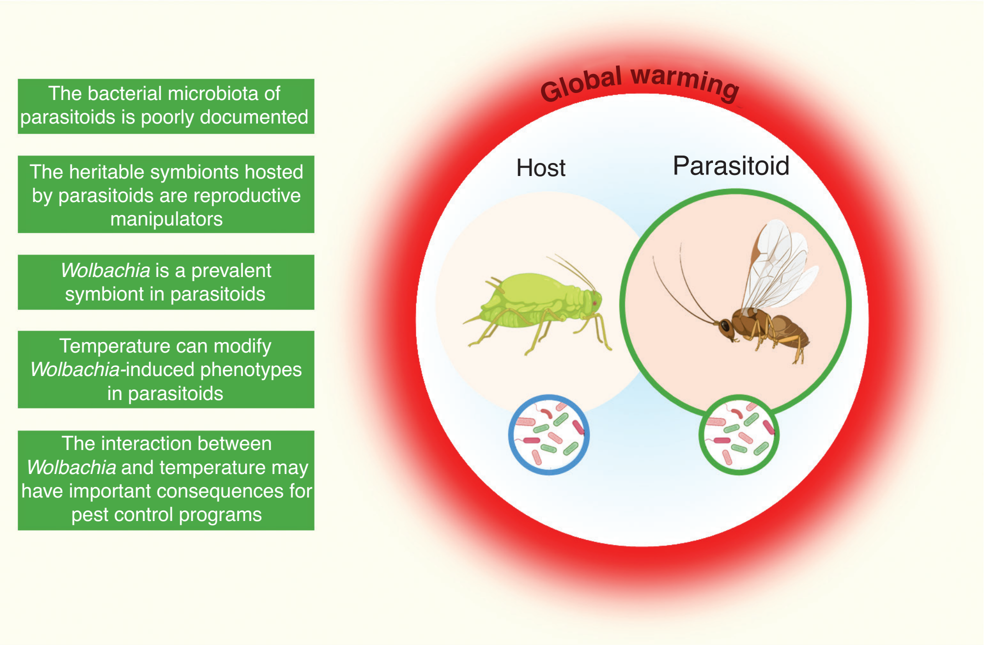
12.4 Parasitoid Microbiota Diversity and Thermal Considerations for Biological Control

12.4.1 Bacterial symbionts associated with parasitoids are mainly reproductive manipulators

By regulating host populations and their dynamics, parasitoids have a strong influence on ecosystems and are key players in crop pest management (Fei *et al*., 2023). Most of them are Hymenoptera, with a parasitic larval stage dependent on a host insect (Mills, 2009). Like most insects, parasitoids host a microbial community (viruses, fungi and bacteria) and these microbial partners influence their life-history traits and more generally their evolutionary ecology (Dicke *et al*., 2020). While the virobiota of parasitoids has been well studied (Beckage and Drezen, 2011; Dicke *et al*., 2020), the bacterial dimension of their microbiota remains poorly documented (Zouache *et al*., 2009; Brucker and Bordenstein, 2012; Nedoluzhko *et al*., 2017). The main heritable symbionts identified in parasitoids to date belong to genera known to have the ability to manipulate the host reproduction, such as *Spiroplasma*, *Cardinium*, *Rickettsia*, *Arsenophonus* and *Wolbachia*, the most frequent symbiont in these insects (Fig. 12.3) (Werren, 1997; Engelstädter and Hurst, 2009; Vavre *et al*., 2009; Taylor *et al*., 2011; Pollmann *et al*., 2022).

12.4.2 *Wolbachia pipientis* is the most common heritable symbiont among parasitoids

Wolbachia pipientis (Alphaproteobacteria) is the most widespread insect symbiont, present in around two-thirds of all insect species, including many parasitoid species (Hilgenboecker *et al*., 2008). This symbiont species is particularly well known for manipulating host reproduction to promote its own spread within insect populations by various strategies such as feminization, male-killing, induction of pathogenesis or cytoplasmic incompatibility (Werren *et al*., 2008; Kaur *et al*., 2021). In parasitoids, two of these strategies have been reported: induction of pathogenesis or cytoplasmic incompatibility. Some strains have been reported to favour thelytokous parthenogenesis, thus preventing the production of males. This was first reported in *Trichogramma* spp. (Hymenoptera: Trichogrammatidae), egg parasitoids widely used for biocontrol of certain lepidopteran pests (Stouthamer *et al*., 1990; 1993), but also in species of the families Pteromalidae (Stouthamer *et al*., 1993), Aphelinidae (Zchori-Fein *et al*., 1995) and Scelionidae (Arakaki *et al*., 2000). Despite lower fecundity, thelytokous *Trichogramma* are often considered to be more effective biological control agents than uninfected arrhenotokous strains because all offspring are female, thus accelerating population growth and reducing production costs (Silva *et al*., 2000). It is therefore in the



