



植物、昆虫和昆虫肠道微生物的互作关系*

李月鲲^{1**} 迪娜·马合萨提^{1,2} 贺娟³ 何玄玉¹ 李建彩^{1***}

(1. 中国科学院分子植物科学卓越创新中心植物性状形成与塑造全国重点实验室, 上海 200032; 2. 新疆大学生命科学与技术学院新疆生物资源与基因工程重点实验室, 乌鲁木齐 830017; 3. 毕节市七星关区农业技术推广站, 毕节 551799)

摘要 植物与昆虫之间全方位的“军备竞赛”使得彼此之间的防御反应和反防御反应逐级递进, 近年来越来越多的研究发现昆虫共生微生物也参与其中。昆虫肠道是共生微生物着生的最重要场所之一, 也是植食性昆虫与寄主植物互作的关键界面。肠道微生物在植食性昆虫及其寄主植物互作过程中的作用是多方面的。首先, 肠道微生物可以为植食性昆虫合成寄主植物不能提供或者提供量不足的营养成分; 其次, 肠道微生物协助昆虫应对寄主植物防御反应, 比如操纵植物的防御信号转导和降解抗虫次生代谢产物等; 最后, 肠道微生物在植食性昆虫、寄主植物与昆虫天敌三级营养关系中也发挥着重要作用。本文综述了植物与昆虫二者之间的“攻防”互作机制, 在此基础上重点探讨了肠道微生物在昆虫适应寄主植物防御方面的作用, 展望了肠道微生物的研究方法及其在害虫综合防治中的应用前景。

关键词 植物-昆虫互作; 肠道微生物; 昆虫适应性; 植物次生代谢物; 代谢组学

The relationship between plants, insects, and gut microbiota

LI Yue-Kun^{1**} Dina · Mahesati^{1,2} HE Juan³ HE Xuan-Yu¹ LI Jian-Cai^{1***}

(1. CAS Key Laboratory of Insect Developmental and Evolutionary Biology, CAS Center for Excellence in Molecular Plant Sciences, Shanghai Institute of Plant Physiology and Ecology, Chinese Academy of Sciences, Shanghai 200032, China;

2. Xinjiang Key Laboratory of Biological Resources and Genetic Engineering, College of Life Science and Technology, Xinjiang University, Urumqi 830017, China; 3. Bijie Municipal Bureau of Agriculture, Bijie 551799, China)

Abstract The evolutionary arms race between plants and herbivorous insects is a complex process that has developed multiple facets over time. Recent studies have increasingly highlighted the role of symbiotic microorganisms in this dynamic co-evolutionary contest. The insect gut serves as a crucial interface for herbivore-plant interactions, and is also the primary habitat for symbiotic microorganisms. These microorganisms influence plant-insect interactions on several levels. First, they can provide essential nutrients that plants may not provide to herbivores. Second, insects often rely on these symbionts to cope with the defensive strategies of their host plants, including the manipulation of defense signaling pathways and the detoxification of harmful compounds. Finally, gut microbes play a significant role in tritrophic interactions between host plants, herbivorous insects and natural enemies. In this article, we review the arms race between plants and insects and emphasize how gut microorganisms help insects counter plant defenses. Furthermore, we discuss cutting-edge methodologies employed to study insect-symbiont interactions and explore the potential applications of gut microbiome research in integrated pest management.

Key words plant-insect interaction; gut microbe; insect adaptation; plant secondary metabolites; metabolomics

植物-昆虫-微生物三者在自然界中相互依存 (Engel and Moran, 2013)。一方面, 依赖植物作为庇护所和食物来源的植食性昆虫, 对植物在抗

虫防御方面的演化能够产生迅速且重大的影响 (Ramos and Schiestl, 2019); 另一方面, 植食性昆虫也演化出适应寄主植物的防御以持续从植

*资助项目 Supported project: 上海自然科学基金 (原创探索类) (23ZR1481600)

**第一作者 First author, E-mail: yuekunli.fay@gamil.com

***通讯作者 Corresponding author, E-mail: jcli@cemps.ac.cn

收稿日期 Received: 2023-05-08; 接受日期 Accepted: 2023-10-08

物获取能量的生存机制。越来越多的研究表明在这种植食性昆虫与植物的攻防互作过程中,昆虫肠道或其他组织中栖息的微生物发挥了不可忽视的作用,并且一定程度上促进了植物-昆虫攻防方式的多样性和进化上的成功 (Schmidt and Engel, 2021)。本文综述了植物与昆虫攻防互作,重点探讨了肠道微生物在该过程中的作用,展望了肠道微生物在农业害虫防治领域的应用前景。

1 植物对植食性昆虫的防御机制

类似于植物应对病原微生物的防御体系 (Yuan *et al.*, 2021b), 植物对昆虫的防御也可以分为激发子诱导 (PAMP-triggered immunity, PTI) 和效应子诱导 (Effector-triggered immunity, ETI) 的 2 种不同层级的防御反应 (Ye *et al.*, 2021; Snoeck *et al.*, 2022)。昆虫口腔分泌物中的激发子能够被植物细胞膜表面的受体所识别, 如叶绿体中的腺嘌呤核苷三磷酸合酶 (ATP synthase) 被昆虫取食消化后, 能够产生 11 个氨基酸的小肽 Inceptin。Inceptin 会被位于植物细胞膜表面的类受体蛋白激酶 INR (Inceptin receptor) 所识别, 并最终诱导植物产生包括释放挥发物在内的一系列防御反应 (Steinbrenner *et al.*, 2020, 2022)。植物识别昆虫的激发子后, 会启动一系列免疫反应, 包括胞外 Ca^{2+} 离子内流、活性氧 (Reactive oxygen species, ROS) 暴发和有丝分裂原活化蛋白激酶 (Mitogen-activated protein kinase, MAPK) 磷酸化等, 并随后进一步激活茉莉酸 (Jasmonate, JA)、水杨酸 (Salicylic acid, SA) 和乙烯 (Ethylene) 等防御信号转导途径 (Chen and Mao, 2020; Gandhi *et al.*, 2021; Yuan *et al.*, 2021a)。另外, 活性氮 (Reactive nitrogen species, RNS) 也是近年来发现的能够参与植物对昆虫的防御信号分子 (Kerchev *et al.*, 2012; Dietz *et al.*, 2016)。不同的信号通路之间会互相影响, 形成交互的网络, 共同决定了植物防御反应的输出形式。比如, 通过对渐狭叶烟草 *Nicotiana attenuata* 进行非靶向代谢组分析发现, 茉莉酸信号通路是调控植物基础防御的决定性因子, 同时乙烯信号通路调控着植物对不同害虫的特异性反应, 2 条

信号通路协同完成了植物对不同害虫的精准防御 (Li *et al.*, 2022)。

识别到植食性昆虫的危害信号后, 经过防御相关的信号转导, 植物会产生许多对昆虫有驱避、拒食或者直接毒性的次生代谢产物, 甚至还可以通过产生挥发性气体吸引害虫天敌实现间接防御 (Aljbory and Chen, 2018; Zogli *et al.*, 2020)。如喜树 *Camptotheca acuminata* 产生的喜树碱能破坏草地贪夜蛾 *Spodoptera frugiperda* 的肠道结构 (Shu *et al.*, 2021)。在甘薯 *Ipomoea batatas* 抗虫品种中, 挥发性次生物质 (E)-4,8-二甲基-1,3,7-壬三烯 (E-4,8-dimethyl-1,3,7-nonatriene, DMNT) 通过诱导甘薯产生或提高石竹烯和十三醛等多种萜烯及醛类化合物含量来提高对斜纹夜蛾 *S. littoralis* 的抗性 (Meents *et al.*, 2019)。茶树在受到茶尺蠖 *Ectropis obliqua* 的取食刺激后会产生 DMNT, DMNT 能够激活邻近植株的 JA 途径, 从而引起邻近植株对茶尺蠖的抗性响应 (Jing *et al.*, 2021)。过表达萜类物质合成基因的水稻可以通过挥发性次生代谢物质招募二化螟 *Chilo suppressalis* 的天敌二化螟盘绒茧蜂 *Cotesia chilonis* (Li *et al.*, 2018)。此外, 有些次生代谢物本来在植物体内是无毒的, 但是被昆虫取食以后会由无毒化合物转变为有毒化合物。如渐狭叶烟草被烟草天蛾 *Manduca sexta* 取食后, 叶片中原本无毒性的二萜经过羟基化修饰, 生成为靶向抑制昆虫鞘脂代谢的有毒化合物, 阻止烟草天蛾进一步取食 (Li *et al.*, 2021a)。与此同时, 植物也能够将化合物储存在体内, 待昆虫取食后生成有毒化合物。如十字花科植物特有的次生代谢物芥子油苷以糖苷的形式储存在植物的 S 细胞中, 负责解离糖苷的黑芥子酶储存在相邻的芥子细胞中; 当叶片细胞被昆虫取食破坏后, 黑芥子与芥子油苷分别从各自的细胞中释放出来, 释放出有毒的氰化物 (Shirakawa *et al.*, 2016)。植物分开储存非活性的次生代谢物和激活这些代谢物的酶, 在受到危害的情况下两者结合释放出有毒物质的体系被称为化学防御的二元系统, 即炸药 (非活性的抗虫化合物) 和点火 (酶) 两部分 (Pentzold *et al.*, 2014)。植物防御的二元系统一般是针对于抗虫代谢物的作用靶

