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# 昆虫共生菌调控宿主温度适应性研究进展

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**摘要:** 昆虫普遍会感染多种共生菌,共生菌在其宿主的生理、生态及进化等方面发挥着至关重要的作用。近年来大量研究表明,昆虫与共生菌的共生关系易受环境温度变化的影响;同时,共生菌直接或间接参与调控昆虫宿主对温度胁迫的响应。该文综述了温度对昆虫与共生菌共生关系的影响和昆虫共生菌在宿主温度适应中的作用、潜在机制及其生态学意义;并基于当前共生菌调控昆虫温度适应性方面的研究进展,建议后续可聚焦于自然条件下变温胁迫对昆虫与共生菌互作的影响、共生菌调控昆虫适应性进化的行为及分子机制和基于共生菌的害虫防治新手段开发与应用等方面开展研究。该文可为全球气候变化和极端温度频发背景下昆虫与共生菌的协同进化研究以及利用共生菌进行害虫防控工作提供参考。

**关键词:** 昆虫; 共生菌; 温度; 种间互作; 生态适应

## Advances in researches on symbiont-mediated thermal adaption in insects

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**Abstract:** Insects harbor a wide variety of symbionts, which play a crucial role in host physiology, ecology, and evolution. A growing number of studies demonstrate that these insect-bacterial symbioses are susceptible to altered temperature regimes. The host's response to temperature stress is also directly or indirectly influenced by their symbionts. Here, the known effects of temperature on symbioses between insects and symbionts were outlined, and the role of symbionts in host thermal adaptation and the underlying mechanisms as well as their ecological significance were summarized. Considering the research advances in symbiont-mediated thermal adaption in insect hosts, further investigations are recommended as follows: the interactions between insects and symbionts in the natural world with varying temperature stress, the behavioral and molecular mechanisms through which symbiotic bacteria regulate insect host temperature-adaptive evolution, and symbionts as potential tools for pest control. This review provides a reference for understanding the co-evolution between insects and symbionts as well as endosymbiont-mediated pest management in the context of global warming and extreme temperatures.

**Key words:** insect; symbiont; temperature; interspecies interaction; ecological adaptation

昆虫普遍会感染多种共生菌,根据共生菌与宿主的关系可将其分为初级(专性)共生菌和次级(兼性)共生菌(Moran et al.,2008)。初级共生菌与宿主形成严格的共生关系,存在于特化的宿主细胞中,是宿主正常生长发育的基础(Douglas,1998);而次级共生菌分布于宿主的生殖器官、血腔、脂肪体、肌肉、

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神经和肠道等组织中，在宿主种群中呈随机分布（Oliver et al.，2010）。在长期的进化过程中，昆虫与共生菌形成复杂的共生关系，共生菌参与调控宿主的生殖（Werren et al.，2008；Engelstädter & Hurst，2009；郑林宇等，2022）、适合度（Gould et al.，2018）、解毒代谢（Sato et al.，2021；Zhang et al.，2021）、营养合成与代谢（Ju et al.，2020）、抵抗天敌与病毒（Haine，2008；Brownlie & Johnson，2009；Gong et al.，2020）和逆境适应性（Raza et al.，2020）等，在宿主生物学、生理生态及进化过程中发挥着重要作用（Feldhaar，2011；Frago et al.，2012）。

近年来，全球气候的快速变化和极端温度的频繁发生，对物种间的互作关系造成了极大威胁（Hoffmann & Sgro，2011；Abarca & Spahn，2021；Ma et al.，2021）。昆虫与共生菌的互作同样不可避免会受到温度等非生物因子胁迫的影响。大量研究表明，温度胁迫可能会导致昆虫与共生菌共生关系的崩溃，为了维持稳定的共生关系，共生菌基因组快速适应性进化，参与调控宿主对温度胁迫的响应（Sgro et al.，2016；Corbin et al.，2017；Renoz et al.，2019）。本文综述了温度胁迫对昆虫与共生菌互作的影响，总结了昆虫共生菌在增强或约束宿主温度适应性方面的进展，归纳了共生菌调控宿主温度适应性的机制及生态学意义，并对该领域未来的研究方向提出展望，旨在为深入了解全球气候变化和极端温度频发背景下昆虫与共生菌的进化以及利用共生菌防控害虫的研究提供新视角。

## 1 温度胁迫对昆虫与共生菌共生关系的影响

当昆虫与共生菌遭受不利温度胁迫时，共生菌对温度的响应速度通常要快于宿主本身（Pintureau-and & Bolland，2001；Moran，2016）。许多共生菌存在于宿主的特定组织中，其生活方式受到宿主严格限制（Brownlie et al.，2007；Bennett & Moran，2013；Sabath et al.，2013），大多数母系遗传内共生菌，如沃尔巴克氏体 *Wolbachia*、*Blochmannia* 和 *Cardinium* 等对高温敏感（Shan et al.，2014），少数共生菌如螺原体 *Spiroplasma* 等对低温的适应性较差（Osaka et al.，2008）（表1）。温度胁迫首先影响共生菌在宿主体内的复制，进而影响其垂直传播和诱导的生物学表型强度（Doremus et al.，2019）。温度对共生菌与宿主的影响程度取决于宿主种类、宿主发育阶段、温度阈值以及温度处理时间等多种因素的综合作用（Hammer et al.，2021）。当不利温度或处理时间超过一定阈值后，昆虫体内的共生菌丢失，导致昆虫与共生菌的共生关系崩溃。

