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**Priyanshu Pawar**
Ph.D. Scholar, Department of Agricultural Entomology, Jawaharlal Nehru Krishi Vishwavidyalaya, Jabalpur, Madhya Pradesh, India

**Nawale Jayant Shyamrao**
SRF, Department of Agricultural Entomology, Mahatma Phule Krishi Vidyapeeth Rahuri, Maharashtra, India

**DK Narwade**
Ph.D. Scholar, Department of Agricultural Entomology, Mahatma Phule Krishi Vidyapeeth Rahuri, Maharashtra, India

**Sunita Yadav**
Ph.D. Scholar, Department of Agricultural Entomology, Jawaharlal Nehru Krishi Vishwavidyalaya, Jabalpur, Madhya Pradesh, India

**Pooja Kumari**
Ph.D. Scholar, Department of Agricultural Entomology, CCS HAU, Hisar, Haryana, India

**Tejaswee Kattumulla**
M.Sc. Scholar, Department of Agricultural Entomology, Kerala Agricultural University, Kerala India

**Corresponding Author:**
**Nawale Jayant Shyamrao**
SRF, Department of Agricultural Entomology, Mahatma Phule Krishi Vidyapeeth Rahuri, Maharashtra, India

# A symbiont-mediated adaptation of aphids to environmental change

**Priyanshu Pawar, Nawale Jayant Shyamrao, DK Narwade, Sunita Yadav, Pooja Kumari and Tejaswee Kattumulla**

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**Abstract**
Aphids (Hemiptera: Aphididae) are a globally important group of herbivores whose ecology and evolutionary trajectories are strongly shaped by intimate associations with bacterial endosymbionts. Their success as pests is not solely due to their high reproductive potential and phenotypic plasticity but is also intricately tied to associations with bacterial endosymbionts. The obligatory symbiont *Buchnera aphidicola*, which is maintained by all aphids, is vital to host nutrition and thermal physiology because it supplies crucial amino acids that are absent in phloem sap. Furthermore, a large number of species are home to facultative (secondary) symbionts, including *Serratia symbiotica*, *Regiella insecticola*, and *Hamiltonella defensa*. These facultative partners can confer conditional benefits, including enhanced tolerance to heat stress, protection against parasitoid wasps and microbial pathogens, and shifts in host plant utilization. In a rapidly changing environment — driven by warming, altered seasonality, and anthropogenic landscape change — symbiont composition, density, and genotype can alter aphid fitness and population dynamics, sometimes in context-dependent and genotype-specific ways. This review synthesizes current knowledge on how aphid–symbiont partnerships mediate adaptation to abiotic (temperature) and biotic (parasitoids, predators, host plants) stressors, discusses mechanistic bases (metabolic provisioning, toxin production, immune modulation), highlights ecological and evolutionary consequences, and outlines key gaps and future research directions, including implications for pest management.

