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Gut microbiota of agricultural insects

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Abstract

Agricultural insect pests rely on a resident gut microbiota that extends their metabolic capacity well beyond what their own genome encodes, and this extension is increasingly recognised as both a driver of pest success and a point of vulnerability that can be exploited for control. The biochemical roles of gut bacteria in phytophagous and stored-product insects, covering the breakdown of recalcitrant plant polymers, nitrogen and vitamin provisioning under nutrient-poor diets, detoxification of plant secondary metabolites, and the modulation of insecticide susceptibility. Findings across taxa are frequently inconsistent: the same bacterial genus can suppress resistance in one host and enhance it in another, and microbial action on a xenobiotic can either neutralise the compound or convert it into a more toxic metabolite, so no single unifying rule adequately describes the microbiota-resistance relationship. Persistent obstacles, including the unculturability of most gut taxa, poor concordance between laboratory and field microbiomes, and the difficulty of establishing causation rather than correlation, are identified as the principal barriers to reliable field application. Closing these gaps will require standardised gnotobiotic insect systems and longitudinal field microbiome surveys rather than further single-species descriptive surveys.

Keywords: Insect gut microbiota, nutritional symbiosis, xenobiotic detoxification, insecticide resistance, paratransgenesis, integrated pest management

Introduction

Insects remain the most taxonomically diverse animal lineage on the planet, and herbivorous forms among them are responsible for a substantial share of the fifteen percent or more of global crop yield lost annually to arthropod feeding (Stork, 2018; Basset *et al.*, 2012) [1, 2]. Climate warming, altered cropping patterns and the geographic redistribution of pest species are widely expected to intensify this burden rather than relieve it (Deutsch *et al.*, 2018) [3]. Against this backdrop, the community of bacteria, and to a lesser extent fungi and archaea, that colonise the insect alimentary canal has moved from a peripheral curiosity to a central object of applied entomological research, largely because these microbes supply functions the insect genome itself cannot (Engel and Moran, 2013; Douglas, 2009) [4, 5]. The insect gut is not a uniform habitat. Its foregut and hindgut are lined by a chitinous cuticle shed at each moult, while the midgut, of endodermal origin, lacks this lining and is where most digestion and absorption, and consequently most microbial colonisation, takes place. Bacterial density and turnover in this compartment routinely exceed those found in the surrounding soil or plant tissue, which has been proposed as one reason insect-associated bacteria display unusually broad catabolic versatility relative to free-living relatives.

The functional catalogue attributed to these symbionts has grown rapidly over the past decade and now spans four broad domains, digestion and nutrient supplementation, detoxification of both natural and synthetic toxins, modulation of host immunity and development, and mediation of interactions with host plants and natural enemies at the third trophic level. Each of these domains has direct bearing on pest management, because a pathway that helps an insect exploit a nutritionally poor or chemically defended host plant is, in principle, a pathway that can be disrupted. Yet the literature on this subject is not a tidy accumulation of concordant findings. The same symbiont genus is reported to confer resistance in one insect-pesticide combination and to have no effect, or even to increase susceptibility, in another.

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Nutritional Symbiosis and the Digestion of Recalcitrant Plant Material

Plant tissue is a poor diet by most nutritional standards, being carbon-rich, nitrogen-poor, and structurally reinforced by polymers that insect digestive enzymes alone cannot efficiently cleave. Cellulose, hemicellulose, pectin and lignin together form a barrier that has to be breached before the more labile nutrients within plant cells become accessible, and gut bacteria are now understood to be central rather than incidental to this process in several lineages. Adams *et al.*, (2011) [6] isolated

Streptomyces and *Pantoea* strains from the gut of the invasive woodwasp *Sirex noctilio* capable of hydrolysing cellulose, and comparable cellulolytic consortia have since been reported from woodboring beetles and stem-boring lepidopterans. Pectin digestion follows a more specialised route in at least one leaf beetle lineage, where Salem *et al.*, (2020) [7] traced the pectinolytic capacity of *Cassida rubiginosa* to an extracellular symbiont, *Stammera*, housed in a purpose-built foregut organ rather than free in the midgut lumen, a compartmentalisation that argues against treating gut symbiosis as a single undifferentiated process across insect orders.