### 1.1 温度影响共生菌的传播

许多共生菌的传播方式主要是通过亲代到子代的垂直传播方式，不利温度会影响共生菌的传播，导致共生菌丢失，例如蚜虫初级共生菌布赫纳氏菌 *Buchnera* 在短期高温处理后，其滴度降低、菌胞破裂，长期高温处理导致布赫纳氏菌丢失（Zhang et al.，2019；Heyworth et al.，2020）。昆虫体内普遍感染的共生菌沃尔巴克氏体对高温敏感，但在不同的昆虫研究体系中，其阈值存在差异，如三色书虱 *Liposcelis tricolor* 和二斑叶螨 *Tetranychus urticae* 在高温32℃或33℃条件下饲养6代，沃尔巴克氏体在宿主种群中完全消失（van Opijnen & Breeuwer，1999；Jia et al.，2009）。埃及伊蚊 *Aedes aegypti* 经过26~37℃的变温处理后，其体内的沃尔巴克氏体 *w*Mel 和 *w*MelPop-CLA 株系不能正常传代（Ross et al.，2017）。单独感染沃尔巴克氏体的截形叶螨 *T. truncatus* 经35℃处理2代后，种群中沃尔巴克氏体感染率不足20%，而同时感染沃尔巴克氏体和螺原体的截形叶螨经35℃处理4代后沃尔巴克氏体感染率依然高达40%（Zhu et al.，2021）。此外，少数共生菌对低温敏感，如灰暗果蝇 *Drosophila nebulosa* 经18℃处理2代后体内的螺原体完全丢失（Anbutsu et al.，2008），黑腹果蝇 *D. melanogaster* 经16.5℃处理1代后体内的螺原体也丢失（Montenegro & Klaczko，2004）。在截形叶螨中，同时感染沃尔巴克氏体和螺原体的截形叶螨品系经20℃处理2代后，螺原体的感染率约为25%，而单独感染螺原体的截形叶螨品系对20℃不敏感（Zhu et al.，2021）。由此可见，共生菌对高低温的敏感性在不同昆虫系统中存在差异。

### 1.2 温度改变共生菌诱导的生物学表型强度

许多广泛分布在昆虫中的共生菌如沃尔巴克氏体、螺原体和 *Cardinium* 等均能调控宿主的生殖或适合度等生物学表型，包括胞质不亲和（cytoplasmic incompatibility，CI）、杀雄、雌性化和孤雌生殖等作用方式（Werren et al.，2008），而温度胁迫会改变共生菌诱导的生物学表型强度，例如波利尼西亚伊蚊 *A. polynesiensis* 幼虫经32~33℃高温处理5~7 d，其沃尔巴克氏体诱导的CI作用消失（Wright & Wang，1980）；同样，高温也会影响沃尔巴克氏体对麦蛾柔茧蜂 *Habrobracon hebetor* 诱导的CI强度（Nasehi et al.，2022）；在苏氏恩蚜小蜂 *Encarsia suzannae* 中，高

温降低了共生菌 *Cardinium* 诱导的CI强度（Doremus et al.，2019）；豆秆野螟 *Ostrinia scapulalis* 幼虫在63℃高温下暴露20~30 min，沃尔巴克氏体的杀雄表型受到抑制（Sakamoto et al.，2008）。共生菌的滴度是影响其传播与诱导生物学表型的关键，共生菌对昆虫温度的响应通常表现出一定的可塑性（Corbin et al.，2017；Doremus et al.，2019）。

**表1 温度胁迫对昆虫与共生菌共生关系的影响案例**

Table 1 Reported cases of the influence of temperature stress on the symbiosis between insects and their symbionts