**Keywords:** Aphids, *Buchnera*, *Hamiltonella*, *Regiella*, facultative symbionts, climate change, adaptation

## Introduction

The rapid expansion of insect pest populations due to climate change poses a significant challenge to contemporary agriculture and food security. This escalating issue underscores the urgent need for innovative monitoring technologies and comprehensive research to uncover the underlying mechanisms of pest proliferation and to design effective, sustainable management strategies (Subedi *et al.*, 2023a) [33]. Among insect pests, aphids (Hemiptera: Aphididae) constitute an ancient yet remarkably adaptable group. Their rapid asexual reproduction has enabled them to thrive globally, emerging as major pests across agricultural, horticultural, and forestry ecosystems, and leading to annual crop losses amounting to billions of US dollars (Skvarla *et al.*, 2017) [32]. The prevalence of widespread synthetic pesticide resistance among these pests further complicates their control, highlighting the urgent need to explore alternative management approaches (Loxdale *et al.*, 2020) [19]. Abiotic factors, particularly temperature, play a crucial role in shaping insect population dynamics, as they significantly impact reproduction, survival rates, fecundity, number of generations (voltinism), interactions with host plants, predator-prey relationships, and patterns of dispersal (Sunil *et al.*, 2023) [34]. Climate change intensifies these influences; however, only a limited number of studies have systematically examined the range expansion and population dynamics of aphid pest species in response to changing climatic conditions (Subedi *et al.*, 2023; Wu *et al.*, 2020) [33, 38]. Among these, the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), is recognized as a major global pest of cereal crops, particularly maize (Zea mays L.). In recent years, its populations have markedly increased across European maize-growing regions including Germany, Poland, Hungary, and Romania resulting in substantial economic losses due to extensive crop damage (Blackman and Eastop, 2000; Csorba *et al.*, 2021, 2022; Emden and Harrington, 2007, 2017) [2, 35]. Currently, control measures for this pest rely largely on synthetic insecticides and hymenopterous parasitoids, with no fully effective monitoring or alternative control technologies yet available (Van Emden and Harrington, 2017) [35]. An additional layer of complexity in aphid population dynamics involves their close associations with bacterial endosymbionts. These symbionts, both obligate (e.g., *Buchnera aphidicola*) and facultative (e.g., *Hamiltonella defensa*, *Regiella insecticola*, *Serratia symbiotica*, *Wolbachia* spp.), contribute to aphid adaptation by influencing thermal tolerance, host plant utilization, defense against natural enemies, and nutrient metabolism (Douglas, 2016; Zepeda-Paulo and Lavandero, 2021) [11, 39]. For example, *B. aphidicola* is implicated in aphid heat sensitivity through modulation of small heat shock proteins, while *S. symbiotica* enhances tolerance to heat stress and aids in nutrient processing (Montllor *et al.*, 2002; Zhang *et al*., 2019; Skaljac *et al.*, 2019) [22, 40, 31]. Similarly, facultative symbionts such as *R. insecticola* and *H. defensa* provide selective advantages against parasitoids or influence host plant performance, highlighting their role in aphid ecological success (Oliver *et al*., 2005; Ramírez-Cáceres *et al*., 2019) [25, 27].

Understanding the interplay between abiotic stressors, such as elevated temperatures under climate change, and biotic factors, including symbionts and pathogens, is therefore critical for developing sustainable aphid management strategies. In this review, we consolidate existing research on how aphids respond to heat stress and examine the influence of bacterial endosymbionts in shaping these responses, with particular emphasis on the economically important corn leaf aphid, *R. maidis*. By integrating insights on host–symbiont interactions and environmental influences, we aim to highlight potential avenues for improving aphid control in a warming world.

## Types of aphid endosymbionts and their basic roles

### Obligate symbiont: *Buchnera aphidicola*

Obligate symbionts are essential for the survival of their hosts and are vertically transmitted from mother to offspring. Among these, the obligate endosymbiont *Buchnera aphidicola* (Enterobacterales: Erwiniaceae) belongs to the γ-proteobacteria and plays a vital role in maintaining host physiology (Bright, M. and Bulgheresi, S., 2010) [3]. This obligate endosymbiotic bacterium supplies its host with vital nutrients, vitamins, and other metabolites that the host cannot synthesize independently, and may also enhance the host's efficiency in nutrient assimilation and overall feeding performance (Salem, H. and Kaltenpoth, M., 2022) [28]. Variation among *Buchnera* strains and their densities within hosts influences host physiology and can affect tolerance to temperature stress through differences in protein stability, gene expression, and metabolic support. *Buchnera* is thermally sensitive, and that both *Buchnera* genotype and titre modulate aphid performance under heat stress.