点具有普遍性的化合物,即这些防御化合物对植物本身也是有毒的,而利用二元系统既可以实现抗虫功能,又避免了有毒化合物对植物自身的伤害 (Li *et al.*, 2022)。

除化学防御外,植物表面的结构也会构成物理性的防御。一些植物表面被有蜡质层,被视为抵抗各类生物胁迫的第一道防线 (Arya *et al.*, 2021)。在小麦与番茄中,抗性品系的毛状体和蜡质均明显多于非抗性品系 (Javed and Qiu, 2020)。部分植物表面布有毛状体 (腺毛和非腺毛),或通过物理结构阻挡昆虫移动 (Andama *et al.*, 2020; Arya *et al.*, 2021; Kortbeek *et al.*, 2021)。由黄蜂传粉的党参 *Codonopsis lanceolata* 和蜜蜂传粉的贝母 *Fritillaria koidzumiana* 的花萼都被光滑的蜡质所覆盖以阻止食蜜蚂蚁窃取果蜜 (Takeda *et al.*, 2021)。物理性防御与化学防御并非孤立,二者还可以互相促进实现最大化的害虫防御效果。比如,分泌型毛状体 (腺毛)除了具备毛状体的物理防御外,还可以合成种类丰富的挥发性或非挥发性次生代谢物,通过化合物实现直接防御或间接防御 (Fiesel *et al.*, 2024)。

2 昆虫对植物防御的适应性机制

针对植物不同层级和方式的防御,昆虫也相应进化出不同的应对策略 (图 1)。昆虫可以通过分泌效应蛋白抑制激发子诱导的防御反应,如刺吸式口器害虫蚜虫口腔分泌物中的 C002、Mp1、Mp10 和 Mp42 (van Bel and Will, 2016; Elston *et al.*, 2023) 及褐飞虱 *Nilaparvata lugens* 口腔分泌物中的 NIShp、NIEG1 和 NISEF1 等 (Huang *et al.*, 2019),其作用机理与植物病原菌效应子介导的感病性 (Effector triggered susceptibility, ETS) (Todd *et al.*, 2022) 相似。咀嚼式昆虫如棉铃虫 *Helicoverpa armigera* 口腔分泌物中鉴定到的效应蛋白 HARP-1 (Chen *et al.*, 2019) 和 HAS-1 (Chen *et al.*, 2023),可以作用于茉莉酸通路关键负调控因子 JAZ 进而抑制植物的防御反应。植物还进化出了针对 ETS 的免疫系统。植物依赖于胞内的受体蛋白 (Nucleotide-binding leucine-rich repeat, NLR) 发挥 ETI 的防

御反应,提高了对植食性昆虫的抗性。最近,有研究鉴定到水稻中关键的抗褐飞虱基因 *BPH14* 能够识别褐飞虱效应蛋白 BISP,并解析了水稻精细调控 ETI 反应对褐飞虱生长抑制作用的分子机制 (Guo *et al.*, 2023),该研究发现植物抗虫基因 (PTI)、效应子诱导的感虫性 (ETS) 和效应子诱导的抗虫性 (ETI) 均参与了植物-昆虫互作过程,证实了经典的植物抗病 Zig-zag 模型 (Jones and Dangl, 2006; Ngou *et al.*, 2022) 同样适用于植物抗虫。

大多数情况下植物的防御反应并不会在防御信号转导层面完全被抑制,信号会继续传递下去诱导次生代谢物质的合成并阻止昆虫的进一步危害。昆虫也进化出了针对于植物次生代谢物的适应性策略。虽然尼古丁是烟草属植物产生的一种重要抗虫生物碱,但是茄科植物专食性昆虫烟草天蛾已经进化出对尼古丁极强的耐受性,可以通过粪便排出几乎所有的尼古丁 (Kumar *et al.*, 2014b),甚至还可以吸收少部分尼古丁驱避其天敌 (Kumar *et al.*, 2014a)。烟粉虱 *Bemisia tabaci* 基因组中包含了开源于植物中的编码酚糖丙二酰基转移酶的同源基因,该酰基转移酶可以通过修饰酚糖类化合物降低其对烟粉虱的毒性 (Xia *et al.*, 2021),说明通过“水平转移”获取解毒基因也是昆虫适应植物抗性的一种手段。对烟草天蛾幼虫的粪便进行代谢组分析,发现烟草天蛾可以通过利用植物自身 2 种防御物质,绿原酸和 17-羟基香叶酰芳樟醇二萜苷 (HGL-DTGs) 来进行相互解毒 (Heiling *et al.*, 2022)。除了对有毒化合物直接加以修饰或转化,植食性昆虫还能隔离植物有毒化合物,利用其抵御天敌也是一种常见的策略 (Beran and Petschenka, 2022)。如强心甙 (Cardenolides) 作为一类植物合成的三萜类化合物,能够作用于昆虫细胞膜表面 Na^+/K^+ 离子通道 (Na^+/K^+ -ATPase); 帝王蝶 *Danaus plexippus* 在演化过程中通过突变 Na^+/K^+ -ATPase 的关键氨基酸位点,阻碍了强心甙与 Na^+/K^+ -ATPase 的结合 (Karageorgi *et al.*, 2019),它们还可以在体内积累高浓度的强心甙,驱避寄生蜂的寄生 (Stenoien *et al.*, 2019)。

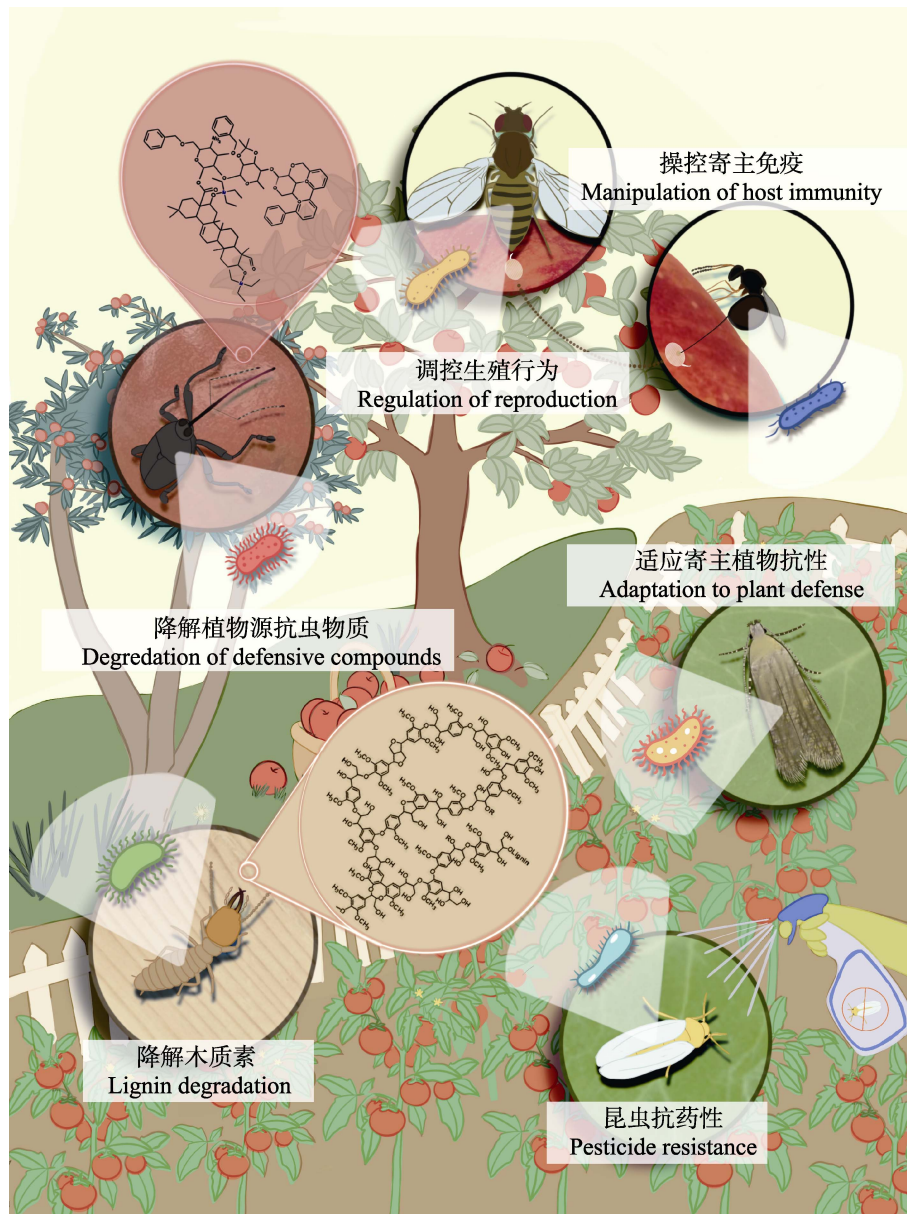


图 1 昆虫的共生微生物能够帮助昆虫更好地适应环境

Fig. 1 Symbiotic microorganisms contribute insects to adapt harsh environments

萝卜肖叶甲属的 *Chrysoschus auratus* 体内的 ABC 转运蛋白能够响应强心甙的诱导并将其转运至储存器官 (Kowalski *et al.*, 2020), 用来应对天敌。除强心甙外, 辣根跳甲 *Phyllotreta armoraciae* 马氏管中的糖转运体能够选择性吸收硫代葡萄糖苷, 利用积累的硫代葡萄糖苷来抵御昆虫天敌 (Yang *et al.*, 2021b)。然而, 转运体如何识别硫代葡萄糖苷、昆虫如何精准调控吸收和利用特定硫代葡萄糖苷等问题仍需要进一步探索。