| 温度类型<br>Temperature type | 宿主昆虫<br>Insect host | 共生菌<br>Symbiont | 温度对共生表型的影响<br>Impact of temperature on symbiosis | 参考文献<br>Reference |
|---|---|---|---|---|
| 热敏感<br>Heat-sensitivity | 甜菜蚜、苜蓿无网长管蚜、豌豆长管蚜<br>*Aphis fabae*, *Acyrthosiphon kondoi*, *Acyrthosiphon pisum* | 初级共生菌：布赫纳氏菌<br>Obligate symbiont: *Buchnera* | 热胁迫可破坏宿主母代与胚胎中共生菌的菌胞<br>Heat causes dramatic disruption in both maternal and embryonic bacteriocytes in hosts | Zhang et al., 2019 |
| | 灰暗果蝇<br>*Drosophila nebulosa* | 次级共生菌：螺原体NSRO株系<br>Facultative symbiont: *Spiroplasma* NSRO | 28℃处理多代后螺原体逐渐丢失<br>Gradual loss of *Spiroplasma* at 28℃ over several generations | Anbutsu et al., 2008 |
| | 杂拟谷盗<br>*Tribolium confusum* | 次级共生菌：沃尔巴克氏体<br>Facultative symbiont: *Wolbachia* | 高温降低了沃尔巴克氏体滴度<br>High temperatures reduce *Wolbachia* density | Gharabigloozare & Bleidorn, 2022 |
| | 西方盲走螨<br>*Metaseiulus occidentalis* | 次级共生菌：沃尔巴克氏体<br>Facultative symbiont: *Wolbachia* | 33℃处理8代后沃尔巴克氏体快速丢失<br>Rapid loss of *Wolbachia* after eight generations at 33℃ | Johanowicz & Hoy, 1998 |
| | 截形叶螨<br>*Tetranychus truncatus* | 次级共生菌：沃尔巴克氏体、螺原体<br>Facultative symbiont: *Wolbachia*, *Spiroplasma* | 35℃导致沃尔巴克氏体和螺原体丢失<br>High temperature (35℃) results in loss of *Wolbachia* and *Spiroplasma* | Zhu et al., 2021 |
| | 二斑叶螨<br>*T. urticae* | 次级共生菌：沃尔巴克氏体<br>Facultative symbiont: *Wolbachia* | 32℃处理6代后沃尔巴克氏体丢失<br>Loss of *Wolbachia* after six generations at 32℃ | van Opijnen & Breeuwer, 1999 |
| | 三色书虱<br>*Liposcelis tricolor* | 次级共生菌：沃尔巴克氏体<br>Facultative symbiont: *Wolbachia* | 33℃处理6代后沃尔巴克氏体被完全消除<br>Complete elimination of *Wolbachia* over six generations at 33℃ | Jia et al., 2009 |
| | 埃及伊蚊<br>*Aedes aegypti* | 次级共生菌：沃尔巴克氏体*w*Mel株系<br>Facultative symbiont: *Wolbachia w*Mel | 高温减少了沃尔巴克氏体滴度<br>High temperatures reduce *Wolbachia* density | Ulrich et al., 2016 |
| | 豌豆蚜<br>*Acyrthosiphon pisum* | 初级或次级共生菌：布赫纳氏菌、*Regiella*、*Fukatsuia*<br>Obligate or facultative symbionts: *Buchnera*, *Regiella*, *Fukatsuia* | 热胁迫降低了共生菌滴度<br>Heat shock reducs the densities of symbionts | Heyworth et al., 2020 |
| | 柑橘木虱<br>*Diaphorina citri* | 次级共生菌：沃尔巴克氏体<br>Facultative symbiont: *Wolbachia* | 40℃处理3 d显著降低了沃尔巴克氏体滴度<br>Significant reduction of *Wolbachia* densities at 40℃ for 3 days | Hussain et al., 2017 |
| | 锈胸弓背蚁<br>*Camponotus chromaiodes* | 初级共生菌：*Blochmannia*<br>Obligate symbiont: *Blochmannia* | 高温处理16周以上可消除部分共生菌<br>Partial elimination of *Blochmannia* after heat treatment for more than 16 weeks | Fan & Wernegreen, 2013 |
| | 麦蛾柔茧蜂<br>*Habrobracon hebetor* | 次级共生菌：沃尔巴克氏体<br>Facultative symbiont: *Wolbachia* | 温度影响共生菌、噬菌体滴度以及*cif*基因表达<br>Temperature affects *Wolbachia* and prophage titers as well as expression levels of *cif* genes | Nasehi et al., 2022 |