Nitrogen scarcity is arguably the more consequential nutritional constraint for herbivores, and gut bacteria address it through at least two distinct routes. Atmospheric nitrogen fixation has been documented in the passalid beetle *Odontotaenius disjunctus*, where Ceja-Navarro *et al.*, (2014) [8] showed that oxygen gradients along the gut create anaerobic microsites permissive for diazotrophic activity, effectively allowing the beetle to manufacture part of its own nitrogen budget. A second and arguably more widespread strategy is nitrogenous waste recycling, in which uric acid and other excretory nitrogen are salvaged and reassembled into essential amino acids; Ren *et al.*, (2022) [9] attributed this capacity in the oriental fruit fly *Bactrocera dorsalis* jointly to *Morganella morganii* and *Klebsiella oxytoca*. Vitamin provisioning rounds out the nutritional contribution, and here the bean bug *Riptortus pedestris* offers one of the more mechanistically resolved cases, with Ohbayashi *et al.*, (2019) [10] demonstrating that its *Burkholderia* symbiont supplies B vitamins that the soy-based diet cannot. A comparable, though strain-variable, capability has been described in ant-associated *Bartonellaceae*, where Bisch *et al.*, (2018) [11] found the gene for vitamin B1 synthesis conserved across the family while the pathway for B3 was present in only one strain, a pattern that cautions against assuming functional uniformity within a bacterial family purely on the basis of taxonomic identity. What the polymer-digestion literature has not fully resolved is the relative contribution of host-encoded and microbially-encoded enzymes in species where both are present. Watanabe and Tokuda (2010) [12] argued that endogenous cellulases are more widespread across insect orders than earlier symbiosis-centred models assumed, while transcriptomic work on the Asian longhorned beetle *Anoplophora glabripennis* by Scully *et al.*, (2014) [13] found gut microbial gene expression shifting substantially with host plant, implying a genuinely shared digestive burden rather than a purely host-driven process. Reconciling these positions probably requires species-by-species enzymatic fractionation rather than a single verdict applied across Coleoptera as a whole, and this remains an underexplored area relative to the volume of descriptive 16S rRNA surveys the field continues to generate. Detoxification of Plant Secondary Metabolites and Synthetic Xenobiotics. Beyond

structural polymers, plants deploy an arsenal of secondary metabolites, alkaloids, terpenoids, phenolics and glucosinolates among them, specifically to deter feeding, and a recurring theme in the gut microbiota literature is that bacterial catabolism converts these compounds into forms the insect can tolerate or even exploit as a carbon source. The coffee berry borer *Hypothenemus hampei* is the best-characterised example of this phenomenon; Ceja-Navarro *et al.*, (2015) [14] showed that its gut bacteria, dominated by *Pseudomonas*, degrade caffeine efficiently enough that axenic insects reared without the microbiota performed markedly worse on a caffeine-containing diet. A parallel case has been built for the pine weevil *Hylobius abietis*, where Berasategui *et al.*, (2017) [15] found gut bacteria not only degrading conifer diterpene acids but using them as a carbon source that measurably improved weevil fitness, converting what should be a defensive compound into a nutritional resource. Isothiocyanate degradation in a flea beetle specialised on Brassicaceae, reported by Shukla and Beran (2020) [16], extends the same principle to a different chemical class and a different insect order, suggesting the underlying logic, bacterial cometabolism turning a deterrent into a tolerated or beneficial substrate, recurs independently across unrelated lineages rather than tracing to a single ancestral symbiosis.

The same catabolic machinery that handles plant allelochemicals appears able to act on synthetic pesticides, and this is where the applied stakes of the research rise sharply. Xia *et al.*, (2018) [17] isolated *Enterococcus*, *Enterobacter* and *Serratia* strains from the gut of the diamondback moth *Plutella xylostella* and tested each against the organophosphate chlorpyrifos; only *Enterococcus* increased larval resistance, *Serratia* if anything reduced it, and *Enterobacter* had no measurable effect, a result that already complicates any assumption that gut bacteria act as a uniform detoxifying shield. In the oriental fruit fly, Cheng *et al.*, (2017) [18] traced trichlorophen resistance to a *Citrobacter* symbiont carrying inducible hydrolase genes, while acetamiprid and imidacloprid degradation by *Rhodococcus* and *Klebsiella* isolates, respectively, has been documented by Phugare and Jadhav (2015) [19] and Phugare *et al.*, (2013) [20] using silkworm bioassays to confirm that the bacterial metabolites themselves retained measurable, if reduced, toxicity rather than being rendered fully inert.