昆虫肠道是解毒的主要场所, 肠道从口开

始, 分为前肠、中肠和后肠, 直到肛门结束 (Terra *et al.*, 2018)。肠道的不同部位环境和结构具有较大差异, 这也导致其在功能上的不同。对于解毒来说, 大多数昆虫的前肠被角质层包被, 如辣根跳甲的前肠几乎被几丁质覆盖, 可以有效应对植物的物理防御, 减少对上皮细胞的破坏; 同时前肠也是芥子油苷吸收的主要部位。选择几丁质覆盖的区域吸收芥子油苷, 可能是为了缩短芥子油苷暴露在黑芥子酶下的时间 (Sporer *et al.*, 2021; Yang *et al.*, 2022)。在前肠降解植物次生

代谢物质, 避免有毒物质继续流向中肠和后肠, 缩短了昆虫暴露在有毒物质中的时间, 这也可能是昆虫应对植物防御性次生代谢物的一种策略。昆虫的后肠则处于相对厌氧和营养贫瘠的环境, 但依然有不少微生物定殖在昆虫的后肠。蜜蜂的肠道寄生虫 *Lotmaria passim* 能够通过降低自身蛋白质翻译、糖酵解和氧自由基清除相关基因的表达而专性寄生于蜜蜂后肠 (Liu *et al.*, 2020b)。

中肠是昆虫消化、免疫和解毒主要发生的场所。大多数昆虫具有独特的围食膜 (Peritrophic membrane, PM) 结构, 半翅目 Hemiptera 和缨翅目 Thysanoptera 昆虫没有围食膜, 但具有微绒毛膜结构 (Perimicrovillar membranes, PMM) (Terra and Ferreira, 2009; Klowden, 2013)。PM 由几丁质与糖蛋白组成, 具有充满孔隙且多层重叠的折叠结构, 也是肠道微生物着生的合适场所。蝗虫肠道中的 PM 结构完整性与肠道微生物定殖数量和传播力相关 (Yang *et al.*, 2021a)。家蚕的 PM 结构在食物丰富时会表现得细密平滑, 一旦饥饿或清除肠道微生物则会变得粗糙且松散 (Zha *et al.*, 2021), 暗示了 PM 在昆虫营养吸收及微生物定殖方面重要的地位。细菌表面的几丁质结合蛋白能够与 PM 上的几丁质结合 (Qin *et al.*, 2020), 帮助细菌更好地附着在鳞翅目昆虫的肠道内。植物的挥发性次生代谢物 DNMT 通过抑制 PM 上编码粘蛋白样蛋白质的 *PxMucin* 基因的表达而破坏了 PM 结构, 最终导致小菜蛾 *Plutella xylostella* 幼虫的死亡 (Chen *et al.*, 2021), 这也可能是由于肠道微生物失衡而引起。

3 肠道微生物在昆虫-植物互作中的研究现状

肠道是包括昆虫在内的所有动物消化和吸收营养的器官, 也是微生物最为富集的器官。昆虫肠道微生物在不同种类的昆虫之间体现出群落结构差异大和分布位置不同的特点。昆虫肠道微生物组成受到宿主紧密调节, 即使在同一种昆虫肠道内, 寄主植物的差异也会导致昆虫肠道微生物结构呈现显著差异。取食 2 种不同山茶树 *Camellia oleifera* 和 *Camellia reticulata* 种子的山

茶花象甲 *Curculio chinensis* 肠道微生物群落结构显著不同, 优势菌门的相对丰度也完全不同 (Zhang *et al.*, 2020)。在取食垂柳 *Salix babylonica*、银白杨 *Populus alba* 和二白杨 *Populus gansuensis* 3 种不同树种的光肩星天牛 *Anoplophora glabripennis* 肠道中, 微生物多样性、组成及结构也具有显著差异 (Wang *et al.*, 2022)。与此同时, 肠道微生物在昆虫肠道中分布的区域十分广泛。家白蚁 *Coptotermes formosanus* 肠道中的原生生物共生体 *Cononympha leidy* 定殖于白蚁后肠 (Nishimura *et al.*, 2020)。不动杆菌 *Acinetobacter* sp. strain 在山茶花象甲前肠、中肠和后肠均有分布, 并且在山茶花象甲危害的茶树附近土壤中, 也检测到不动杆菌 (Zhang *et al.*, 2022), 表明肠道微生物的来源或许与寄主和生境有关。黑腹果蝇 *Drosophila melanogaster* 前肠定殖的醋酸杆菌 *Acetobacter thailandicus* 可以提高果蝇生殖力, 缩短发育历期, 并且该菌可以通过食物作为介质水平传播至群体中的其他果蝇甚至子代 (Pais *et al.*, 2018; Stoffolano, 2019)。部分定殖在中肠隐窝处的细菌 (Sato *et al.*, 2021), 由于接触面积受限, 在昆虫体内解毒的效率可能受到隐窝特有的褶皱结构影响。

肠道微生物的功能多种多样 (Blow *et al.*, 2020)。锥蝽 *Rhodnius prolixus* 中肠内多种细菌参与了 B 族维生素的生物合成 (Tobias *et al.*, 2020)。臭蝽属 *Megacopta punctatissima* 中肠第 4 区域定殖的细菌 *Ishikawaella* 能够给宿主提供必需氨基酸, 如支链氨基酸和芳香族氨基酸; 失去了共生菌的臭蝽若虫颜色变浅、生长缓慢、体型减小, 且存活率降低 (Moriyama and Fukatsu, 2022), 暗示了肠道微生物与寄主不可分割的共生关系。有意思的是, 共生菌 *Ishikawaella* 的垂直传播依赖于臭蝽产卵时产生的“共生胶囊”, 若虫通过咬破胶囊来获得共生菌, 未能获得该菌的初孵幼虫的生长受到严重抑制 (Koga *et al.*, 2021)。这一看似“冗余”的胶囊结构, 实际上确保了臭蝽若虫能够在孵化后第一时间获取有益共生菌, 大大提高了若虫获取共生微生物的效率, 促进了后代种群繁衍。点蜂缘蝽 *Riptortus*

pedestris 中肠定殖的 *Burkholderia* 属细菌可以将寄主昆虫的代谢废物（如尿酸）转化为氨基酸，但 *Burkholderia* 对胁迫更敏感且丧失了运动能力，细胞表面也与体外培养的状态具有很大差别，表现出对寄主更强的依赖性（Ohbayashi *et al.*, 2019）。肠道微生物还会参与调节昆虫的免疫反应，如红棕象甲 *Rhynchophorus ferrugineus* 的肠道共生菌群通过上调病原体识别受体、核因子- κ B 和抗菌肽相关基因来增强宿主的免疫能力（Muhammad *et al.*, 2019），从而提高红棕象甲幼虫对粘质沙雷菌的抗性。值得一提的是，由于原生生物不易被观察到，其功能基因有可能会被误判为属于真菌或细菌。对肠道不同来源或分类的微生物的观察，有助于进一步了解昆虫肠道中尚未发现的微生物种类。另一个有趣的现象是，同一属的肠道微生物可能在不同昆虫中具有普遍的功能。如魏斯氏菌 *Weissella* 介导了德国小蠊 *Blattella germanica* 的聚集行为（Wada-Katsumata *et al.*, 2015），在具有同样聚集行为的沙漠蝗 *Schistocerca gregaria* 和东亚飞蝗 *Locusta migratoria* 的肠道中魏斯氏菌也被发现占有主导地位（Lavy *et al.*, 2020）。尽管在沙漠蝗产卵时分泌的泡沫栓状物中发现含有定殖的部分肠道菌，魏斯氏菌却没有在垂直传播的过程中被传播给下一代（Lavy *et al.*, 2021），暗示了蝗虫聚集行为的复杂性。魏斯氏菌在昆虫成长中后期才占有主导地位可能是由于其生长消耗了寄主大量能量，在生长期无法保证能量供应导致。