### Facultative (secondary) symbionts

Facultative γ-proteobacterial symbionts, unlike obligate ones, are not essential for all hosts and can influence their hosts in diverse ways—yielding beneficial, detrimental, or neutral outcomes (Guo, J. *et al.*, 2017) [14]. Overall, these symbionts are not required for the host's normal growth, development, or reproductive processes (Douglas, A. E., 2015) [10]. Facultative symbionts contribute to the acquisition and transmission of key ecological traits in their hosts through horizontal gene transfer (HGT). These traits include enhanced defense against parasitoids, improved thermal tolerance (Montllor *et al.*, 2002; Russell and Moran, 2006) [22, 16], and increased resistance to fungal pathogens (Scarborough *et al.*, 2005; Łukasik *et al.*, 2015) [29, 20]. Major examples include:

- *Hamiltonella defensa* — often confers protection against parasitoid wasps, a benefit that in many systems depends on associated bacteriophages (APSE) that encode toxins. The protection is strain-specific and can show high specificity toward particular parasitoid species.
- *Regiella insecticola* — linked to altered host plant use and protection against some natural enemies; effects vary by strain and aphid species.
- *Serratia symbiotica*, *Arsenophonus*, *Spiroplasma* and others — can affect thermal tolerance, metabolism, resistance to pathogens, or interact with host ecology in complex ways.

## Mechanisms by which symbionts mediate adaptation

### Nutritional and metabolic provisioning

*Buchnera* synthesizes essential amino acids (e.g., tryptophan, leucine) and vitamins, directly altering host nutrition and fecundity. Changes in *Buchnera* gene expression or numbers can shift aphid developmental rates and reproduction under resource limitation or thermal stress.

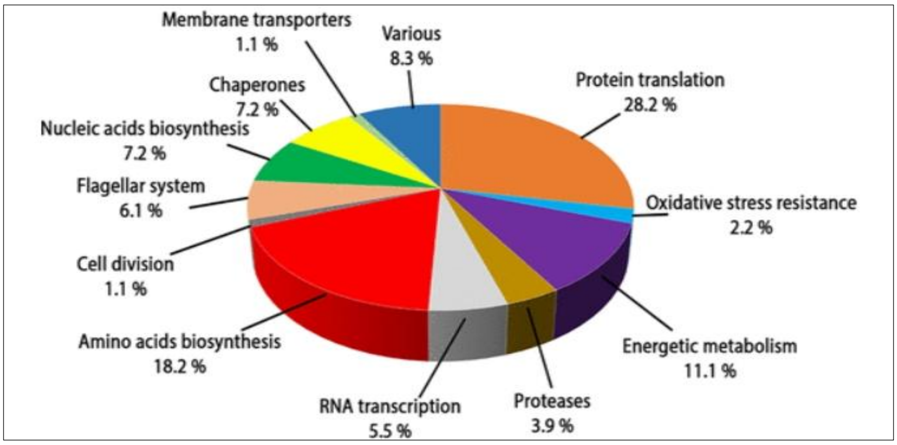


**Fig 1:** Shows Functional classification of all *B. aphidicola* proteins

**Thermal tolerance and temperature sensitivity**

Symbionts affect aphid responses to temperature extremes through multiple mechanisms. To begin with, *Buchnera* proteins exhibit reduced thermal stability when compared to their homologous counterparts found in closely related free-living bacterial species (van Ham *et al.*, 2003) [36]. Second, similar to other insect endosymbionts (Kupper *et al.*, 2014) [18], *Buchnera* continuously produces elevated levels of heat shock proteins, including GroEL and DnaK, which play a crucial role in restoring misfolded proteins during periods of thermal stress (Fares *et al.*, 2002) [13]. Functional expression of *Buchnera* enzymes in Escherichia coli requires either GroEL overexpression (Huang *et al.*, 2008) [15] or growth at lower temperatures (Price and Wilson, 2014) [12]. Thirdly, specific *Buchnera* genotypes associated with the pea aphid (*Acyrthosiphon pisum*) display pronounced sensitivity to elevated temperatures, which has been linked to a recurrent mutation in the heat shock promoter region of ibpA, a gene encoding a universal small heat shock protein (Burke *et al.*, 2010; Dunbar *et al.*, 2007) [4, 12]. Aphids possessing this particular haplotype experience a substantial or complete loss of *Buchnera* populations when exposed to heat stress, leading to a marked decline in reproductive capacity; experimental substitution of this haplotype has been shown to improve thermal tolerance (Moran and Yun, 2015) [23]. Furthermore, the facultative symbiont *Serratia symbiotica* has been found to alleviate heat-induced damage in *A. pisum* (Montllor *et al.*, 2002; Russell and Moran, 2006) [22, 16], most likely by stabilizing *Buchnera* populations and synthesizing protective metabolites (Burke *et al.*, 2010) [5]. Finally, in some cases, *Buchnera* densities in aphids decline at elevated temperatures (Chen *et al.*, 2009) [7].