Insecticide Resistance

The proposition that gut microbiota drive insecticide resistance is now well established in outline, but the mechanistic detail resists the kind of generalisation that would make the phenomenon easy to exploit for control. Temperature-sensitive symbiosis illustrates the point sharply. Zhang *et al.*, (2023) [21] compared geographically distinct strains of the brown planthopper *Nilaparvata lugens* and found microbiome composition correlating with insecticide susceptibility in a manner that shifted with rearing temperature, and field populations showed no consistent relationship between *Wolbachia* carriage and resistance phenotype despite laboratory evidence, from Cai *et al.*, (2021) [22], that *Wolbachia* upregulates the detoxifying cytochrome P450 gene *NICYP4CE1* under imidacloprid stress. The disconnect between a mechanistically plausible laboratory pathway and an inconsistent field correlation is not a minor caveat; it is arguably the central unresolved problem in this literature, because most practical resistance-

management decisions have to be made at the field population level rather than in a controlled colony.

A second complication is that gut bacteria do not uniformly detoxify; in some documented cases they activate a proinsecticide into a more potent form. *Wolfe and Scharf* (2022) ^[23] showed that antibiotic treatment of German cockroaches reduced bacterial load and simultaneously increased survival after indoxacarb exposure, meaning the intact microbiota had been converting the proinsecticide indoxacarb into the more toxic metabolite DCJW, the opposite of a protective role. *Paddock et al.*, (2021) ^[24] reported a structurally analogous finding for *Bacillus thuringiensis* Cry toxin resistance in western corn rootworm, where altered bacterial community composition was linked to resistance, but through interference with toxin activation rather than through direct degradation of the toxin itself. Taken together with the diamondback moth data described above, these results support a working principle rather than a single mechanism, that the net effect of the gut microbiota on pesticide susceptibility is determined jointly by the insecticide's own mode of activation, the specific bacterial taxa present, and the physiological state of the host, and that none of these three variables can be assumed constant across populations, seasons or geography.

Immune Modulation and Third-Trophic-Level Signalling

Gut bacteria do not act only on nutrients and toxins; they also shape how the host insect interacts immunologically with itself and chemically with the wider community of plants and natural enemies around it. In the honeybee, *Guo et al.*, (2023) ^[25] linked reactive oxygen species production,

regulated jointly by the Immune Deficiency and Toll signalling pathways, to the maintenance of host-specific gut bacterial composition, indicating that immune surveillance is not merely a defence against pathogens but an active mechanism for curating a beneficial community. Herbivore-associated bacteria can also be deployed offensively against the plant itself. *Chung et al.*, (2013) ^[26] demonstrated that oral secretions of the Colorado potato beetle, carrying endosymbiotic bacteria, suppress jasmonic acid-mediated defences in tomato by enhancing the competing salicylic acid pathway, effectively using bacteria as a chemical weapon against the plant's own signalling network.

The same bacterial volatiles that shape plant defence can cut in either direction for the herbivore at the third trophic level. Honeydew-associated bacteria from the brown planthopper elicit indirect defences in rice that recruit the herbivore's own natural enemies, as shown by *Wari et al.*, (2019) ^[27], which is disadvantageous for the insect that produced the honeydew in the first place. Conversely, *Frago et al.*, (2017) ^[28] found that the aphid symbiont *Hamiltonella defensa* reduces the volatile signal that would otherwise attract parasitoid wasps, protecting the aphid rather than exposing it. Whether a given gut or honeydew bacterium ultimately helps or harms its insect host at this trophic interface appears to depend on the specific volatile compounds it induces and how the local community of natural enemies is tuned to detect them, and this context sensitivity mirrors the pattern already noted for insecticide resistance, reinforcing the broader conclusion that insect gut symbiosis functions as a set of conditional, ecologically contingent interactions rather than a fixed beneficial partnership.