**续表1 Continued**

| 温度类型<br>Temperature type | 宿主昆虫<br>Insect host | 共生菌<br>Symbiont | 温度对共生表型的影响<br>Impact of temperature on symbiosis | 参考文献<br>Reference |
|---|---|---|---|---|
| | 苏氏恩蚜小蜂<br>*Encarsia suzannae* | 次级共生菌：*Cardinium*<br>Facultative symbiont: *Cardinium* | 热胁迫降低了共生菌滴度、垂直传播效率及胞质不亲和修饰与营救强度<br>Warm temperatures reduce symbiont density, vertical transmission rate, and the strength of both cytoplasmic incompatibility (CI) modification and rescue | Doremus et al., 2019 |
| | 埃及伊蚊<br>*A. aegypti* | 次级共生菌：沃尔巴克氏体*w*Mel、*w*AlbB和*w*MelPop-CLA株系<br>Facultative symbiont: *Wolbachia w*Mel, *w*AlbB and *w*MelPop-CLA | 26~37℃的变温处理导致*w*Mel和*w*MelPop-CLA株系不能隔代传播<br>*w*Mel and *w*MelPop-CLA infections are not transmitted to the next generation when hosts are exposed to 26−37℃ | Ross et al., 2017 |
| | 豆秆野螟<br>*Ostrinia scapulalis* | 次级共生菌：沃尔巴克氏体<br>Facultative symbiont: *Wolbachia* | 63℃处理幼虫20~30 min抑制共生菌杀雄表型<br>Exposing larval female moths to 63℃ for 20−30 min suppresses the male-killing phenotype | Sakamoto et al., 2008 |
| | 波利尼西亚伊蚊<br>*A. polynesiensis* | 次级共生菌：沃尔巴克氏体<br>Facultative symbiont: *Wolbachia* | 32~33℃处理幼虫5~7 d导致胞质不亲和作用消失<br>CI eliminated by exposure of larvae to 32−33℃ for 5−7 days | Wright & Wang, 1980 |
| 冷敏感<br>Cold-sensitivity | 灰暗果蝇<br>*Drosophila nebulosa* | 次级共生菌：螺原体NSRO<br>Facultative symbiont: *Spiroplasma* NSRO | 18℃处理约2代后螺原体快速丢失<br>Rapid loss of *Spiroplasma* at 18℃ after two generations | Anbutsu et al., 2008 |
| | 黑腹果蝇<br>*D. melanogaster* | 次级共生菌：螺原体MSRO<br>Facultative symbiont: *Spiroplasma* MSRO | 16.5℃处理1代后螺原体丢失<br>Loss of *Spiroplasma* at 16.5℃ after one generation | Montenegro & Klaczko, 2004 |
| | 黑腹果蝇<br>*D. melanogaster* | 次级共生菌：沃尔巴克氏体*w*Mel株系<br>Facultative symbiont: *Wolbachia w*Mel | 低温降低了沃尔巴克氏体*w*Mel株系的菌胞丰度及传播效率<br>Cool temperature reduces the abundance of *Wolbachia w*Mel bacteriocytes and transmission efficiency | Hague et al., 2022 |
| | 苏氏恩蚜小蜂<br>*E. suzannae* | 次级共生菌：*Cardinium*<br>Facultative symbiont: *Cardinium* | 低温降低了细菌滴度，增强了胞质不亲和作用<br>Cool temperatures reduce symbiont density, but enhance CI | Doremus et al., 2019 |
| | 截形叶螨<br>*T. truncatus* | 次级共生菌：沃尔巴克氏体、螺原体<br>Facultative symbiont: *Wolbachia*, *Spiroplasma* | 20℃处理降低了螺原体的滴度和传播效率，对沃尔巴克氏体无影响<br>Exposure of mites to 20℃ reduces the density and transmission of *Spiroplasma* but not *Wolbachia* | Zhu et al., 2021 |

## 2 共生菌在宿主昆虫温度适应性中的作用及机制

### 2.1 共生菌在宿主温度适应性中的双重作用

由于共生菌的基因组通常远小于宿主昆虫的基因组，因此在面对不利温度胁迫时，与宿主昆虫相比，共生菌基因组的适应性进化更加迅速（Bennett & Moran，2013；Lo et al.，2016；Latorre & Manzano-Marín，2017）。共生菌在宿主温度适应过程中发挥着双重作用，即可以提高或约束宿主对温度的适应性，其作用方式与宿主和共生菌种类密切相关（表2）。

**表2 共生菌在宿主昆虫温度适应过程中的作用案例**

Table 2 Case studies of the role of symbiotic bacteria in thermal adaptation of insect hosts

