

共生菌 *Wolbachia* 调控昆虫温度偏好行为的研究进展*

段雅心^{1**} 王欣宇¹ 王子涵¹ 朱玉溪^{1***} 杜予州^{1,2***}

(1. 扬州大学植物保护学院, 扬州 225009; 2. 江苏省绿色农药工程研究中心, 扬州 225009)

摘要 环境温度的变化显著影响昆虫与其共生菌的共生关系, 而共生菌可通过快速的适应性进化, 调控宿主应对温度的胁迫。*Wolbachia* 是昆虫中分布最广泛的内共生菌之一, 在宿主的生理、生态及进化中发挥着重要作用。近年来研究发现, *Wolbachia* 感染可影响宿主昆虫的温度偏好行为, 协助宿主在微环境中规避不利温度的胁迫。本文综述了温度胁迫对昆虫与 *Wolbachia* 共生关系的影响, 重点阐述 *Wolbachia* 在调控宿主昆虫温度偏好行为中的作用、潜在机制及其生态学意义。该综述有助于深入理解在全球气候变化和极端温度频发背景下, 共生菌 *Wolbachia* 调控宿主应对温度胁迫的行为策略, 并为利用 *Wolbachia* 在害虫生物防控中的应用提供理论依据。

关键词 共生菌; *Wolbachia*; 温度偏好; 生态适应

Advances in research on *Wolbachia*-mediated thermal preferences in insects

DUAN Ya-Xin^{1**} WANG Xin-Yu¹ WANG Zi-Han¹
ZHU Yu-Xi^{1***} DU Yu-Zhou^{1,2***}

(1. College of Plant Protection, Yangzhou University, Yangzhou 225009, China;

2. Jiangsu Province Engineering Research Center of Green Pesticides, Yangzhou University, Yangzhou 225009, China)

Abstract Symbiotic relationships between insects and their symbionts are profoundly influenced by fluctuations in ambient temperature. Conversely, symbionts can undergo rapid adaptive evolution to modulate host responses to thermal stress. *Wolbachia*, one of the most prevalent intracellular symbionts in insects, plays a pivotal role in shaping host physiology, ecology, and evolution. Emerging evidence has shown that infection can modify the thermal preferences of insect hosts, causing them to avoid microhabitats with ambient temperatures deleterious to *Wolbachia*. This review synthesizes current knowledge of the impact of thermal stress on insect-*Wolbachia* symbiosis, with a focus on *Wolbachia*'s role in regulating host thermal preferences, the underlying molecular and behavioral mechanisms underlying this regulation, and its broader ecological consequences. These insights deepen our understanding of rapid, behavioral adaptation in host-symbiont systems during global climate change and increasing temperature extremes, and offer a theoretical foundation for the application of *Wolbachia* in insect pest management.

Key words symbionts; *Wolbachia*; thermal preference; ecological adaptation

全球气候变暖及极端温度的频繁发生, 对生物和生态系统造成显著影响 (Ma *et al.*, 2021, 2025)。昆虫是地球上最丰富的动物类群, 其体

内蕴藏着丰富的微生物类群 (Moran *et al.*, 2008)。在长期的协同进化过程中, 部分微生物与宿主昆虫形成了相互依赖的紧密关系 (Douglas,

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**第一作者 First author, E-mail: 221804305@stu.yzu.edu.cn

***共同通讯作者 Co-Corresponding authors, E-mail: yuxizhu@yzu.edu.cn; yzdu@yzu.edu.cn

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1998; 杨义婷等, 2014)。其中, *Wolbachia* 是一种母系遗传共生菌, 广泛分布于约 66% 的昆虫物种中 (Hilgenboecker *et al.*, 2008), 能够通过多种方式 (如细胞质不亲和、孤雌生殖、雌性化、杀雄等) 调控宿主的生殖 (Adams *et al.*, 2021; 郑林宇等, 2022; Hochstrasser, 2023), 并影响宿主的行为、生理、生态与进化 (Werren *et al.*, 2008; Bi and Wang, 2020; Kaur *et al.*, 2021; Porter and Sullivan, 2023)。