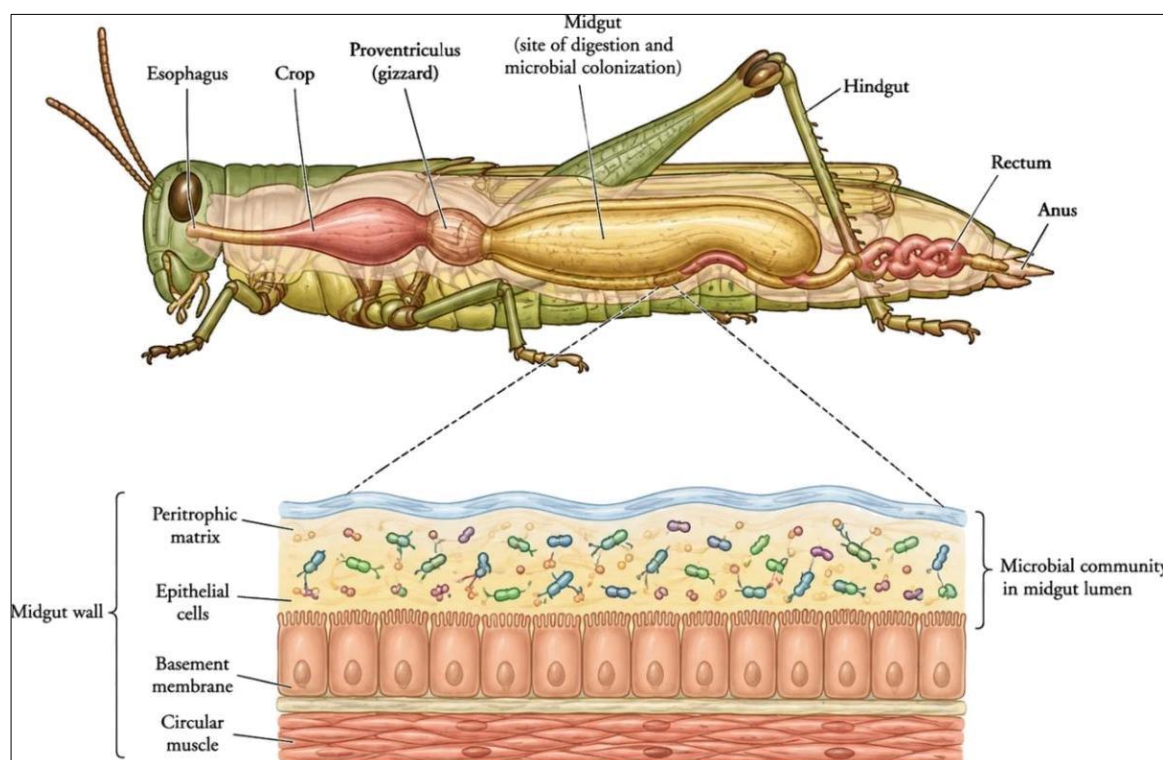


Fig 1: Integrated model of insect gut microbiota functions across host physiology and trophic interactions

Applications, Gaps and the Path Toward Microbiome-Informed Pest Management

The applied promise of this body of work rests on the idea that a pathway an insect depends on for host exploitation or toxin tolerance is also a pathway that can be interrupted deliberately. Paratransgenesis, in which a culturable gut

symbiont is genetically engineered to secrete an antipest or anti-pathogen effector and then reintroduced to the host, has moved furthest in the mosquito system, where *Wang et al.*, (2012) ^[29] and later *Wang et al.*, (2017) ^[30] engineered *Serratia* and *Pantoea* strains from *Anopheles* mosquitoes to secrete anti-*Plasmodium* effectors and demonstrated

reduced parasite development on feeding. The same principle has been extended tentatively into agricultural pests; *Elston et al.*, (2020) ^[31] engineered a culturable strain of *Serratia symbiotica* isolated from the black bean aphid, establishing feasibility even though field deployment for a crop pest has not yet been achieved. Symbiont-mediated RNA interference offers a related but mechanistically distinct route, using gut bacteria as a continuous *in situ* source of double-stranded RNA rather than as a chemical factory; *Taracena et al.*, (2015) ^[32] achieved this in the Chagas disease vector *Rhodnius prolixus* by modifying its symbiont *Rhodococcus rhodnii*, and *Xu et al.*, (2021) ^[33] found that in the leaf beetle *Plagioderma versicolora*, the insecticidal benefit of orally delivered dsRNA arose partly from degradation products of the dsRNA itself reshaping the gut community toward pathogenic taxa, rather than solely from gene silencing, a mechanistic subtlety that complicates simple predictions about RNAi efficacy in the field.

Three structural obstacles currently limit how far any of these approaches can be pushed toward routine field use. The first is culturability. Most gut bacterial taxa identified by sequencing have never been isolated in pure culture, and although culturomic approaches have expanded the recoverable fraction, *Diakite et al.*, (2019) ^[34] still found that even intensive multi-medium culturing recovered only a subset of the diversity visible by metagenomics, which restricts both mechanistic testing and any engineering-based application to an unrepresentative sliver of the community. The second is the persistent gap between laboratory-adapted and field microbiomes; *Gomes et al.*, (2020) ^[35] found that bacteria isolated from field-collected fall armyworm larvae metabolised multiple insecticides more actively than those from laboratory-selected resistant colonies, which raises a serious question about how much of the mechanistic