**Defensive toxins and bacteriophages**

Protection against parasitoids is commonly mediated by symbiont-encoded toxins or toxin-encoding bacteriophages (e.g., APSE associated with *Hamiltonella*). The presence/absence and genotype of APSE phages across *Hamiltonella* strains determines efficacy and specificity of defense against different parasitoid species. This genomic mosaicism explains why symbiont-conferred resistance often displays strong genotype × genotype specificity.

**Immune and physiological modulation**

Some symbionts influence host immune function—such as haemocyte counts or immune gene expression—affecting susceptibility to pathogens and natural enemies, with these effects often changing under environmental stress. Such immunomodulation can create trade-offs between growth, reproduction, and defense. Recent research indicates that certain facultative symbionts engage in direct interactions with the aphid's innate immune system. For instance, aphids harboring specific strains of *Regiella* display a reduction in circulating immune cell counts (Schmitz *et al.*, 2012) [30] along with decreased expression and protein levels of phenoloxidase, a key enzyme in immune defense (Nichols *et al.*, 2021; Luo *et al.*, 2020) [24, 21]. Moreover, RNAi-mediated suppression of phenoloxidase (PO1) has been shown to elevate *Regiella* densities (Nichols *et al.*, 2021) [24]. Similarly, certain strains of the facultative symbiont *Hamiltonella defensa* can proliferate to high densities while concurrently downregulating host immune-related genes (Kaech *et al.*, 2021) [17].

**Behavioural and chemical ecology changes**

Symbionts can change aphid behavior (e.g., feeding, movement) and plant volatile emission profiles, potentially altering attraction of natural enemies or vectors and feeding preferences for host plants (Fig.2). Such changes can influence transmission of plant viruses and the ecological networks aphids inhabit.

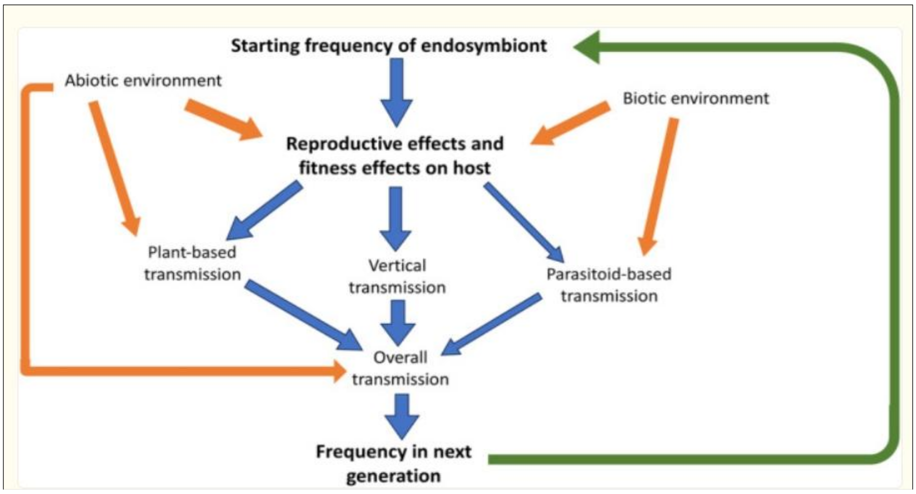


**Fig 2:** Endosymbiont population dynamics in natural ecosystems.

Fig 2. In natural ecosystems, the dynamics of endosymbiont populations are governed by factors that affect their transmission, replication, and overall influence on host fitness. These interactions are intricately connected to both abiotic and biotic components of the surrounding environment.