昆虫与 *Wolbachia* 的共生关系对环境温度较为敏感, 极端温度胁迫会显著抑制 *Wolbachia* 在宿主体内的增殖和垂直传播, 进而威胁共生系统的稳定性, 甚至导致共生关系的破裂 (Corbin *et al.*, 2017)。然而, 相较于宿主基因组, *Wolbachia* 基因组具有更高的进化速率, 这使其在温度剧烈波动的环境中具有较强的适应能力, 能够快速响应并调节宿主的生理与行为反应, 以维持共生体系的稳定性 (Renoz *et al.*, 2019; Serbus *et al.*, 2020)。近年来, 大量研究发现 *Wolbachia* 能够影响宿主昆虫对温度的偏好, 其调控效应在不同宿主种类与菌株间存在显著差异 (Truitt *et al.*, 2018; Hague *et al.*, 2020)。*Wolbachia* 对昆虫宿主的温度偏好性调控, 可能是“共生驱动”的环境选择策略, 通过影响宿主的温度选择行为, 帮助宿主在微环境中逃避不利温度的胁迫 (Hague *et al.*, 2020)。本文综述了温度胁迫对昆虫与 *Wolbachia* 共生关系的影响, 系统阐述 *Wolbachia* 在调控宿主昆虫温度偏好行为中的作用、潜在机制及其生态学意义, 并展望了该研究领域的未来发展方向。该综述有助于深化我们对气候变化背景下“昆虫-共生菌”互作机制的理解, 揭示 *Wolbachia* 在调控宿主行为以应对温度胁迫过程中的适应性策略, 也为将 *Wolbachia* 应用于昆虫害虫的生物防控提供理论依据。

1 温度对昆虫与 *Wolbachia* 共生关系的影响

温度胁迫显著影响昆虫与共生菌的互作关系 (Vidal *et al.*, 2021; Hague *et al.*, 2022)。

对于初级共生菌而言, 其热敏感性常成为宿主的“阿喀琉斯之踵 (Achilles' Heel)”, 如蚜虫初级共生菌 *Buchnera* 限制了宿主的耐热性 (Zhang *et al.*, 2019)。*Wolbachia* 作为典型的次级共生菌, 其与宿主的共生关系同样表现出温度的敏感性, 这一现象已在果蝇、蚊子、飞虱、叶螨等多种昆虫 (螨) 中得到证实 (Shan *et al.*, 2014; Gruntenko *et al.*, 2017; Ross *et al.*, 2017; Ju *et al.*, 2020; Zhu *et al.*, 2021)。首先, 温度胁迫会影响 *Wolbachia* 在宿主体内的增殖及在种群内的垂直传播效率。例如, 高温处理会显著降低杂拟谷盗 *Tribolium confusum*、埃及伊蚊 *Aedes aegypti* 和柑橘木虱 *Diaphorina citri* 等昆虫体内的 *Wolbachia* 滴度 (Ulrich *et al.*, 2016; Hussain *et al.*, 2017; Gharabigloozaire and Bleidorn, 2022); 高温处理埃及伊蚊幼虫后, 其体内 *Wolbachia* wMel 和 wMelPop-CLA 株系不能跨代传播 (Ross *et al.*, 2017), 低温同样会降低黑腹果蝇 *Drosophila melanogaster* 体内 wMel 株系的菌胞丰度及传播效率 (Hague *et al.*, 2022)。大多数情况下, 多种 *Wolbachia* 株系对高温较为敏感, 而对低温胁迫的耐受性较强。其次, 温度改变 *Wolbachia* 诱导的宿主生物学表型强度。例如, 高温削弱了 *Wolbachia* 诱导豆秆野螟 *Ostrinia scapulalis* 的杀雄表型 (Sakamoto *et al.*, 2008), 并影响麦蛾柔茧蜂 *Habrobracon hebetor* 的胞质不相容效应 (Nasehi *et al.*, 2022)。综上, 温度主要通过调控 *Wolbachia* 的增殖、垂直传播效率以及宿主生物学表型, 进而影响昆虫与 *Wolbachia* 共生关系的稳定性。而这种影响的强度通常取决于多个因素, 包括 *Wolbachia* 的株系差异、宿主种类、性别、发育阶段、温度阈值以及胁迫持续时间等 (朱玉溪等, 2022)。