植食性昆虫的肠道微生物在昆虫与植物互动过程中同样重要。在植物防御早期的信号转导阶段，肠道微生物能够通过直接作用于植物防御信号转导或植物代谢物的方式参与昆虫适应植物的防御反应。如豌豆蚜 *Acyrtosiphon pisum* 唾液腺中的沙雷氏菌 *Serratia symbiotica* 可以利用富含组氨酸的 Ca^{2+} 结合蛋白 ApHRC 抑制植物中 Ca^{2+} 离子通道和 ROS 积累，从而抑制植物对昆虫的防御反应（Wang *et al.*, 2020）。稻绿蝽 *Nezara viridula* 的共生微生物 *Sodalis* sp. 可以抑制植物 JA 通路上调，因此也有可能直接抑制植

物的脂肪族硫代葡萄糖苷防御途径（Coolen *et al.*, 2024）。反之，植物也会通过识别昆虫的肠道微生物群落，直接启动对昆虫的防御功能。如玉米叶片上着生的腺毛含有几丁质酶，草地贪夜蛾取食后会导致肠道的 PM 结构被严重破坏，肠内微生物流出至血腔进一步抑制草地贪夜蛾的生长（Mason *et al.*, 2019）。目前，尚不清楚相对于直接识别昆虫取食过程中分泌的唾液激发子，识别肠道微生物的优势有哪些，未来研究亟需解析肠道微生物在昆虫-植物互作的信号转导过程发挥作用的生态学优势。

肠道微生物在昆虫适应植物的次生代谢物方面也发挥重要作用，如参与解毒有害的糖苷、萜类化合物和生物碱（Salem and Kaltentpoth, 2022）。不动杆菌 *Acinetobacter* sp. strain AS23 能够有效帮助山茶花象甲降解茶皂苷（Zhang *et al.*, 2020）。假单胞杆菌 *Pseudomonas fulva* 在咖啡果小蠹 *Hypothenemus hampei* 肠道中定殖，可以帮助咖啡果小蠹降解咖啡因，并通过卵垂直传播给子代（Ceja-Navarro *et al.*, 2015; Vega *et al.*, 2021）。卷心菜茎跳蚤甲虫 *Psylliodes chrysocephala* 的肠道菌 *Pantoea* 参与降解异硫氰酸酯类次生代谢物质 4-甲基亚磺酸丁基硫代葡萄糖苷（4MSOB GLS）（Shukla and Beran, 2020）。根大小蠹 *Dendroctonus rhizophagus* 肠道内的共生酵母 *Cyberlindnera americanake* 能够降解单萜，帮助小蠹虫应对韧皮部中的高毒性萜烯类次生代谢物质（Soto-Robles *et al.*, 2019）。马铃薯甲虫 *Leptinotarsa decemlineata* 的肠道共生菌肠杆菌 *Enterobacter* BC-8 能够帮助昆虫在取食时抑制植物因受到机械损伤而引起的过氧化物反应和酚类物质积累（Sorokan *et al.*, 2020）。针对细胞壁加厚、木质化和栓质化等植物的物理防御，肠道微生物还可以直接协助昆虫破碎植物细胞壁，如木质素的降解。家白蚁 *Coptotermes formosanus* 肠道中的原生生物共生体 *C. leidy* 参与了降解木质素（Nishimura *et al.*, 2020）。肠道微生物帮助昆虫适应形态各异和营养不均衡的植物，反映了三者互动关系的多样性和可塑性，以及肠道微生物功能繁多的潜力（表 1）。

表 1 不同昆虫肠道微生物的功能及研究方法
Table 1 The function and methodology of insect symbiotic microorganisms

微生物名称 Name	可否分离 培养 Culturable or not	寄主昆虫 Host insect	体内定位 Localization	传播方式 Transmission	对宿主的功能 Function	测定方法 Methodology	参考文献 Reference
<i>Ishikawaella</i>	Y	凹斑豆龟蜡 <i>Megacopta punctatissima</i>	中肠 Midgut	经体外胶囊垂 直传播 Vertical transmission via capsules	提供必须氨基酸 Supply essential amino acids	表型观察 Phenotype quantification	Koga <i>et al.</i> , 2021; Moriyama and Fukatsu, 2022
<i>Enterobacter ludwigii</i>	Y	棉铃虫 <i>Helicoverpa zea</i>	肠道 Gut	未知 Unknown	增强寄主免疫 Enhance host immunity	检测免疫相关基 因表达量 Quantification of immunity-related gene expression	Wang <i>et al.</i> , 2018
<i>Acetobacter thailandicus</i>	Y	黑腹果蝇 <i>Drosophila melanogaster</i>	前肠 Foregut	以食物为介质 进行水平和垂 直传播 Horizontal and vertical transmission via foods	促进生长发育 Promote growth and development	无菌体系和生物 测定 Axenic system and bioassay	Pais <i>et al.</i> , 2018; Stoffolano, 2019
<i>Acetobacter pomorum</i> & <i>Bacillus</i> sp.	Y	布拉迪小环腹 瘿蜂 <i>Leptopilina boulardi</i>	未知 Unknown	未知 Unknown	决定寄生能否 成功 Defining host permissiveness for parasites	无菌体系和生物 测定 Axenic system and bioassay	Zhou <i>et al.</i> , 2022
<i>Weissella</i>	Y	德国小蠊 <i>Blattella germanica</i> 沙漠蝗虫 <i>Schistocerca gregaria</i>	粪便 Feces	通过泡沫塞垂 直传播 Vertical transmission via foam plug	诱导聚集行为 Triggering aggregation	无菌体系和生物 测定 Axenic system and bioassay	Wada-Katsumata <i>et al.</i> , 2015; Lavy <i>et al.</i> , 2020; Lavy <i>et al.</i> , 2021
<i>Pantoea</i>	Y	卷心菜茎跳蚤 甲虫 <i>Psylliodes chrysocephala</i>	肠道 Gut	未知 Unknown	降解植物抗虫物 质 Degradation of 4MSOB-GLS	无菌体系和生物 测定 Axenic system and bioassay	Shukla and Beran, 2020
<i>Cyberlindnera americana</i>	Y	根大小蠹 <i>Dendroctonus rhizophagus</i>	全身多 处/粪便 Body and Feces	未知 Unknown	对萜类化合物进 行解毒 Detoxification of Terpenoids	转录组学 Transcriptome	Soto-Robles <i>et al.</i> , 2019
<i>Cononympha leidyi</i>	N	家白蚁 <i>Coptotermes formosanus</i>	后肠 Hindgut	未知 Unknown	降解木质素 Degradation lignin	单细胞测序 Single-cell sequencing	Jasso-Selles <i>et al.</i> , 2020; Nishimura <i>et al.</i> , 2020
<i>Pseudomonas fulva</i>	Y	咖啡果小蠹 <i>Hypothenemus hampei</i>	肠道/ 粪便 Gut and Feces	随卵垂直传播 Vertical transmission via eggs	降解咖啡因 Degradation of caffeine	质谱检测 Mass spectrum detection	Ceja-Navarro <i>et al.</i> , 2015; Vega <i>et al.</i> , 2021
<i>Acinetobacter</i> sp. AS23	Y	山茶花象甲 <i>Curculio chinensis</i>	肠道 Gut	Horizontal transmission via environments	降解茶皂苷 Degradation of saponin	质谱检测 Mass spectrum detection	Zhang <i>et al.</i> , 2020; Zhang <i>et al.</i> , 2022

续表 1 (Table 1 continued)

微生物名称 Name	可否分离 培养 Culturable or not	寄主昆虫 Host insect	体内定位 Localization	传播方式 Transmission	对宿主的功能 Function	测定方法 Methodology	参考文献 Reference
<i>Enterobacter</i> BC-8	Y	马铃薯甲虫 <i>Leptinotarsa</i> <i>decemlineata</i>	肠道 Gut	未知 Unknown	抑制植物抗虫性 Inhibiting plant defense	微生物接种和植 物抗性评估 Bacteria inoculation and plant defense evaluation	Sorokan <i>et al.</i> , 2020
<i>Hamiltonella</i> <i>defensa</i>	N	狄草谷网蚜 <i>Sitobion</i> <i>miscanthi</i> , 烟粉虱 <i>Bemisia tabaci</i>	后肠、 卵巢 Hindgut and ovary	垂直和水平 传播 Horizontal and vertical transmission	提高抗药性 Enhancing pesticide- resistance	原位杂交 Insite hybridization	Shan <i>et al.</i> , 2019; Kaech and Vorburger, 2020; Li <i>et al.</i> , 2021b; Yao <i>et al.</i> , 2023