| 共生菌<br>Symbiont | 昆虫宿主<br>Insect host | 作用<br>Role | 潜在作用机制<br>Underlying mechanism | 参考文献<br>Reference |
|---|---|---|---|---|
| 初级共生菌：布赫纳氏菌<br>Obligate symbiont: *Buchnera* | 棉蚜、甜菜蚜、苜蓿无网长管蚜、豌豆长管蚜<br>*Aphis gossypii*, *Aphis fabae*, *Acyrthosiphon kondoi*, *Acyrthosiphon pisum* | 限制宿主耐热性<br>Limiting host thermal tolerance | 共生菌影响宿主*Hsp*及*GroEL*基因的表达<br>Affecting host *Hsp* and *GroEL* gene expression | Zhang et al., 2019 |
| 初级共生菌：布赫纳氏菌<br>Obligate symbiont: *Buchnera* | 豌豆蚜<br>*A. pisum* | 提高宿主耐热性<br>Enhancing host thermal tolerance | 共生菌点突变赋予宿主耐热性<br>Thermal tolerance is governed by a point mutation in bacterial symbionts | Dunbar et al., 2007 |
| 次级共生菌：沃尔巴克氏体<br>Facultative symbiont: *Wolbachia* | 果蝇属<br>*Drosophila* | 提高宿主耐热性<br>Increasing the heat stress tolerance of the host | 增强多巴胺代谢<br>Intensifying dopamine metabolism | Gruntenko et al., 2017 |
| 次级共生菌：沃尔巴克氏体、醋酸杆菌<br>Facultative symbiont: *Wolbachia*, *Acetobacter* | 黑腹果蝇<br>*D. melanogaster* | 沃尔巴克氏体和醋酸杆菌影响宿主耐热及耐寒性<br>Thermal and cool tolerance affected by *Wolbachia* and *Acetobacter* | 未知<br>Unknown | Moghadam et al., 2018 |
| 次级共生菌：沃尔巴克氏体、螺原体<br>Facultative symbiont: *Wolbachia*, *Spiroplasma* | 截形叶螨<br>*T. truncatus* | 提高或限制宿主耐热性<br>Enhancing or limiting host thermal tolerance | 调控宿主温度偏好性或影响宿主*Hsp*基因的表达<br>*Wolbachia* modifies host temperature preference or *Hsp* gene expression | Zhu et al., 2021 |
| 次级共生菌：*Cardinium*<br>Facultative symbiont: *Cardinium* | MED型烟粉虱<br>*Bemisia tabaci* MED | 提高宿主耐热性<br>Increasing the thermal tolerance of host | 未知<br>Unknown | Yang et al., 2021 |
| 次级共生菌：立克次氏体、*Regiella*、*Fukatsuia*<br>Facultative symbiont: *Rickettsia*, *Regiella*, *Fukatsuia* | 豌豆蚜<br>*A. pisum* | 增强宿主耐热性<br>Enhancing host thermal tolerance | 未知<br>Unknown | Montllor et al., 2002; Heyworth et al., 2020 |
| 次级共生菌：立克次氏体<br>Facultative symbiont: *Rickettsia* | B型烟粉虱<br>*Bemisia tabaci* B biotype | 提高宿主耐热性<br>Enhancing host thermal tolerance | 诱导耐热性相关基因表达<br>Inducing the expression of genes required for thermotolerance | Brumin et al., 2011 |
| 次级共生菌：沙雷氏菌、*Hamiltonella defensa*、*Regiella insecticola*<br>Facultative symbiont: *Serratia symbiotica*, *Hamiltonella defensa*, *Regiella insecticola* | 豌豆蚜<br>*A. pisum* | 赋予宿主耐热性<br>Conferring tolerance to high temperatures | 未知<br>Unknown | Russell & Moran, 2006 |
| 初级或次级共生菌：布赫纳氏菌、沙雷氏菌等<br>Obligate or facultative symbionts: *Buchnera*, *Serratia*, etc. | 禾谷缢管蚜、麦长管蚜<br>*Rhopalosiphum padi*, *Sitobion avenae* | 提高宿主耐热性<br>Enhancing host thermal tolerance | 未知<br>Unknown | Majeed et al., 2022 |
| 肠道共生菌：克雷伯杆菌BD177<br>Gut symbiotic bacteria: *Klebsiella michiganensis* BD177 | 橘小食蝇<br>*Bactrocera dorsalis* | 增强宿主耐寒性<br>Enhancing host resistance to low-temperature stress | 调控宿主精氨酸与脯氨酸代谢通路<br>Stimulating host arginine and proline metabolism pathway | Raza et al., 2020 |
| 肠道共生菌：不动杆菌、短芽胞杆菌、芽胞杆菌、肠杆菌、肠球菌、假单胞菌、葡萄球菌<br>Gut symbiotic bacteria: *Acinetobacter*, *Brevibacillus*, *Bacillus*, *Enterobacter*, *Enterococcus*, *Pseudomonas*, *Staphylococcus* | 橘小食蝇<br>*B. dorsalis* | 帮助宿主克服温度胁迫<br>Helping the host to overcome temperature stress | 未知<br>Unknown | Ayyasamy et al., 2021 |
| 肠道共生菌<br>Gut symbiotic bacteria | 亚暗果蝇<br>*Drosophila subobscura* | 提高宿主耐热性<br>Enhancing host thermal tolerance | 未知<br>Unknown | Jaramillo & Castañeda, 2021 |
| 肠道共生菌<br>Gut symbiotic bacteria | 黑腹果蝇<br>*D. melanogaster* | 提高宿主耐寒性<br>Enhancing host resistance to low-temperature | 未知<br>Unknown | Henry & Colinet, 2018 |