面对温度胁迫时, 昆虫-共生菌系统演化出多层次适应策略 (Fares *et al.*, 2004; 单红伟等, 2016; Ferguson *et al.*, 2024)。在微观分子生物学层面上, 共生菌参与调控宿主昆虫热应激基因或蛋白的表达水平, 影响宿主对不利温度的适应能力 (Zhu *et al.*, 2021; Hague *et al.*, 2022; Ling *et al.*, 2024)。例如, 蚜虫次级共生菌 *Serratia*

通过与初级共生菌 *Buchnera* 形成互补的 DNA 错配修复系统,降低初级共生菌基因组的突变发生频率,提高热胁迫下小热激蛋白 *ibpA* 的转录效率,抑制菌胞细胞骨架 *actin* 变性聚集,进而促进蚜虫种群的热适应性 (Ling *et al.*, 2024);在截形叶螨 *Tetranychus truncatus* 中, *Wolbachia* *wTtr* 通过改变宿主热激蛋白基因 (*Hsps*) 的表达模式,调控宿主的耐热性 (Zhu *et al.*, 2021)。在宏观生态学层面上,共生菌改变昆虫宿主的生理代谢或温度选择行为,调节宿主对温度胁迫的响应 (Hague *et al.*, 2020; Zhu *et al.*, 2024b)。如 *Wolbachia* 感染增强麦蛾柔茧蜂和黑腹果蝇脂质与碳水化合物代谢 (Karpova *et al.*, 2023; Kryukova *et al.*, 2023), 潜在影响宿主昆虫的温度耐受能力;同时, *Wolbachia* 可通过合成维生素、血红素等代谢物或重塑宿主代谢谱来应对环境温度胁迫 (Ju *et al.*, 2020; Zhu *et al.*, 2024b)。除此之外,近期研究发现 *Wolbachia* 感染调节昆虫的温度偏好性,这种“共生驱动”的环境选择策略,通过引导宿主主动趋避特定温区,优化共生菌的生存环境,对维持共生稳定性及拓展宿主生态位具有深远意义 (Truitt *et al.*, 2018; Hague *et al.*, 2020)。

2 *Wolbachia* 对宿主温度偏好的调控作用及潜在机制

目前关于 *Wolbachia* 调控宿主温度偏好的研

究主要集中于果蝇、斑潜蝇及叶螨等模式生物 (表 1)。在拟果蝇 *Drosophila simulans*、*Drosophila sechellia*、*Drosophila teissieri*、截形叶螨等昆虫 (螨) 中,感染 *Wolbachia* 株系 *wRi*、*wHa*、*wSh*、*wTei*、*wMau*、*wTtr* 的宿主偏好温度显著低于未感染个体 ($P < 0.05$), 偏好温度变化范围在 0.50-2.26 °C, 表明 *Wolbachia* 感染的个体偏好相对低的温度 (表 1);相反, *Drosophila mauritana* 感染 B 类群株系 *wMau* 的个体偏好相对高的温度 (Hague *et al.*, 2020), 推测存在 *Wolbachia* 株系与宿主特异性互作。有趣的是,黑腹果蝇的研究中存在分歧,Truitt 等 (2018) 与 Arnold 等 (2019) 发现感染 *wMelCS* 及 *wMelPop* 菌株的个体倾向于较低温度,而 Hague 等 (2020) 研究表明感染 *wMelCS* 菌株的个体偏好较高温,这种差异可能与宿主的驯化历史相关。在南美斑潜蝇 *Liriomyza huidobrensis* 云南种群中,感染 *wLhui* 的个体温度偏好性比未感染个体低约 0.90 °C, 但两者之间无统计显著差异 ($P > 0.05$), 可能与种群内个体差异较大有关 (Zhu *et al.*, 2024a)。综合分析, *Wolbachia* 调控宿主温度偏好的表型强度可能与宿主种类、*Wolbachia* 株系与滴度紧密相关,该现象在节肢动物中广泛存在,且具有可塑性 (Truitt *et al.*, 2018; Arnold *et al.*, 2019; Hague *et al.*, 2020; Zhu *et al.*, 2021)。

Wolbachia 诱导的宿主温度偏好变化可能代表了宿主-共生菌相互作用的行为适应 (Lewis

表 1 *Wolbachia* 调控昆虫温度偏好行为的案例
Table 1 Reported cases of *Wolbachia*-mediated host thermal preference