Y, Yes, 是; N, No, 否。

不仅如此，肠道微生物还参与了昆虫-天敌之间军备竞赛(Beran and Petschenka, 2022; Speer, 2022)，在昆虫与捕食性或寄生性天敌的协同进化进程中扮演着重要角色。如黄粉虫 *Tenebrio molitor* 被缩小膜壳绦虫 *Hymenolepis diminuta* 寄生后，缩小膜壳绦虫在失去肠道共生菌的宿主上的寄生成功率会显著降低(Fredensborg *et al.*, 2020)，肠道微生物的结构和群落结构发生了明显变化；此类现象在膜翅目昆虫中也具报道，如清除宿主肠道共生菌后，布拉迪小环腹瘿蜂 *Leptopilina boulardi* 无法在黑腹果蝇上完成完整的生活史(Zhou *et al.*, 2022)。

4 肠道菌群在害虫综合防治的研究展望

肠道微生物在植食性昆虫适应环境和寄主植物抗性方面发挥着重要作用，越来越多的研究指出靶向肠道微生物的农业害虫防治措施是植物保护发展的重要方向之一(Jordan *et al.*, 2021)。如植物共生菌假单胞菌 *Pseudomonas protegens* 既可以诱导植物防御、抑制植物病害，又可以靶向昆虫肠道微生物菌群，显著改变了菜粉蝶 *Pieris brassicae* 幼虫肠道内肠杆菌 *Enterobacteriaceae* 家族的丰度，最终实现抑制菜粉蝶生长的同时也增强植物抗病性(Vacheron *et al.*, 2019)。通过肠道微生物进行害虫防治，可

以达到“一举两得”的效果。狄草谷网蚜 *Sitobion miscanthi* 共生菌 *Hamiltonella defensa* 能够通过增加解毒酶活性显著降低狄草谷网蚜对低剂量杀虫剂的敏感性，提高其解毒能力(Li *et al.*, 2021b)。去除该共生菌为提高狄草谷网蚜的防治效果提供了另一视角。清除共生菌 *Hamiltonella defensad* 导致烟粉虱无法完成正常受精，仅能产生雄性后代(Shan *et al.*, 2019; Yao *et al.*, 2023)。基于共生菌 *Wolbachia* 的胞质不相容技术(Incompatible insect technique-IIT)结合基于辐射的昆虫不育技术(Sterile insect technique-SIT)，可以成功清除入侵物种白纹伊蚊 *Aedes albopictus* 种群(Zheng *et al.*, 2019)，克服了基因编辑外溢的风险，有效减少了白纹伊蚊的数量。因此，全面揭示肠道微生物对农业害虫适应、农药降解和作物抗性方面的功能，针对性地清除或积累对农业害虫防控不同方面具有协同效果的肠道微生物是农业害虫防控的新路径。

对于植食性昆虫肠道微生物的深入研究，能够从宏观的角度理解环境-植物-昆虫三者微生物网络，进一步服务于农业害虫防治和生态保护。一方面，进行害虫防治时需关注原有微生物的减少或流失，预防由于当地微生物群落结构改变而引起病虫害的暴发或加剧。如杀虫剂的持续使用会降低土壤微生物的多样性，伯克霍尔德氏菌 *Burkholderia* 可以降解杀虫剂杀螟硫磷，在持续用药的土壤中成为优势菌群，协助点蜂缘蝽增

强抗药性 (Itoh *et al.*, 2018)。事实上, 昆虫肠道微生物、植物根际微生物和土壤微生物三者在群落构成上存在共享种群。碳氮循环和极端天气等宏观尺度的变化会对土壤微生物造成显著影响, 土壤环境的改变也能够重塑植物根际微生物 (Jansson and Hofmockel, 2020); 土壤微生物群落可以进一步影响植物对昆虫的抗性 (Pineda *et al.*, 2020), 并影响昆虫肠道微生物群落构成, 在空间和时间的尺度上改变昆虫肠道微生物的优势种群 (Hannula *et al.*, 2019; Gomes *et al.*, 2020)。因此, 害虫的传播及定殖与其所在环境空间关系密切, 二者互为因果。另一方面, 外来微生物的引入可能会改变原有生态系统的平衡, 在水平或垂直方向发生溢出效应, 动态改变昆虫生存的原生生态系统 (Thakur *et al.*, 2019; Xia *et al.*, 2021)。外来物种入侵的过程中, 微生物会随之一同迁入新的栖息地, 如果条件适宜则会随着宿主定殖于新的生态系统中 (Thakur *et al.*, 2019)。如伴生真菌 *Leptographium procerum* 可以通过松树害虫红脂大小蠹 *Dendroctonus valens* 招募当地菌群, 通过降解酚类物质柚皮素和加速真菌碳水化合物等代谢途径组成复杂的共生体, 使入侵昆虫的适应性显著增强, 最终成功定殖于不同国家, 造成对松树的全球性破坏 (Cheng *et al.*, 2018; Liu *et al.*, 2020a)。因此, 保护当地土壤微生物种群的丰富度, 关注动植物入侵所伴随的微生物入侵, 是农业害虫防治和生态管理需要关注的新方向 (Carrasco-Espinosa *et al.*, 2022)。区别于传统的“植物-昆虫”二元关系, 从“植物-昆虫-微生物”三者关系, 甚至“植物-昆虫-微生物-天敌”四者之间立体耦合的互作网络考虑更有助于治理外来入侵物种和农药评估对环境的影响。

5 结语

作为“看不见的大多数”, 在地下环境和极端气候条件下, 微生物甚至可能是惟一的生命体形式 (Cavicchioli *et al.*, 2019)。了解包括肠道微生物在内的共生微生物, 对于系统理解昆虫与植物的互作关系和农业害虫防治至关重要。自 1923

年人们关注到昆虫肠道微生物与其生存环境至今 (Cleveland, 1923), 越来越多的研究发现微生物不仅对昆虫的生长发育不可或缺, 还参与“植物-昆虫”之间的攻防互作。肠道微生物对于昆虫及其寄主植物的重要性, 不仅体现在协助昆虫应对植物次生代谢产物以及其他寄主植物对昆虫的防御机制, 更体现在肠道微生物在植食性昆虫-寄主植物-昆虫天敌的三级营养关系中, 彼此协同进化的互作模式。植物、昆虫与其共生微生物共同经历着遗传与生理生化的演化, 三者的关联不仅塑造了植物和昆虫的表型, 更进一步影响了植物和昆虫相互作用的方式, 甚至是物种的进化轨迹 (Gupta and Nair, 2020; Smee *et al.*, 2021)。植物在进化的角度上发展出更多类型的次生代谢物质应对昆虫, 极大扩增了天然产物的多样性。在植物不同的防御模式下, 促使昆虫进化出多变的策略用以应对有毒的植物次生代谢物质, 昆虫与肠道微生物动态的共生效应也促使昆虫或昆虫肠道微生物协同进化。植物、昆虫与昆虫肠道微生物三者的互作关系体现出重要的生态和经济价值 (van den Bosch and Welte, 2017; Bai *et al.*, 2021), 为农业管理提供了全新角度。未来有望从群落结构整体出发, 设计出更具有绿色和特色的生物防治产品。

参考文献 (References)

- Aljbory Z, Chen MS, 2018. Indirect plant defense against insect herbivores: A review. *Insect Science*, 25(1): 2–23.
- Andama JB, Mujiono K, Hojo Y, Shinya T, Galis I, 2020. Nonglandular silicified trichomes are essential for rice defense against chewing herbivores. *Plant Cell & Environment*, 43(9): 2019–2032.
- Arya GC, Sarkar S, Manasherova E, Aharoni A, Cohen H, 2021. The plant cuticle: An ancient guardian barrier set against long-standing rivals. *Frontiers in Plant Science*, 12: 663165.
- Bai S, Yao Z, Raza MF, Cai Z, Zhang H, 2021. Regulatory mechanisms of microbial homeostasis in insect gut. *Insect Science*, 28(2): 286–301.
- Beran F, Petschenka G, 2022. Sequestration of plant defense compounds by insects: From mechanisms to insect-plant coevolution. *Annual Review of Entomology*, 67: 163–180.