**Context dependence: environment × symbiont × host interactions**

Symbiont effects are rarely absolute; instead, they vary with abiotic context (temperature, humidity), biotic context (parasitoid community composition, predators, host plant species), and host/symbiont genotype. Key patterns from experiments and field surveys include:

- **Temperature can flip costs/benefits:** Rising temperatures can alter the balance of costs and benefits associated with harboring facultative symbionts. In some cases, warming reduces both the protective advantages and the reproductive penalties of carrying such microbes, while in others, heat stress compromises *Buchnera* function, lowering overall aphid performance. Consequently, climate change can unpredictably reshape the selective pressures influencing symbiont prevalence. For example, fluctuations in temperature can modify the level of parasitoid resistance conferred by *Hamiltonella defensa* in aphids and by *Spiroplasma* in drosophilids (Bensadia *et al.*, 2006) [1], as well as influence the antiviral protection mediated by *Wolbachia* in drosophilid hosts (Chrostek *et al.*, 2020) [6]. Similarly, symbiont-driven detoxification processes that contribute to insecticide resistance—such as *Wolbachia* in planthoppers—can be thermally sensitive (Zhang *et al*., 2021) [41].

- **Specificity of defensive protection:** *Hamiltonella defensa* provides resistance against parasitoid wasps by producing phage-encoded toxins integrated into its genome. However, this protection is often highly specific: strains that defend against a dominant parasitoid species in one region may fail to provide benefits elsewhere, shaping geographic variation in symbiont frequencies. In addition, harboring *Hamiltonella* can impose physiological costs, such as reduced longevity or increased mortality in some aphid species (Wernegreen, 2012) [37]. Different *Hamiltonella* genotypes also vary in their effectiveness against particular parasitoid species, further influencing local host–parasite dynamics (Moran and Yun, 2015) [23].
- **Trade-offs and pleiotropy:** Symbiont conferred resistance can come at the expense of growth or reproduction under some conditions; these trade-offs influence the maintenance and spread of symbionts across environmental gradients.

## Eco-Evolutionary Perspectives on Aphid Management and Conservation

Symbiont-mediated adaptation fundamentally reshapes strategies for managing aphid populations, particularly when evaluated through the interconnected lenses of environmental, regulatory, management, and stochastic factors (Fig.3). Defensive endosymbionts, such as *Hamiltonella defensa*, can significantly reduce the efficacy of biological control agents like parasitoid wasps by conferring resistance traits to their hosts. These protective effects may be amplified or diminished depending on abiotic conditions; for example, elevated temperatures associated with climate change can interact with symbiont physiology to alter both the strength and stability of defensive benefits. Similarly, changes in cropping systems and reduced plant diversity can shift the balance between aphids, their symbionts, and natural enemies, further complicating biological control outcomes. Agricultural management practices are equally influential, as inputs like fertilizers, pesticides, and irrigation not only directly impact aphid population dynamics but also shape the distribution, abundance, and functional performance of their associated symbionts. Crop rotation and intercropping strategies may alter host plant availability and indirectly shape symbiont-mediated fitness outcomes. On a broader scale, policy and regulatory frameworks—such as pesticide bans, the promotion of integrated pest management (IPM), or incentives for habitat diversification—intervene to shape the ecological context in which aphid–symbiont interactions unfold. Stochastic forces, including extreme climatic events, novel invasive weeds, or unexpected pathogen outbreaks, add additional layers of complexity and unpredictability.

In light of these interacting pressures, pest management demands a systems-based approach that explicitly incorporates the ecological and evolutionary roles of endosymbionts. Promising avenues include manipulating landscape features to enhance natural enemy efficacy, integrating symbiont surveillance into pest monitoring programs, and developing novel interventions that disrupt symbiont-derived defenses, such as bacteriophage-targeted tools. By combining ecological, regulatory, and biological insights, future management strategies will be better equipped to anticipate shifts in aphid populations, safeguard biological control efficacy, and promote the long-term resilience and sustainability of agroecosystems.