初级共生菌的去除会导致宿主死亡或正常生长受限。初级共生菌的温度敏感性限制了昆虫对不利温度的响应。在这个层面上，昆虫宿主与初级共生菌高度依赖的相互作用可能是昆虫对不利温度响应的“阿喀琉斯之踵”。最典型的例子就是蚜虫与其初级共生菌布赫纳氏菌，布赫纳氏菌为宿主提供营养，当该共生菌缺失时蚜虫不能存活，但布赫纳氏菌通常对高温敏感，热胁迫会导致该共生菌丢失，因此布赫纳氏菌限制了宿主蚜虫的热耐受性(Zhang et al.，2019)。然而，当布赫纳氏菌基因组点突变后，可以在一定高温范围内提高宿主的耐热性(Dunbar et al.，2007；Burke et al.，2010)。因此，昆虫与共生菌的共生关系可能随着外界胁迫的改变而在互利共生与拮抗作用间相互转换(Renoz et al.，2019)。相反，次级共生菌可能增强了宿主对高低温的耐受性，帮助宿主适应高低温胁迫，例如在橘小实蝇 *Bactrocera dorsalis* 中，肠道细菌克雷伯杆菌 *Klebsiella michiganensis* BD177能提高宿主的抗寒能力(Raza et al.，2020)，其他肠道菌如不动杆菌 *Acinetobacter*、短芽胞杆菌 *Brevibacillus* 和芽胞杆菌 *Bacillus* 等均能帮助宿主克服温度胁迫(Ayyasamy et al.，2021)；蚜虫体内的多种共生菌如沙雷氏菌 *Serratia symbiotica*、*Hamiltonella defensa*、*Regiella insecticola*、*Regiella* 和 *Fukatsuia* 等均参与了调控宿主的耐热性(Russell & Moran，2006；Heyworth et al.，2020；Majeed et al.，2022)；在烟粉虱 *Bemisia tabaci* 和果蝇等研究体系中，立克次氏体 *Rickettsia*、沃尔巴克氏体、*Cardinium*、醋酸杆菌 *Acetobacter* 及肠道细菌也可增强宿主的耐热性(Henry & Colinet，2018；Jaramillo & Castañeda，2021；Yang et al.，2021)。在截形叶螨中，单独感染共生菌沃尔巴克氏体或螺原体时会降低宿主的耐热性，而同时感染两者时可以提高宿主对高温的适应性(Zhu et al.，2021)。这些结果表明共生菌参与调控昆虫宿主的温度耐受性及适应性，且具有宿主特异性和表型可塑性等特点。

### 2.2 共生菌调控宿主温度适应的潜在机制

基于共生菌分布的普遍性及其在调控宿主昆虫温度适应过程中的重要生态学意义，国内外学者们对其调控机制的研究从未间断。大量研究表明，共生菌可以通过改变宿主的行为、生理及细胞代谢等多种途径来调控宿主对不利温度的响应(表2、图1)。

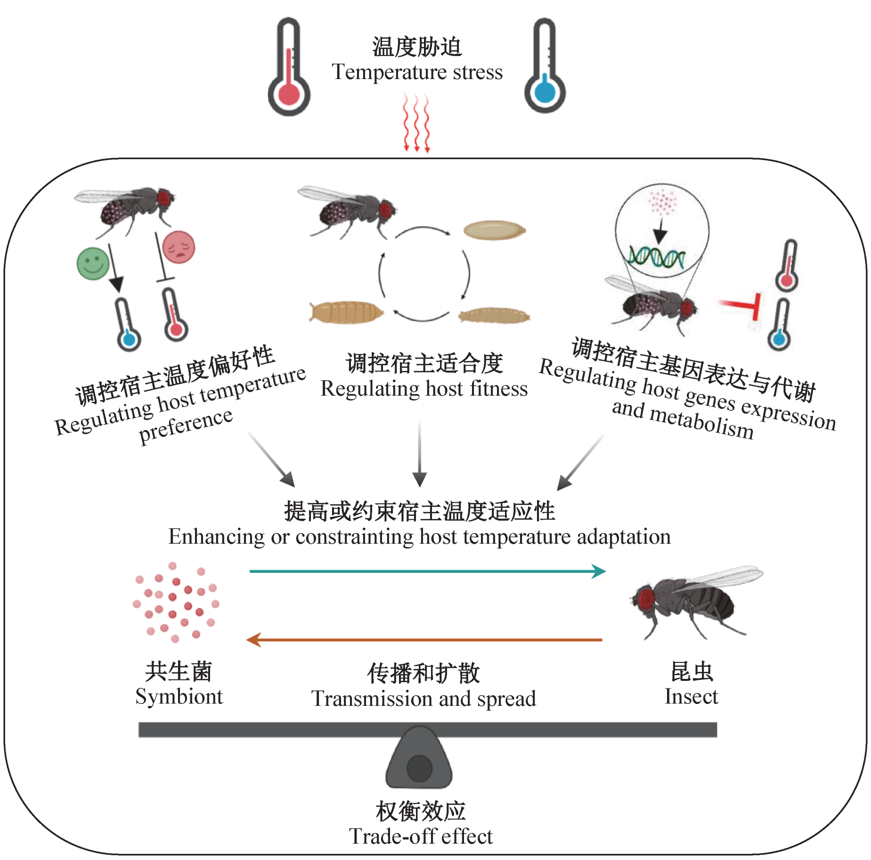


**图1 共生菌调控昆虫温度适应的作用方式示意图**

Fig. 1 A hypothetical scenario for the underlying mechanisms of symbiotic bacteria-mediated adaptation of insect hosts to different temperatures