The bacterial microbiota of parasitoids is poorly documented

The heritable symbionts hosted by parasitoids are reproductive manipulators

Wolbachia is a prevalent symbiont in parasitoids

Temperature can modify *Wolbachia*-induced phenotypes in parasitoids

The interaction between *Wolbachia* and temperature may have important consequences for pest control programs

Fig. 12.3. The diversity of parasitoids' bacterial microbiota must be considered in biological control programmes.

interest of biological control to have *Wolbachia*-infected control agents.

In parasitoids, *Wolbachia* can also cause cytoplasmic incompatibility (CI), a phenomenon resulting in high embryonic mortality when mating occurs between infected males and uninfected females due to sperm modifications, as reported in the parasitoid *Encarsia inaron* (Hymenoptera: Aphelinidae) (White *et al.*, 2009). *Wolbachia* maintains a high prevalence in insect populations thanks to its efficient vertical transmission rates (typically 100%), its ability to manipulate host reproduction and its propensity for horizontal transmission between species that are sometimes phylogenetically far apart. This is particularly true for parasitoids, due to the close interaction maintained with the host, as first demonstrated by Werren *et al.* (1997) with *Nasonia vitripennis* (Hymenoptera: Pteromalidae) and its fly host. Superparasitism, i.e. the oviposition behaviour of parasitoid females that lay their eggs in an already parasitized host, also appears to be a cause of horizontal transmission when infected and uninfected larvae are in the same host egg, as reported by Huigens *et al.* (2000).

Beyond the effects of manipulating parasitoid reproduction, *Wolbachia* can also have an impact on the fitness of these insects. In the *Drosophila* parasitoid wasp *Leptopilina heterotoma* (Hymenoptera: Figitidae), *Wolbachia* can significantly decrease certain fitness traits such as fecundity, host survival and locomotor performance (Fleury *et al.*, 2000). Recent evidence suggests that *Wolbachia* may have an impact on mating preferences in parasitoid wasps, by making infected females less selective in their choice of mating, but the actual implications of decrease in female selectivity by *Wolbachia* are not yet clear (Amini *et al.*, 2024). In very rare cases, the *Wolbachia*–parasitoid association may have evolved into a strictly mutualistic relationship, as shown by Dedeine *et al.* (2001) in *A. tabida*, where the presence of *Wolbachia* strain *w*Atab3 became necessary for host oogenesis. This is the only reported case, and the extent of *Wolbachia*-based obligate mutualism in parasitoids remains unknown.

12.4.3 *Wolbachia*-temperature interaction: Implications for the host parasitoid

The interaction between *Wolbachia* and temperature can have implications for the parasitoid host at several levels. First, *Wolbachia* tends to influence the temperature preference of host insects. This has mainly been demonstrated in *Drosophila* (Truitt *et al.*, 2019; Hague *et al.*, 2020; Ferguson *et al.*, 2024). Hague *et al.* (2020) demonstrated that these effects are strain dependent. *Drosophila* flies' hosts tend to prefer cooler or warmer temperatures. For example, some *Wolbachia* strains appear to have the ability to increase insect tolerance to heat stress, as has been found in *Drosophila melanogaster* (Diptera: Drosophilidae) where *Wolbachia* do so by stimulating dopamine metabolism (Gruntenko *et al.*, 2017; Burdina *et al.*, 2021). However, Ferguson *et al.* (2024) reported opposite results: they found that *Wolbachia* infection has a negative impact on heat tolerance in *Drosophila simulans* (Diptera: Drosophilidae). The impact of *Wolbachia* on host heat tolerance undoubtedly depends on the genotype of both host and symbiont. Results concerning the impact of *Wolbachia* on temperature preference and heat tolerance come mainly from the *Drosophila* model but no data are available for parasitoids. Yet this is a crucial issue to address in the context of biological control of pests under global warming. Testing the influence of *Wolbachia* on the temperature preference and heat tolerance of parasitoids is an area for future study.