- Blow F, Ankrah NYD, Clark N, Koo I, Allman EL, Liu Q, Anitha M, Patterson AD, Douglas AE, 2020. Impact of facultative bacteria on the metabolic function of an obligate insect-bacterial symbiosis. *mBio*, 11: e00402-20
- Carrasco-Espinosa K, Avitia M, Barron-Sandoval A, Abbruzzini TF, Salazar Cabrera UI, Arroyo-Lambauer D, Uscanga A, Campo J, Benitez M, Wegier A, Rosell JA, Reverchon F, Hernandez G, Boege K, Escalante AE, 2022. Land-use change and management intensification is associated with shifts in composition of soil microbial communities and their functional diversity in coffee agroecosystems. *Microorganisms*, 10(9):1763.
- Cavicchioli R, Ripple WJ, Timmis KN, Azam F, Bakken LR, Baylis M, Behrenfeld MJ, Boetius A, Boyd PW, Classen AT, Crowther TW, Danovaro R, Foreman CM, Huisman J, Hutchins DA, Jansson JK, Karl DM, Koskella B, Mark Welch DB, Martiny JBH, Moran MA, Orphan VJ, Reay DS, Remais JV, Rich VI, Singh BK, Stein LY, Stewart FJ, Sullivan MB, van Oppen MJH, Weaver SC, Webb EA, Webster NS, 2019. Scientists' warning to humanity: Microorganisms and climate change. *Nature Reviews Microbiology*, 17(9): 569–586.
- Ceja-Navarro JA, Vega FE, Karaoz U, Hao Z, Jenkins S, Lim HC, Kosina P, Infante F, Northen TR, Brodie EL, 2015. Gut microbiota mediate caffeine detoxification in the primary insect pest of coffee. *Nature Communications*, 6: 7618.
- Chen C, Chen H, Huang S, Jiang T, Wang C, Tao Z, He C, Tang Q, Li P, 2021. Volatile DMNT directly protects plants against *Plutella xylostella* by disrupting the peritrophic matrix barrier in insect midgut. *Elife*, 10: e63938.
- Chen CY, Liu YQ, Song WM, Chen DY, Chen FY, Chen XY, Chen ZW, Ge SX, Wang CZ, Zhan S, Chen XY, Mao YB, 2019. An effector from cotton bollworm oral secretion impairs host plant defense signaling. *Proceedings of National Academy of Science of the United States of America*, 116(28): 14331–14338.
- Chen CY, Mao YB, 2020. Research advances in plant-insect molecular interaction. *F1000Res*, 9: F1000 Faculty Rev-198.
- Chen X, Liu YQ, Wu MN, Yan L, Chen CY, Mu YP, Liu YJ, Wang MY, Chen XY, Mao YB, 2023. A highly accumulated secretory protein from cotton bollworm interacts with basic helix-loop-helix transcription factors to dampen plant defense. *New Phytologist*, 237(1): 265–278.
- Cheng C, Wickham JD, Chen L, Xu D, Lu M, Sun J, 2018. Bacterial microbiota protect an invasive bark beetle from a pine defensive compound. *Microbiome*, 6(1): 132.
- Cleveland LR, 1923. Correlation between the food and morphology of termites and the presence of intestinal protozoa. *American Journal of Epidemiology*, 3(4): 444–461.
- Coolen S, Rogowska-van der Molen MA, Kwakernaak I, van Pelt JA, Postma JL, van Alen T, Jansen RS, Welte CU, 2024. Microbiota of pest insect *Nezara viridula* mediate detoxification and plant defense repression. *The ISME Journal*, 18(1): wrae097.
- Dietz KJ, Mittler R, Noctor G, 2016. Recent progress in understanding the role of reactive oxygen species in plant cell signaling. *Plant Physiology*, 171(3): 1535–1539.
- Elston KM, Maeda GP, Perreau J, Barrick JE, 2023. Addressing the challenges of symbiont-mediated RNAi in aphids. *PeerJ*, 11: e14961.
- Engel P, Moran NA, 2013. The gut microbiota of insects-diversity in structure and function. *FEMS Microbiology Reviews*, 37(5): 699–735.
- Fiesel PD, Kerwin RE, Jones AD, Last RL, 2024. Trading acyls and swapping sugars: Metabolic innovations in solanum trichomes. *Plant Physiology*, 196(2): 1231–1253.
- Fredensborg BL, Fossdal IKI, Johannesen TB, Stensvold CR, Nielsen HV, Kapel CMO, 2020. Parasites modulate the gut-microbiome in insects: A proof-of-concept study. *PLoS ONE*, 15(1): e0227561.
- Gandhi A, Kariyat R, Harikishore A, Ayati M, Bhunia A, Sahoo N, 2021. Deciphering the role of ion channels in early defense signaling against herbivorous insects. *Cells*, 10(9): 2219.
- Gomes SIF, Kielak AM, Hannula SE, Heinen R, Jongen R, Keesmaat I, De Long JR, Bezemer TM, 2020. Microbiomes of a specialist caterpillar are consistent across different habitats but also resemble the local soil microbial communities. *Animal Microbiome*, 2(1): 37.
- Guo J, Wang H, Guan W, Guo Q, Wang J, Yang J, Peng Y, Shan J, Gao M, Shi S, Shangguan X, Liu B, Jing S, Zhang J, Xu C, Huang J, Rao W, Zheng X, Wu D, Zhou C, Du B, Chen R, Zhu L, Zhu Y, Walling LL, Zhang Q, He G, 2023. A tripartite rheostat controls self-regulated host plant resistance to insects. *Nature*, 618(7966): 799–807.
- Gupta A, Nair S, 2020. Dynamics of insect-microbiome interaction influence host and microbial symbiont. *Frontiers in Microbiology*, 11: 1357.
- Hannula SE, Zhu F, Heinen R, Bezemer TM, 2019. Foliar-feeding insects acquire microbiomes from the soil rather than the host plant. *Nature Communications*, 10(1): 1254.
- Heiling S, Li J, Halitschke R, Paetz C, Baldwin IT, 2022. The downside of metabolic diversity: Postingestive rearrangements

- by specialized insects. *Proceedings of National Academy of Science of the United States of America*, 119(24): e2122808119.
- Huang HJ, Zhang CX, Hong XY, 2019. How does saliva function in planthopper-host interactions? *Archives of Insect Biochemistry and Physiology*, 100(4): e21537.
- Itoh H, Hori T, Sato Y, Nagayama A, Tago K, Hayatsu M, Kikuchi Y, 2018. Infection dynamics of insecticide-degrading symbionts from soil to insects in response to insecticide spraying. *The ISME Journal*, 12(3): 909–920.
- Jansson JK, Hofmockel KS, 2020. Soil microbiomes and climate change. *Nature Reviews Microbiology*, 18(1): 35–46.
- Jasso-Selles DE, De Martini F, Velenovsky JFt, Mee ED, Montoya SJ, Hileman JT, Garcia MD, Su NY, Chouvenec T, Gile GH, 2020. The complete protist symbiont communities of *Coptotermes formosanus* and *Coptotermes gestroi*: Morphological and molecular characterization of five new species. *The Journal of Eukaryotic Microbiology*, 67(6): 626–641.
- Javed K, Qiu D, 2020. Protein elicitor peb11 of *Brevibacillus laterosporus* enhances resistance against *Myzus persicae* in tomato. *Pathogens*, 9(1): 57.
- Jing T, Du W, Gao T, Wu Y, Zhang N, Zhao M, Jin J, Wang J, Schwab W, Wan X, Song C, 2021. Herbivore-induced DMNT catalyzed by CYP82D47 plays an important role in the induction of JA-dependent herbivore resistance of neighboring tea plants. *Plant Cell & Environment*, 44(4): 1178–1191.
- Jones JD, Dangl JL, 2006. The plant immune system. *Nature*, 444(7117): 323–329.
- Jordan C, de Carvalho VR, Mascarin GM, Dos Santos Oliveira LR, Dunlap CA, Wilcken CF, 2021. First record of a new microsporidium pathogenic to *Gonipterus platensis* in Brazil. *Scientific Reports*, 11(1): 10971.
- Kaeck H, Vorburger C, 2020. Horizontal transmission of the heritable protective endosymbiont *Hamiltonella defensa* depends on titre and haplotype. *Frontiers in Microbiology*, 11: 628755.
- Karageorgi M, Groen SC, Sumbul F, Pelaez JN, Verster KI, Aguilar JM, Hastings AP, Bernstein SL, Matsunaga T, Astourian M, Guerra G, Rico F, Dobler S, Agrawal AA, Whiteman NK, 2019. Genome editing retraces the evolution of toxin resistance in the monarch butterfly. *Nature*, 574(7778): 409–412.
- Kerchev PI, Fenton B, Foyer CH, Hancock RD, 2012. Plant responses to insect herbivory: Interactions between photosynthesis, reactive oxygen species and hormonal signalling pathways. *Plant Cell & Environment*, 35(2): 441–453.
- Klowden MJ, 2013. *Physiological Systems in Insects*. Idaho: Academic Press. 306.
- Koga R, Tanahashi M, Nikoh N, Hosokawa T, Meng XY, Moriyama M, Fukatsu T, 2021. Host's guardian protein counters degenerative symbiont evolution. *Proceedings of National Academy of Science of the United States of America*, 118(25): e2103957118.
- Kortbeek RWJ, Galland MD, Muras A, van der Kloet FM, Andre B, Heilijgers M, van Hijum S, Haring MA, Schuurink RC, Bleeker PM, 2021. Natural variation in wild tomato trichomes; selecting metabolites that contribute to insect resistance using a random forest approach. *BMC Plant Biology*, 21(1): 315.
- Kowalski P, Baum M, Korten M, Donath A, Dobler S, 2020. ABCB transporters in a leaf beetle respond to sequestered plant toxins. *Proceedings of National Academy of Science of the United States of America*, 287(1934): 20201311.
- Kumar P, Pandit SS, Steppuhn A, Baldwin IT, 2014a. Natural history-driven, plant-mediated RNAi-based study reveals CYP6b46's role in a nicotine-mediated antipredator herbivore defense. *Proceedings of National Academy of Science of the United States of America*, 111(4): 1245–1252.
- Kumar P, Rath P, Schottner M, Baldwin IT, Pandit S, 2014b. Differences in nicotine metabolism of two *Nicotiana attenuata* herbivores render them differentially susceptible to a common native predator. *PLoS ONE*, 9(4): e95982.
- Lavy O, Gophna U, Ayali A, Gihaz S, Fishman A, Gefen E, 2021. The maternal foam plug constitutes a reservoir for the desert locust's bacterial symbionts. *Environmental Microbiology*, 23(5): 2461–2472.
- Lavy O, Gophna U, Gefen E, Ayali A, 2020. Locust bacterial symbionts: An update. *Insects*, 11(10): 655.
- Li F, Li W, Lin YJ, Pickett JA, Birkett MA, Wu K, Wang G, Zhou JJ, 2018. Expression of lima bean terpene synthases in rice enhances recruitment of a beneficial enemy of a major rice pest. *Plant Cell & Environment*, 41(1): 111–120.
- Li J, Baldwin IT, Li D, 2022. Harmonizing biosynthesis with post-ingestive modifications to understand the ecological functions of plant natural products. *Natural Product Reports*, 39(7): 1383–1392.
- Li J, Halitschke R, Li D, Paetz C, Su H, Heiling S, Xu S, Baldwin IT, 2021a. Controlled hydroxylations of diterpenoids allow for plant chemical defense without autotoxicity. *Science*, 371(6526): 255–260.
- Li Q, Sun J, Qin Y, Fan J, Zhang Y, Tan X, Hou M, Chen J, 2021b. Reduced insecticide susceptibility of the wheat aphid *Sitobion*