在宏观生态学层面上，共生菌调控宿主温度适应的作用机制包括2个方面。第一，共生菌参与调控宿主的温度偏好性，作为响应温度胁迫的应激性行为，帮助宿主躲避或逃避微环境中不利温度压力，例如在果蝇与叶螨的研究中发现感染沃尔巴克氏体的个体通常比未感染沃尔巴克氏体的个体更偏好低温（Hague et al.，2020；Zhu et al.，2021）。沃尔巴克氏体对宿主的温度选择行为调控可能是宿主适应温度胁迫的普遍行为策略之一（Arnold et al.，2018；Truitt et al.，2019；Hague et al.，2020）。虽然沃尔巴克氏体对宿主的温度偏好调控可能在昆虫体内普遍存在，但对其广谱性及调控机制仍有待进一步研究。第二，共生菌通过调控宿主的营养代谢（Russell & Moran，2006）及其诱导的生殖调控和适合度代价减弱或消失（Pintureau et al.，1999；Anbutsu et al.，2008；Bordenstein & Bordenstein，2011）来直接或间接影响宿主的耐热性或耐寒性。在蚜虫体内至少有3种共生菌，包括*Hamiltonella*、沙雷氏菌和布赫纳氏菌，在高温环境条件下，沙雷氏菌可以通过合成氨基酸来增强宿主的存活或生殖能力（Russell & Moran，2006；Heyworth & Ferrari，2015；Chong & Moran，2018）。在果蝇中共生菌沃尔巴克氏体通过增加多巴胺的代谢可提高宿主的耐热性（Gruntenko et al.，2017）。在橘小实蝇中克雷伯杆菌能提高宿主的精氨酸和脯氨酸代谢能力，增强其抗寒能力（Raza et al.，2020）。在灰飞虱*Laodelphax striatellus*、褐飞虱*Nilaparvata lugens*、豌豆蚜*Acyrthosiphon pisum*和烟粉虱等多种昆虫体内，共生菌沃尔巴克氏体、沙雷氏菌和*Hamiltonella*等可为宿主补充代谢物，从而可能间接影响宿主的温度适应性（Ju et al.，2020；Ren et al.，2020；Zhou et al.，2021）。

在微观分子生物学层面上，昆虫宿主的表型不仅受自身基因组的调节，也受其体内共生菌基因组的影响（Iltis et al.，2022）。昆虫共生菌编码不稳定的蛋白质，并表现出对热胁迫的脆弱性，共生菌的热敏感性可能会限制寄主的热耐受性和适应性（Wernegreen，2012）。例如，黑腹果蝇沃尔巴克氏体*w*Mel株系中，表面蛋白WspB中的一个衍生的终止密码子可能与沃尔巴克氏菌的热敏性有关（Hague et al.，2022）。豌豆蚜共生菌布赫纳氏菌中的热激相关基因*iboA*编码热激蛋白，在高温激发下该基因的表达量迅速增加，当*iboA*发生突变后，高温下该基因的表达量极低，突变体蚜虫的生殖能力减弱（Dunbar et al.，2007）。将布赫纳氏菌人工注射到突变体蚜虫中，替换共生菌后的蚜虫表现出较强的抗热性，验证了共生菌*iboA*基因在寄主昆虫抗热中的功能（Moran & Yun，2015）。此外，蚜虫共生菌布赫纳氏菌伴侣蛋白GroEL在高温下持续表达，可能调控宿主对温度的适应性（Baumann et al.，1996；Fares et al.，2004；Zhang et al.，2019）。共生菌也可能参与调控宿主温度应激基因的表达（Brumin et al.，2011），间接调控宿主对温度的应激反应（Moran & Yun，2015；Harmon et al.，2009）。例如感染共生菌立克次氏体的烟粉虱，在常温下一些微丝和细胞骨架基因表达量较高，如肌动蛋白基因、原肌球蛋白基因以及肌凝蛋白基因等，这些基因的表达对烟粉虱抵御高温有着潜在作用（Brumin et al.，2011）。截形叶螨体内共生菌沃尔巴克氏体和螺原体通过诱导*Hsp70*等热激蛋白基因的表达来调控宿主的温度耐受性（Zhu et al.，2021）。然而，目前对共生菌调控宿主昆虫温度适应性的分子机制仍知之甚少，随着近年来高通量测序技术的快速发展，为研究其分子机制提供了更便利的条件。

## 3 共生菌调控宿主温度适应的生态学意义

共生菌对宿主温度适应性的调控一般趋向于互利共赢的适应性进化方式，对维持昆虫与共生菌共生关系的稳定具有重要意义（Feldhaar，2011；Corbin et al.，2017；Lemoine et al.，2020）。在生态学层面上，共生菌对宿主温度适应的调控通常会引起级联效应：一方面，对于宿主来说，从个体到种群及群落水平，导致生态位扩张和种间竞争减少，有助于昆虫的扩散与暴发，共生菌对宿主温度适应的调控也决定了昆虫的时空分布；另一方面，昆虫种群的暴发反过来促进共生菌的传播与扩散（图1）。因此，在自然界中，共生菌的分布与宿主所处温度环境密切相关，呈现独特的时空分布模型（Tsuchida et al.，2002；Zhu et al.，2018；Hague et al.，2022）。