12.4.4 Effect of temperature on *Wolbachia*-induced phenotypes

Numerous studies have examined the impact of the thermal environment on the expression of parasitic reproductive phenotypes due to *Wolbachia*. While most results have been obtained on *Drosophila* flies (Corbin *et al.*, 2017), some studies have been conducted on parasitoid wasps (Girin and Boulétreau, 1995; Pintureau *et al.*, 1999; Mouton *et al.*, 2006; 2007; Bordenstein and Bordenstein, 2011; Zhou *et al.*, 2019; Power *et al.*, 2022). In general, high temperatures tend to reduce the expression of the parasitic reproductive phenotypes. For example, Bordenstein and Bordenstein (2011) reported that high temperatures reduced *Wolbachia* densities and the penetrance of cytoplasmic incompatibility in the parasitoid wasp *N. vitripennis*. Mouton *et al.* (2006) also investigated the impact of temperature on cytoplasmic incompatibility in *L. heterotoma*, but although they reported temperature-dependent density variability, they found no change in the expression of cytoplasmic incompatibility under the different temperature regimes applied, but perhaps because they did not test the critical warm conditions for the *Wolbachia* strain. In the thelytokous species *Trichogramma cordubensis* (Hymenoptera: Trichogrammatidae) infected by *Wolbachia*, high-temperature treatments (30°C) tend to 'inactivate' the symbiont, resulting in induction of male production (Pintureau *et al.*, 1999). In *Ooencyrtus mirus* (Hymenoptera: Encyrtidae), Power *et al.* (2022) found that the sex ratio was skewed in favour of males in offspring from *Wolbachia*-infected parents reared at 34°C and 36°C (high temperatures). In this species, the population growth rate without male generation is highest at 30°C.

These studies teach us some important lessons for biological control programmes. First, *Wolbachia* can be hijacked to produce more female parasitoids, the sex that enables pest control in the field. Second, temperature conditions are essential for the expression of *Wolbachia*-induced phenotypes. Understanding how temperature influences *Wolbachia*-induced phenotypes is therefore essential for optimizing the mass rearing of parasitoids dedicated for pest control.

One thing to bear in mind is that symbiont within-host density is an important parameter in the interaction between the host insect and its symbiont because it can significantly influence transmission and the amplitude of expression of the symbiont-induced phenotypes (Martinez *et al.*, 2017; López-Madrigal and Duarte, 2019). For the insect host, the higher the density of symbionts, the greater the fitness costs can be (Chrostek and Teixeira, 2015; Martinez *et al.*, 2017; Parker *et al.*, 2021). However, at the same time, a high symbiont density can also mean greater benefits for the host, as it correlates with the degree of expression of induced phenotypes (Martinez *et al.*, 2017; López-Madrigal and

Duarte, 2019; Parker *et al.*, 2021; Drew and King, 2022). And temperature is a highly influential parameter when it comes to within-host density symbiont (Mouton *et al.*, 2006; Anbutsu *et al.*, 2008; Doremus *et al.*, 2018). Thus, understanding the thermal niche of heritable symbionts and the influence of temperature on their within-host density is crucial for grasping how the costs, benefits and parasitic reproductive phenotypes are expressed in parasitoid wasps and their hosts, and finally for understanding how this modulates parasitoidism with the aim of optimizing biological control in a context of climate change.

12.5 Concluding Remarks and Perspectives

Global change is causing a general rise in temperatures and a greater incidence of extreme climatic events. In this context, insects, which are ectotherms and therefore particularly sensitive to thermal conditions, are exposed to a greater frequency of heat stress events, which could destabilize the coevolutionary processes in which they are involved and which have been shaped over millions of years in a relatively stable climatic context (van Baaren *et al.*, 2010; Harvey *et al.*, 2023). In this context, host–parasitoid relationships could be turned upside down: the life-history traits, development times and metabolism of hosts and parasitoids could be affected. On a broader scale, the geographical distribution of species involved in these interactions and phenological synchronization between trophic levels could be disrupted. The aim of this chapter is to highlight the importance of invisible players that have a key role in the evolutionary ecology of their hosts and can influence parasitoidism: heritable symbionts. Indeed, temperature highly influences the effects these microbes can have on their host, and therefore host–parasitoid interactions.