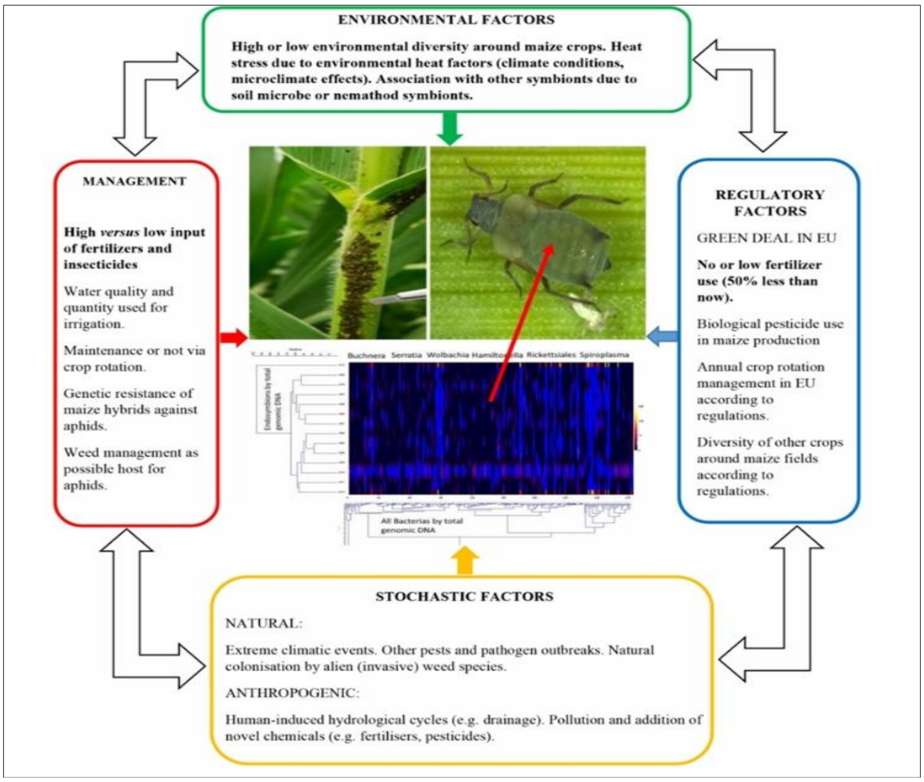


**Fig 3:** Schematic representation of the main factors influencing maize–aphid–symbiont interactions.

## Conclusions

Bacterial endosymbionts are increasingly recognized as pivotal drivers of aphid responses to environmental change. The obligate symbiont *Buchnera aphidicola* plays a vital role in aphid nutrition by synthesizing essential amino acids and vitamins that are lacking in the phloem sap on which the host feeds. However, *Buchnera* is also thermally fragile, and its loss or reduced functionality at elevated temperatures can directly constrain aphid performance and limit range expansion under warming climates. Similarly, facultative (secondary) symbionts such as *Hamiltonella defensa*, *Regiella insecticola*, and *Serratia symbiotica* provide context-dependent advantages that go beyond nutritional support. These benefits include increased resistance to parasitoid wasps and fungal pathogens, as well as, in certain cases, improved tolerance to thermal stress and adaptability to different host plants. Nevertheless, such benefits often come at fitness costs, and their expression is strongly context-dependent, varying across environments, aphid genotypes, and community interactions. As global change accelerates through climate warming, altered precipitation regimes, intensified agriculture, and habitat modification, the selective pressures governing symbiont maintenance and spread are expected to shift. This will generate complex eco-evolutionary dynamics in aphid populations, shaping not only their abundance and distribution but also their interactions with natural enemies and crops. For pest management, these dynamics pose both challenges and opportunities: defensive symbionts may undermine classical biological control strategies, yet symbiont biology itself may offer novel intervention targets. To anticipate and guide these outcomes, future research must integrate comparative genomics, mechanistic physiology, community ecology, and predictive modeling. Such interdisciplinary approaches will be essential to understand, forecast, and ultimately manage the consequences of symbiont-mediated adaptation in aphids under rapid environmental change.

## Author Declarations

The authors declare that they have no known conflicts of interest associated with this publication.

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