宿主 Host	<i>Wolbachia</i> 菌株 (类群) <i>Wolbachia</i> strain (group)	宿主偏好温度 (°C) Temperature preference (Tp) (°C)				参考文献 Reference
		Tp <i>Wolbachia</i> 感染 Tp <i>Wolbachia</i> -infected			差异水平 Significant difference level	
		Tp <i>Wolbachia</i> 未感染 Tp <i>Wolbachia</i> -uninfected				
南美斑潜蝇(云南种群) <i>Liriomyza huidobrensis</i> (Yunnan population)	wLhui (A 类群) wLhui (A group)	19.30	20.20	- 0.90	ns	Zhu <i>et al.</i> , 2024a
南美斑潜蝇(新疆种群) <i>Liriomyza huidobrensis</i> (Xinjiang population)	wLhui (A 类群) wLhui (A group)	19.70	19.60	0.10	ns	Zhu <i>et al.</i> , 2024a

续表 1 (Table 1 continued)

宿主 Host	Wolbachia 菌株 (类群) Wolbachia strain (group)	宿主偏好温度 (°C) Temperature preference (Tp) (°C)				参考文献 Reference
		Tp <i>Wolbachia</i> 感染 Tp <i>Wolbachia</i> -infected	Tp <i>Wolbachia</i> 未感染 Tp <i>Wolbachia</i> -uninfected	ΔTp	差异水平 Significant difference level	
截形叶螨 (<i>Wolbachia</i> 感染种群) <i>Tetranychus truncatus</i> (<i>Wolbachia</i> -infected population)	wTtr (B 类群) wTtr (B group)	20.21	22.47	- 2.26	<i>P</i> < 0.05	Zhu <i>et al.</i> , 2021
截形叶螨 (<i>Wolbachia</i> - <i>Spiroplasma</i> 感染种群) <i>Tetranychus truncatus</i> (<i>Wolbachia</i> - <i>Spiroplasma</i> co-infected population)	wTtr (B 类群) wTtr (B group)	20.74	22.47	- 1.73	<i>P</i> < 0.05	Zhu <i>et al.</i> , 2021
拟果蝇 <i>Drosophila simulans</i>	wRi (A 类群) wRi (A group)	21.72	23.12	- 1.40	<i>P</i> < 0.05	Hague <i>et al.</i> , 2020
拟果蝇 <i>Drosophila simulans</i>	wHa (A 类群) wHa (A group)	23.56	24.89	- 1.30	<i>P</i> < 0.05	Hague <i>et al.</i> , 2020
<i>Drosophila sechellia</i>	wSh (A 类群) wSh (A group)	23.32	23.98	- 0.66	<i>P</i> < 0.05	Hague <i>et al.</i> , 2020
<i>Drosophila teissieri</i>	wTei (A 类群) wTei (A group)	22.70	23.70	- 1.00	<i>P</i> < 0.01	Hague <i>et al.</i> , 2020
<i>Drosophila mauritana</i>	wMau (B 类群) wMau (B group)	21.15	19.67	1.48	<i>P</i> < 0.01	Hague <i>et al.</i> , 2020
黑腹果蝇 <i>Drosophila melanogaster</i>	wMelCS (A 类群) wMelCS (A group)	-	-	- 0.50	ns	Hague <i>et al.</i> , 2020
黑腹果蝇 <i>Drosophila melanogaster</i>	wMel (A 类群) wMel (A group)	-	-	- 0.50	ns	Hague <i>et al.</i> , 2020
<i>Drosophila yakuba</i>	wYak (A 类群) wYak (A group)	-	-	- 0.50	ns	Hague <i>et al.</i> , 2020
黑腹果蝇 <i>Drosophila melanogaster</i>	wMel (未知) wMel (unknown)	23.20	24.40	- 1.20	<i>P</i> < 0.05	Truitt <i>et al.</i> , 2018
黑腹果蝇 <i>Drosophila melanogaster</i>	wMelCS (未知) wMelCS (unknown)	20.40	24.40	- 4.00	<i>P</i> < 0.05	Truitt <i>et al.</i> , 2018
黑腹果蝇 <i>Drosophila melanogaster</i>	wMelPop (未知) wMelPop (unknown)	20.50	24.40	- 3.90	<i>P</i> < 0.05	Truitt <i>et al.</i> , 2018
黑腹果蝇 <i>Drosophila melanogaster</i>	wMelCS (未知) wMelCS (unknown)	25.06	25.78	- 0.72	<i>P</i> < 0.05	Arnold <i>et al.</i> , 2019