从应用的视角出发，共生菌作为一种害虫防控的新策略具有巨大的应用潜力（Gao et al.，2020；Wang et al.，2022）。尤其是基于共生菌沃尔巴克氏体技术，在以蚊为代表的卫生害虫和以稻飞虱为代表的农业害虫防治领域已取得重要进展（Bian et al.，2013；Zheng et al.，2019；Gong et al.，2020）。在这些研究中，通过规模化释放人工转染共生菌沃尔巴克氏体的昆虫株系，利用种群压制或种群替换策略达到防虫抑毒的效果。然而，在自然界中释放的昆虫带菌株系易受环境温度的影响，而共生菌对宿

主温度适应性的正向调控可增强共生菌在复杂温度环境中的稳定性，提高其应用潜力。

## 4 展望

昆虫与其共生微生物组成共生功能体（Iltis et al.，2022），当面临生物与非生物胁迫时，昆虫与共生菌作为一个整体经历着复杂的被动选择和主动适应过程。温度胁迫时，对宿主有利的共生菌被保留下来，而在温度胁迫解除时，共生菌由于消耗宿主营养和适合度代价等原因导致其数量减少。因此，推测共生菌与宿主犹如跷跷板的两端，共生菌在宿主体内的多样性和动态变化可能是宿主响应不利温度胁迫的权衡结果（图1）。在昆虫与共生菌长期的协同进化过程中，为了维持稳定的共生关系，共生菌基因组快速的适应性进化，直接或间接调控宿主对温度胁迫的响应。目前，有关共生菌调控蚜虫和果蝇等模式昆虫温度适应性的研究已取得一些进展，但仍然有许多科学问题亟待进一步研究。

第一，探究自然条件下变温胁迫对昆虫与共生菌互作的影响。前期大多数研究主要集中在实验室条件下，不能完全真实呈现自然环境中昆虫与共生菌的互作（Stoks et al.，2017）。在自然条件下，不同时空温度变化较为复杂，变温对昆虫与共生菌共生关系的影响在很大程度上仍然未知。未来的研究需要模拟田间温度环境，深入探究变温条件下昆虫自然种群中共生菌的多样性、传播方式和功能等方面的动态变化模型。另外，在空间与时间的大尺度上，应持续关注全球气候变化对昆虫与共生菌共生关系的影响。

第二，解析共生菌调控昆虫温度适应性的行为及分子机制。共生菌介导宿主的温度选择行为，可能是昆虫在微环境中逃避和适应温度胁迫的普遍性行为策略，但共生菌如何调控宿主对温度胁迫的感应、胁迫信号的转导及行为选择调节机制尚待进一步研究。前期研究表明共生菌感染也可诱导宿主温度应答基因的表达及生理代谢的改变（Brumin et al.，2011；Zhu et al.，2021），但对于共生菌确切的作用方式仍然未知。这可能受限于大多数可遗传的胞内共生菌不能体外培养，下一步研究需要借助细胞系等工具深入研究共生菌调控宿主温度适应性的分子机制（Masson et al.，2018；Li et al.，2021）。除了可遗传的共生菌外，昆虫体内共生菌与其他细菌间也存在复杂的联系（Jang & Kikuchi，2020），共生菌是否与其他细菌发生相互作用，通过多种作用方式协同调控宿主的温度适应性有待进一步研究验证。此外，在不同研究系统中，即使是同一种共生菌，对宿主的温度适应调控作用也存在很大差异，这可能是共生菌在不同昆虫中独特的适应性进化结果。从进化的视角而言，共生菌与宿主间存在许多水平转移基因（Husnik & McCutcheon，2018），这些水平转移基因在宿主温度适应过程中的功能也是未来研究的侧重点之一。

第三，基于共生菌的害虫防治新手段开发与应用。共生菌作为防控害虫的新手段，虽然具有巨大的潜力与优势，但同时存在许多局限性。在利用沃尔巴克氏体防控蚊子及稻飞虱的应用技术研究中，释放人工转染共生菌沃尔巴克氏体的昆虫株系，首先需考虑变温环境中共生菌及其对宿主表型调控的稳定性（Zheng et al.，2019；Gong et al.，2020）。随着分子生物学技术的快速发展，未来可以借助基因编辑等分子生物学手段，改变共生菌对极端温度的敏感性，提高其在复杂温度环境下的稳定性，增强其应用潜力（李维华等，2022；Wang et al.，2022）。深入探究温度变化下昆虫与共生菌的互作关系，对预测共生菌在宿主适应气候变化的响应与适应以及利用共生菌靶向防控害虫具有重要意义。

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