- miscanthi after infection by the secondary bacterial symbiont *Hamiltonella defensa*. *Pest Management Science*, 77(4): 1936–1944.
- Liu F, Wickham JD, Cao Q, Lu M, Sun J, 2020a. An invasive beetle-fungus complex is maintained by fungal nutritional-compensation mediated by bacterial volatiles. *The ISME Journal*, 14(11): 2829–2842.
- Liu Q, Lei J, Darby AC, Kadowaki T, 2020b. Trypanosomatid parasite dynamically changes the transcriptome during infection and modifies honey bee physiology. *Communication Biology*, 3(1): 51.
- Mason CJ, Ray S, Shikano I, Peiffer M, Jones AG, Luthe DS, Hoover K, Felton GW, 2019. Plant defenses interact with insect enteric bacteria by initiating a leaky gut syndrome. *Proceedings of National Academy of Science of the United States of America*, 116(32): 15991–15996.
- Meents AK, Chen SP, Reichelt M, Lu HH, Bartram S, Yeh KW, Mithofer A, 2019. Volatile DMNT systemically induces Jasmonate-independent direct anti-herbivore defense in leaves of sweet potato (*Ipomoea batatas*) plants. *Scientific Reports*, 9(1): 17431.
- Moriyama M, Fukatsu T, 2022. Host's demand for essential amino acids is compensated by an extracellular bacterial symbiont in a hemipteran insect model. *Frontiers in Physiology*, 13: 1028409.
- Muhammad A, Habineza P, Ji T, Hou Y, Shi Z, 2019. Intestinal microbiota confer protection by priming the immune system of red palm weevil *Rhynchophorus ferrugineus* Olivier (Coleoptera: Dryophthoridae). *Frontiers in Physiology*, 10: 1303.
- Ngou BPM, Ding P, Jones JDG, 2022. Thirty years of resistance: Zig-zag through the plant immune system. *Plant Cell*, 34(5): 1447–1478.
- Nishimura Y, Otagiri M, Yuki M, Shimizu M, Inoue JI, Moriya S, Ohkuma M, 2020. Division of functional roles for termite gut protists revealed by single-cell transcriptomes. *The ISME Journal*, 14(10): 2449–2460.
- Ohbayashi T, Futahashi R, Terashima M, Barriere Q, Lamouche F, Takeshita K, Meng XY, Mitani Y, Sone T, Shigenobu S, Fukatsu T, Mergaert P, Kikuchi Y, 2019. Comparative cytology, physiology and transcriptomics of *Burkholderia insecticola* in symbiosis with the bean bug *Riptortus pedestris* and in culture. *The ISME Journal*, 13(6): 1469–1483.
- Pais IS, Valente RS, Sporniak M, Teixeira L, 2018. *Drosophila melanogaster* establishes a species-specific mutualistic interaction with stable gut-colonizing bacteria. *PLoS Biology*, 16(7): e2005710.
- Pentzold S, Zagrobelny M, Rook F, Bak S, 2014. How insects overcome two-component plant chemical defence: Plant beta-glucosidases as the main target for herbivore adaptation. *Biological Reviews*, 89(3): 531–551.
- Pineda A, Kaplan I, Hannula SE, Ghanem W, Bezemer TM, 2020. Conditioning the soil microbiome through plant-soil feedbacks suppresses an aboveground insect pest. *New Phytologist*, 226(2): 595–608.
- Qin J, Tong Z, Zhan Y, Buisson C, Song F, He K, Nielsen-LeRoux C, Guo S, 2020. A bacillus thuringiensis chitin-binding protein is involved in insect peritrophic matrix adhesion and takes part in the infection process. *Toxins (Basel)*, 12(4): 252.
- Ramos SE, Schiestl FP, 2019. Rapid plant evolution driven by the interaction of pollination and herbivory. *Science*, 364(6436): 193–196.
- Salem H, Kaltenpoth M, 2022. Beetle-bacterial symbioses: Endless forms most functional. *Annual Review of Entomology*, 67: 201–219.
- Sato Y, Jang S, Takeshita K, Itoh H, Koike H, Tago K, Hayatsu M, Hori T, Kikuchi Y, 2021. Insecticide resistance by a host-symbiont reciprocal detoxification. *Nature Communications*, 12(1): 6432.
- Schmidt K, Engel P, 2021. Mechanisms underlying gut microbiota-host interactions in insects. *Journal of Experimental Biology*, 224(Pt 2): jeb207696.
- Shan HW, Luan JB, Liu YQ, Douglas AE, Liu SS, 2019. The inherited bacterial symbiont *Hamiltonella* influences the sex ratio of an insect host. *Proceeding of The Royal Society B-Biology Science*, 286(1915): 20191677.
- Shirakawa M, Ueda H, Shimada T, Hara-Nishimura I, 2016. Fama: A molecular link between stomata and myrosin cells. *Trends in Plant Science*, 21(10): 861–871.
- Shu B, Zou Y, Yu H, Zhang W, Li X, Cao L, Lin J, 2021. Growth inhibition of *Spodoptera frugiperda* larvae by camptothecin correlates with alteration of the structures and gene expression profiles of the midgut. *BMC Genomics*, 22(1): 391.
- Shukla SP, Beran F, 2020. Gut microbiota degrades toxic isothiocyanates in a flea beetle pest. *Molecular Ecology*, 29(23): 4692–4705.
- Smee MR, Raines SA, Ferrari J, 2021. Genetic identity and genotype x genotype interactions between symbionts outweigh species level effects in an insect microbiome. *The ISME Journal*, 15(9): 2537–2546.