Δ Tp = Tp *Wolbachia* 感染 - Tp *Wolbachia* 未感染; ns: 无显著性差异。

Δ Tp = Tp *Wolbachia*-infected - Tp *Wolbachia*-uninfected; ns: No significant difference.

and Lizé, 2015; Truitt *et al.*, 2018; Hague *et al.*, 2021)。然而, 目前关于 *Wolbachia* 调控昆虫温度偏好行为的机制尚不清楚。我们推测 *Wolbachia* 通过直接或间接作用方式调控宿主的温度选择

行为: 一方面, 许多昆虫 *Wolbachia* 分布于宿主的脑部或肠道 (Strunov and Kiseleva, 2016), 且大多数 *Wolbachia* 基因组存在完整的 T4SS 分泌系统 (Carpinone *et al.*, 2018; Sinha *et al.*,

2019), *Wolbachia* 可能通过 T4SS 分泌系统将效应因子递送到宿主神经细胞, 或通过“肠-脑轴”(李子园等, 2024), 靶向宿主神经行为通路, 直接调控宿主的温度选择行为; 另一方面, *Wolbachia* 会改变宿主细胞或个体的代谢谱, 宿主的代谢状态可能间接驱动其自身的温度选择行为, 以寻求更适合能量平衡的温度(Zhu *et al.*, 2024b)。因 *Wolbachia* 难以体外培养, 其功能研究长期受限。近年来, 借助细胞系、基因组学及基因编辑等技术手段, 为解析其调控机制提供了新思路。

3 *Wolbachia* 调控宿主温度偏好的生态学意义

3.1 共生关系维持

Wolbachia 对宿主温度偏好性的调控通常偏向于对宿主和共生菌有利的方向(Corbin *et al.*, 2017; Lemoine *et al.*, 2020), 通过引导宿主选择更利于共生稳定的温区, 形成级联保护效应: 对于共生菌而言, 适宜的温度有利于共生菌在宿主体内的增殖, 如感染 *Wolbachia* wRi、wHa、wSh、wTei 株系的果蝇偏好较凉爽的地区, 较低的温度环境下 *Wolbachia* 滴度稳定(Hague *et al.*, 2020), 保证了共生菌在宿主种群中的稳定垂直传播(Corbin *et al.*, 2017); 此外, 对于宿主而言, 由于 *Wolbachia* 感染个体通常偏好相对较低的温度(表 1), 低温不仅削弱了宿主的适合度代价, 还能提升宿主存活率并延长寿命(Arnold *et al.*, 2019), 进而促进共生菌的传播扩散(Hague *et al.*, 2020)。因此, *Wolbachia* 介导的宿主温度偏好行为可被视为宿主与共生体协同进化形成的一种微生境的适应策略, 确保了双方在温度波动环境中的稳定共存(图 1)。

3.2 害虫种群的分布、扩张和暴发

温度是决定昆虫分布、扩张与暴发的关键生态因子之一(Ma *et al.*, 2021; Lahondère and Bonizzoni, 2022)。*Wolbachia* 对宿主温度偏好性的调控, 理论上能够提升昆虫宿主对微环境的