The question that motivates our discussion is: 'How can temperature influence parasitoidism through heritable symbiosis?'. Our review highlights the difficulty of predicting this. Indeed, the diversity of the microbial players involved is great, and the nature of the interactions they can have with their host on the parasitism–mutualism evolutionary continuum can be extremely variable, depending on various genetic and environmental factors. Heat tolerance of insects can be limited by their endosymbionts. This is especially true for insects harbouring obligate symbionts. In a warming environment, the thermosensitivity of the obligate symbionts of many pests could lead to a reduction in their quality for parasitoids and/or lead to their geographical redistribution. At the same time, facultative symbionts can change this paradigm. Some symbionts can rescue old, heat-sensitive symbioses while others, by being costly to their host, inflict on them a double penalty in a stressful environment (Renoz *et al.*, 2019). Defensive symbiosis can also be disrupted, perhaps to the advantage of parasitoids. Reproductive manipulators, such as *Wolbachia*, which are widespread in parasitoids, could also be impacted by thermal changes. This could have consequences for the sex ratio of parasitoid populations, depending on the species and the thermal niche of their symbionts. From an applied point of view, this is a crucial aspect that needs to be further studied; a better understanding of the thermal niches of reproductive manipulators is needed for optimized, more effective biological control. *Wolbachia* is undoubtedly an important tool to be considered in biological control (and still too neglected) to increase yields in terms of mass production of parasitoid females.

On the other hand, both the host and the parasitoid may carry symbionts that react in opposite directions to temperature increases and extremes. Determining the fate of such systems with the information we currently have is virtually impossible. To resolve these questions, complex interaction experiments need to be set up, for example with aphids carrying *S. symbiotica* facing a parasitoid carrying *Wolbachia*, under fluctuating temperatures, with all the necessary positive and negative controls. This type of experiment is difficult but not impossible to carry out in a microcosm, for example, and it is also essential if we want to make predictions that will hold up in the future.

In the same way, one aspect that is sorely lacking is the absence of long-term data on changes in the various components of trophic levels in the field. Field studies that consider thermal or seasonal variables and evaluate the success of biological control programmes in the context of aphid–parasitoid–microbiota interactions are still lacking (Gimmi *et al.*, 2023). Moreover, among the sample of field studies conducted, the trend appears to be surprisingly reversed from interpretations supported by laboratory results (Smith *et al.*, 2015; Doremus *et al.*, 2018; Hudson *et al.*, 2024). It is imperative to go out into the field and monitor changes in pest populations and their natural enemies, as well as the symbionts they contain. Metagenomic/metabarcoding approaches currently provide us with the tools we need to do this but require us to set up sampling protocols involving different types of organism that may be involved. In addition, studies should focus more on the transmission of endosymbionts under natural conditions to better understand the dynamics of infection within host populations.

One of the key factors in the future evolution of climate is the speed of change. This speed is such that it generates selection pressures that are too severe to enable adaptation, and selection could therefore lead to extinction. Phenotypic plasticity, especially thermal plasticity, should allow faster adaptation to these changes and may even be heritable (Svensson *et al.*, 2020). Future populations should therefore be characterized by greater phenotypic plasticity in response to temperature. In this case, however, it is clear that selection pressures are exerted on both the host and its obligate and facultative symbionts. Selection should therefore favour groups of organisms that allow the host and its partners to develop, survive and be as fertile as possible under stress conditions; in other words, greater phenotypic plasticity of the holobiont (i.e. the assemblage of a host and the many other species living in or around it). Similarly, parasitoids also exert a selection pressure on the composition of their host populations by favouring those that harbour protective symbionts, leading to dynamic coevolution between these species. In an environment where warmer temperatures become the norm, symbiont-induced genotypes conferring better heat resistance are likely to be selected. By a cascade effect, associations of strains that are both protective against parasitoids and heat tolerant will become more frequent. These coinfections should have an impact on the physical quality and fecundity of the pests. In short, we could be witnessing a subtle interplay of the effects of high temperatures, which can result in faster pest population growth because the age of first reproduction is earlier and the host is protected by the endosymbionts it carries.

Finally, we have dealt here with only a small part of the possible interactions, and only with certain organisms. We did not cover the case of prey–predator interactions, although many predators used in biological control are infected with *Wolbachia* (Sokolova *et al.*, 2002; Li *et al.*, 2021), and there is evidence that prey symbionts have an impact on predator fitness (Kovacs *et al.*, 2017). Also, the question of the virobiota is only just beginning to be addressed, although it has a considerable influence on the life-history traits and behaviour of the insects concerned (Murhububa *et al.*, 2024). Moreover, at the level of insect vectors, there seems to be a clear potential interaction between the viruses transmitted and the presence of symbionts. We lack data to understand these interactions and the influence that temperature fluctuations or an increase in mean temperature could have on them.

Fortunately, more and more data are accumulating that will eventually enable us to make predictions and perhaps even envisage new biological control techniques directly involving micro-organisms that live in close interaction with their hosts and thus modify their plastic response capacity to sudden variations in environmental conditions.

Acknowledgement

This paper was made possible thanks to the grant that Thierry Hance received from the SPWFeder-Interreg TransPest project (grant number 0100226).

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