- Snoeck S, Guayazan-Palacios N, Steinbrenner AD, 2022. Molecular tug-of-war: Plant immune recognition of herbivory. *Plant Cell*, 34(5): 1497–1513.
- Sorokan AV, Burkhanova GF, Benkovskaya GV, Maksimov IV, 2020. Colorado potato beetle microsymbiont *Enterobacter* BC-8 inhibits defense mechanisms of potato plants using crosstalk between Jasmonate- and salicylate-mediated signaling pathways. *Arthropod-Plant Interactions*, 14(2): 161–168.
- Soto-Robles LV, Torres-Banda V, Rivera-Orduna FN, Curiel-Quesada E, Hidalgo-Lara ME, Zuniga G, 2019. An overview of genes from *Cyberlindnera americana*, a symbiont yeast isolated from the gut of the bark beetle *Dendroctonus rhizophagus* (Curculionidae: Scolytinae), involved in the detoxification process using genome and transcriptome data. *Frontiers in Microbiology*, 10: 2180.
- Speer KA, 2022. Microbiomes mediate host-parasite interactions. *Molecular Ecology*, 31(7): 1925–1927.
- Sporer T, Kornig J, Wielsch N, Gebauer-Jung S, Reichelt M, Hupfer Y, Beran F, 2021. Hijacking the mustard-oil bomb: How a glucosinolate-sequestering flea beetle copes with plant myrosinases. *Frontiers in Plant Science*, 12: 645030.
- Steinbrenner AD, Munoz-Amatriain M, Chaparro AF, Aguilar-Venegas JM, Lo S, Okuda S, Glauser G, Dongiovanni J, Shi D, Hall M, Crubaugh D, Holton N, Zipfel C, Abagyan R, Turlings TCJ, Close TJ, Huffaker A, Schmelz EA, 2020. A receptor-like protein mediates plant immune responses to herbivore-associated molecular patterns. *Proceedings of National Academy of Science of the United States of America*, 117(49): 31510–31518.
- Steinbrenner AD, Saldivar E, Hodges N, Guayazan-Palacios N, Chaparro AF, Schmelz EA, 2022. Signatures of plant defense response specificity mediated by herbivore-associated molecular patterns in legumes. *Plant Journal*, 110(5): 1255–1270.
- Stenoien CM, Meyer RA, Nail KR, Zalucki MP, Oberhauser KS, 2019. Does chemistry make a difference? Milkweed butterfly sequestered cardenolides as a defense against parasitoid wasps. *Arthropod-Plant Interactions*, 13(6): 835–852.
- Stoffolano JG, 2019. Fly foregut and transmission of microbes. *Advances in Insect Physiology*, 57: 27–95.
- Takeda K, Kadokawa T, Kawakita A, 2021. Slippery flowers as a mechanism of defence against nectar-thieving ants. *Annals of Botany*, 127(2): 231–239.
- Terra WR, Dias RO, Oliveira PL, Ferreira C, Venancio TM, 2018. Transcriptomic analyses uncover emerging roles of mucins, lysosome/secretory addressing and detoxification pathways in insect midguts. *Current Opinion in Insect Science*, 29: 34–40.
- Terra WR, Ferreira C, 2009. Digestive System, Encyclopedia of Insects (second edition). Burlington: Academic Press. 273–281.
- Thakur MP, van der Putten WH, Cobben MMP, van Kleunen M, Geisen S, 2019. Microbial invasions in terrestrial ecosystems. *Nature Reviews Microbiology*, 17(10): 621–631.
- Tobias NJ, Eberhard FE, Guarneri AA, 2020. Enzymatic biosynthesis of B-complex vitamins is supplied by diverse microbiota in the *Rhodnius prolixus* anterior midgut following *Trypanosoma cruzi* infection. *Compute Structure Biotechnology Journal*, 18: 3395–3401.
- Todd JNA, Carreon-Anguiano KG, Islas-Flores I, Canto-Canche B, 2022. Microbial effectors: Key determinants in plant health and disease. *Microorganisms*, 10(10): 1980.
- Vacheron J, Pechy-Tarr M, Brochet S, Heiman CM, Stojiljkovic M, Maurhofer M, Keel C, 2019. T6ss contributes to gut microbiome invasion and killing of an herbivorous pest insect by plant-beneficial *Pseudomonas* protegens. *The ISME Journal*, 13(5): 1318–1329.
- van Bel AJ, Will T, 2016. Functional evaluation of proteins in watery and gel saliva of aphids. *Frontiers in Plant Science*, 7: 1840.
- van den Bosch TJM, Welte CU, 2017. Detoxifying symbionts in agriculturally important pest insects. *Microbial Biotechnology*, 10(3): 531–540.
- Vega FE, Emche S, Shao J, Simpkins A, Summers RM, Mock MB, Ebert D, Infante F, Aoki S, Maul JE, 2021. Cultivation and genome sequencing of bacteria isolated from the coffee berry borer (*Hypothenemus hampei*), with emphasis on the role of caffeine degradation. *Frontiers in Microbiology*, 12: 644768.
- Wada-Katsumata A, Zurek L, Nalyanya G, Roelofs WL, Zhang A, Schall C, 2015. Gut bacteria mediate aggregation in the german cockroach. *Proceedings of National Academy of Science of the United States of America*, 112(51): 15678–15683.
- Wang J, Yang M, Song Y, Acevedo FE, Hoover K, Zeng R, Felton GW, 2018. Gut-associated bacteria of *Helicoverpa zea* indirectly trigger plant defenses in maize. *Journal of Chemical Ecology*, 44(7/8): 690–699.
- Wang L, Li C, Wang X, Wang G, Shang S, Dou Z, Luo Y, 2022. Gut lignocellulose activity and microbiota in Asian longhorned beetle and their predicted contribution to larval nutrition. *Frontiers in Microbiology*, 13: 899865.
- Wang Q, Yuan E, Ling X, Zhu-Salzman K, Guo H, Ge F, Sun Y, 2020. An aphid facultative symbiont suppresses plant defense by

- manipulating aphid gene expression in salivary glands. *Plant Cell & Environment*, 43(9): 2311–2322.
- Xia J, Guo Z, Yang Z, Han H, Wang S, Xu H, Yang X, Yang F, Wu Q, Xie W, Zhou X, Dermauw W, Turlings TCJ, Zhang Y, 2021. Whitefly hijacks a plant detoxification gene that neutralizes plant toxins. *Cell*, 184(7): 1693–1705.
- Yang X, Koci J, Smith AA, Zhuang X, Sharma K, Dutta S, Rana VS, Kitsou C, Yas OB, Mongodin EF, Pal U, 2021a. A novel tick protein supports integrity of gut peritrophic matrix impacting existence of gut microbiome and lyme disease pathogens. *Cellular Microbiology*, 23(2): e13275.
- Yang ZL, Nour-Eldin HH, Hanniger S, Reichelt M, Crocoll C, Seitz F, Vogel H, Beran F, 2021b. Sugar transporters enable a leaf beetle to accumulate plant defense compounds. *Nature Communications*, 12(1): 2658.
- Yang ZL, Seitz F, Grabe V, Nietzsche S, Richter A, Reichelt M, Beutel R, Beran F, 2022. Rapid and selective absorption of plant defense compounds from the gut of a sequestering insect. *Frontiers in Physiology*, 13: 846732.
- Yao YL, Ma XY, Wang TY, Yan JY, Chen NF, Hong JS, Liu BQ, Xu ZQ, Zhang N, Lv C, Sun X, Luan JB, 2023. A bacteriocyte symbiont determines whitefly sex ratio by regulating mitochondrial function. *Cell Reports*, 42(2): 112102.
- Ye J, Zhang L, Zhang X, Wu X, Fang R, 2021. Plant defense networks against insect-borne pathogens. *Trends in Plant Science*, 26(3): 272–287.
- Yuan M, Jiang Z, Bi G, Nomura K, Liu M, Wang Y, Cai B, Zhou JM, He SY, Xin XF, 2021a. Pattern-recognition receptors are required for NLR-mediated plant immunity. *Nature*, 592(7852): 105–109.
- Yuan M, Ngou BPM, Ding P, Xin XF, 2021b. PTI-ETI crosstalk: An integrative view of plant immunity. *Current Opinion in Plant Biology*, 62: 102030.
- Zha XL, Wang H, Sun W, Zhang HY, Wen J, Huang XZ, Lu C, Shen YH, 2021. Characteristics of the peritrophic matrix of the silkworm, *bombyx mori* and factors influencing its formation. *Insects*, 12(6): 516.
- Zhang S, Li Z, Shu J, Xue H, Guo K, Zhou X, 2022. Soil-derived bacteria endow camellia weevil with more ability to resist plant chemical defense. *Microbiome*, 10(1): 97.
- Zhang S, Shu J, Xue H, Zhang W, Zhang Y, Liu Y, Fang L, Wang Y, Wang H, 2020. The gut microbiota in camellia weevils are influenced by plant secondary metabolites and contribute to saponin degradation. *mSystems*, 5(2): e00692-19.
- Zheng X, Zhang D, Li Y, Yang C, Wu Y, Liang X, Liang Y, Pan X, Hu L, Sun Q, Wang X, Wei Y, Zhu J, Qian W, Yan Z, Parker AG, Gilles JRL, Bourtzis K, Bouyer J, Tang M, Zheng B, Yu J, Liu J, Zhuang J, Hu Z, Zhang M, Gong JT, Hong XY, Zhang Z, Lin L, Liu Q, Hu Z, Wu Z, Baton LA, Hoffmann AA, Xi Z, 2019. Incompatible and sterile insect techniques combined eliminate mosquitoes. *Nature*, 572(7767): 56–61.
- Zhou S, Lu Y, Chen J, Pan Z, Pang L, Wang Y, Zhang Q, Strand MR, Chen XX, Huang J, 2022. Parasite reliance on its host gut microbiota for nutrition and survival. *The ISME Journal*, 16(11): 2574–2586.
- Zogli P, Pingault L, Grover S, Louis J, 2020. Ento(o)mics: The intersection of ‘omic’ approaches to decipher plant defense against sap-sucking insect pests. *Current Opinion in Plant Biology*, 56: 153–161.