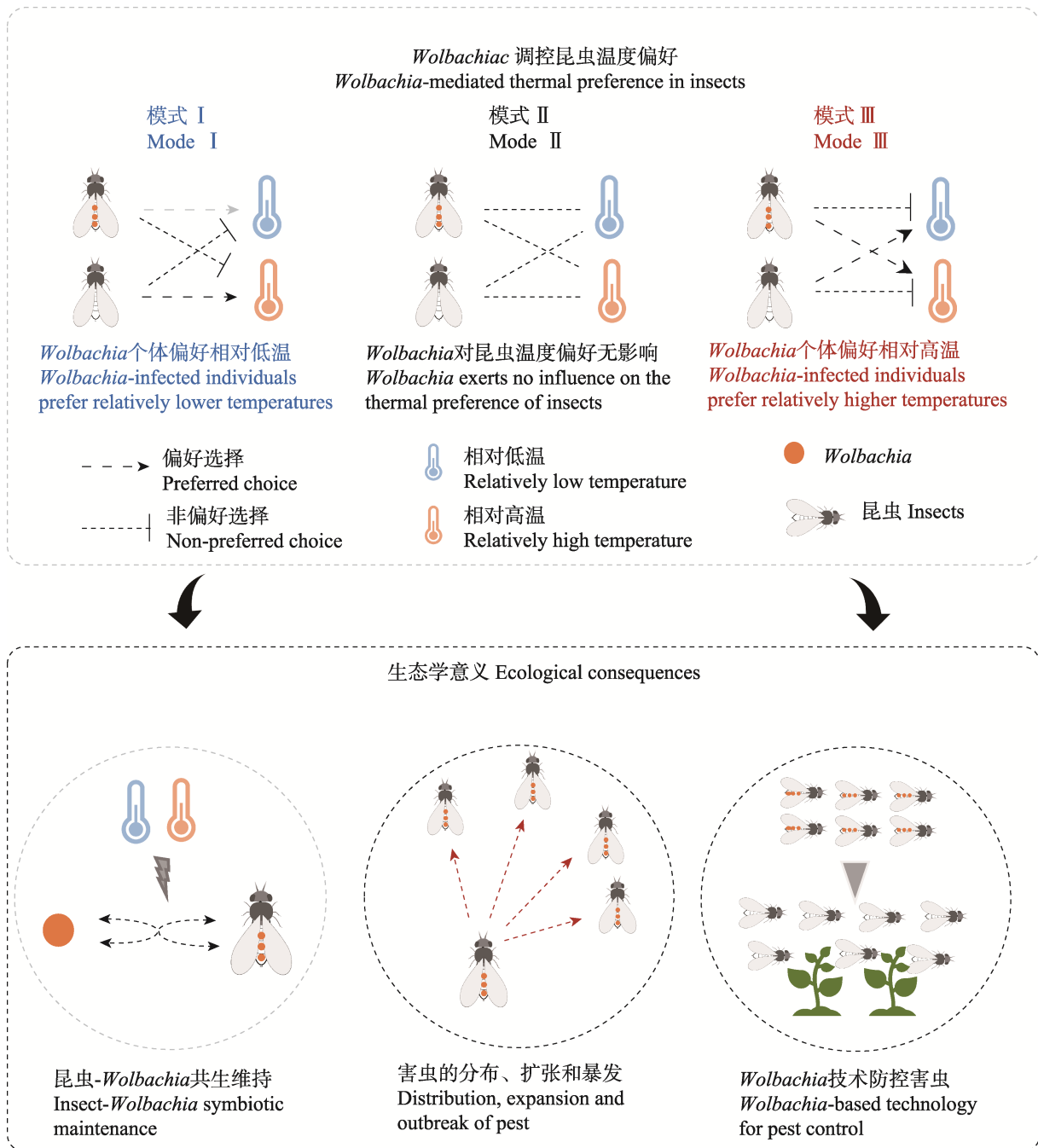
区域性适应潜力(Truitt *et al.*, 2018), 从而改变宿主的地理分布范围(Hague *et al.*, 2022)。例如, 感染 wMel 的黑腹果蝇个体, 在高纬度地区的种群扩张速率较未感染个体快 2 倍(Kriesner *et al.*, 2016)。此外, 在短期极端温度胁迫下, *Wolbachia* 介导的温度行为选择帮助宿主规避温度胁迫, 提高宿主生存概率(Hague *et al.*, 2022), 在一定程度上促进宿主的适应性进化(Lemoine *et al.*, 2020)。因此, 这种调控机制不仅增强了宿主在波动环境中的生存优势, 也可能推动昆虫种群的区域性扩散与爆发(Lemoine *et al.*, 2020)(图 1)。

3.3 害虫防治

近年来, *Wolbachia* 在害虫防治领域引起了广泛关注, 基于 *Wolbachia* 技术的害虫防治策略显现出巨大的应用潜力(Hoffmann *et al.*, 2015; 王四宝和曲爽, 2017; Ross *et al.*, 2019)。该技术基于大规模释放人工转染 *Wolbachia* 的昆虫, 利用“种群压制”或“种群替换”的策略, 控制害虫、阻断虫媒病传播和防控农业害虫(Gong *et al.*, 2023), 目前已在蚊子和稻飞虱等卫生和农业害虫防治中取得重要进展(Bian *et al.*, 2013; Zheng *et al.*, 2019; Gong *et al.*, 2020)。然而, 基于 *Wolbachia* 的害虫防治技术(种群压制/替换策略)面临温度敏感性挑战, 不利温度可能影响 *Wolbachia* 诱导的表型及共生关系, 导致防控的失效。因此, 在复杂的自然温度条件下, 害虫与 *Wolbachia* 共生关系的稳定维持是保证防控有效性的关键因素之一(Iltis *et al.*, 2022)。*Wolbachia* 对宿主温度偏好的有利调节, 增强其在复杂温度下的共生稳定性, 提高害虫防治的应用潜力(图 1)。

4 展望

在全球气候变化加剧的背景下, 昆虫-*Wolbachia* 共生功能体(Holobiont)的温度适应性研究亟待突破(Zheng *et al.*, 2023)。*Wolbachia* 介导的宿主温度偏好行为, 作为应对环境胁迫的新策略, 其广谱性及机制解析对理解共生进化与

图 1 共生菌 *Wolbachia* 调控昆虫温度偏好行为及生态学意义Fig. 1 Thermal preference mediated by *Wolbachia* and its ecological implications in insects

害虫防控具有双重意义。未来研究需聚焦以下核心问题：

第一，*Wolbachia* 对昆虫温度偏好的调控是否具有普遍性？现有研究主要围绕果蝇、斑潜蝇和叶螨等昆虫（螨）类群，且供试昆虫主要为实验室品系，未来需要针对更多的昆虫物种与 *Wolbachia* 株系，深入探究自然种群中 *Wolbachia*

对昆虫温度偏好调控的普遍性。

第二，*Wolbachia* 是否与其他微生物协同调控宿主的温度偏好性？*Wolbachia* 是许多昆虫体内的优势微生物，由于对宿主空间和营养的竞争，*Wolbachia* 感染可能影响宿主的微生物群落多样性及组成，导致感染与未感染 *Wolbachia* 的个体微生物存在差异（Audsley *et al.*, 2018；

Brinker *et al.*, 2019; Duan *et al.*, 2020); 此外, 网络分析表明 *Wolbachia* 与其他微生物存在显著相关性 (Duan *et al.*, 2025)。因此, 现有研究不能完全排除 *Wolbachia* 与其他微生物协同调控宿主温度偏好表型的可能性, 未来需要实验性的证据进一步验证。

第三, *Wolbachia* 对昆虫温度偏好性的调控机制? *Wolbachia* 调控宿主温度偏好的表型强度可能与宿主种类、*Wolbachia* 株系、滴度及组织分布紧密相关, 不同研究系统间 *Wolbachia* 诱导的表型差异的主导因素未知 (Truitt *et al.*, 2018; Hague *et al.*, 2020)。此外, 为深入解析 *Wolbachia* 调控昆虫温度偏好性的分子机制, *Wolbachia* 调控宿主温度偏好行为的效应因子、宿主靶标及其作用方式有待挖掘。

第四, *Wolbachia* 调控宿主温度偏好行为对基于 *Wolbachia* 技术防控害虫的应用局限性? 从宿主与 *Wolbachia* 共进化的视角, 这种调控作用是 *Wolbachia* 的主动适应进化, 还是宿主适应环境的被动权衡? 一般情况下, 昆虫应对温度的方式很多 (Renoz *et al.*, 2019; Serbus *et al.*, 2020), *Wolbachia* 介导的宿主温度适应对于宿主与共生菌共生关系的影响程度有多大? 此外, *Wolbachia* 调控宿主温度偏好行为, 主要适用于宿主对短期温度胁迫下的微环境调节, 极端温度的长期胁迫, 打破共生关系, 可能会限制 *Wolbachia* 技术的防控效果。

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