literature, generated overwhelmingly on colony insects, actually generalises to the populations that resistance management programmes need to target. The third obstacle is a persistent conflation of correlation with causation in survey-based studies; sequencing a resistant population and finding an enriched bacterial taxon does not establish that the taxon caused the resistance, and axenic or gnotobiotic rearing, which would allow that causal test, remains technically difficult and has been achieved for only a limited number of pest species, a constraint discussed at length by *Wu et al.*, (2023) ^[36]. *Kikuchi et al.*, (2012) ^[37] demonstrated one of the clearer causal tests available in this literature, using a soil-acquired *Burkholderia* symbiont to confer fenitrothion resistance on the bean bug, and studies of this design, isolation, reintroduction, and functional confirmation in a defined host background, remain the standard the field should be working toward rather than the exception. Where the field appears to be converging, cautiously, is on the idea that gut microbiota manipulation is most likely to succeed as one component within an integrated resistance management strategy rather than as a standalone control method. Targeting the specific bacterial taxa implicated in the bioactivation-resistance pathway described in the previous section, for instance, could in principle restore susceptibility to an insecticide that has lost field efficacy, and *Xia et al.*, (2013) ^[38] had already flagged this possibility for chlorpyrifos resistance in the diamondback moth over a decade ago, yet a field-validated demonstration of deliberately engineered microbiome suppression restoring insecticide efficacy in an open agricultural setting has still not been published for any major crop pest, which remains the clearest indication that the discipline has advanced further in mechanistic description than in applied translation.

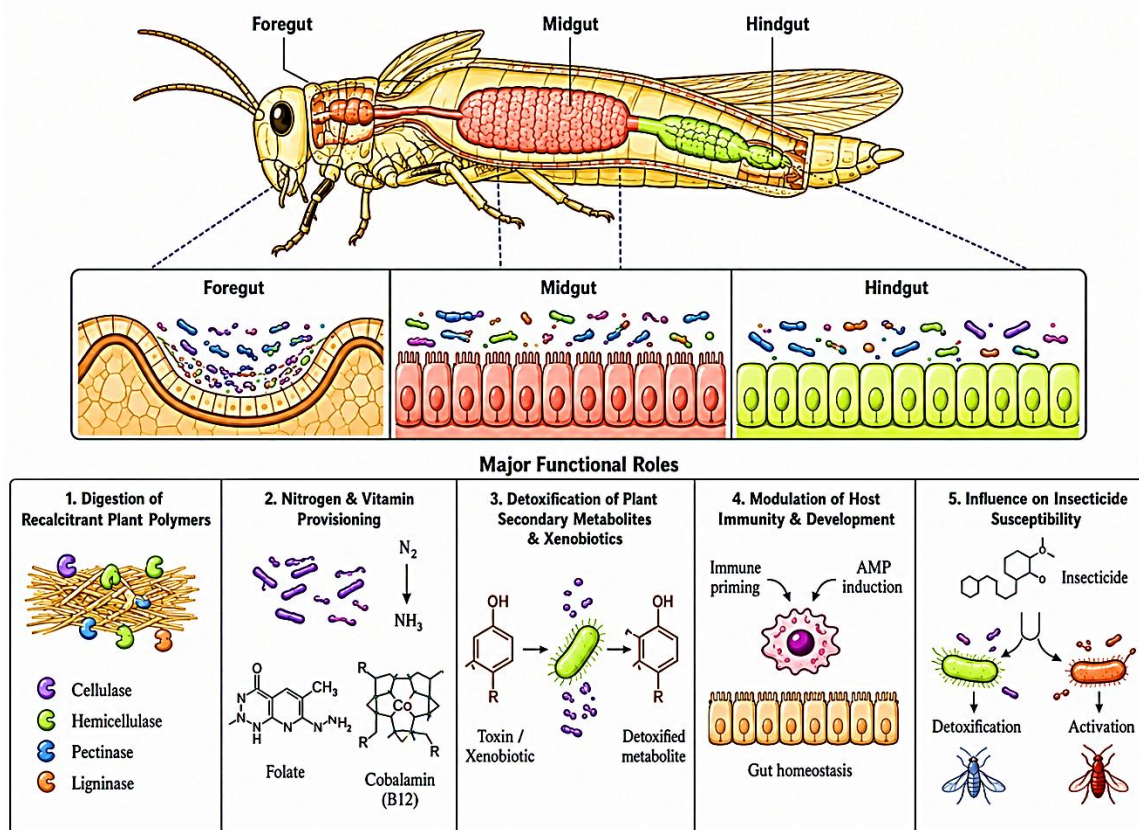


Fig 2: Decision framework for translating gut microbiota research into pest management interventions.

Table 1: Documented nutritional and detoxification functions of gut bacteria across agriculturally important insect orders

Insect (order)	Gut bacterium	Function	Reference
<i>Sirex noctilio</i> (Hymenoptera)	<i>Streptomyces</i> , <i>Pantoea</i>	Cellulose hydrolysis for wood-feeding	Adams <i>et al.</i> , (2011) ^[1]
<i>Cassida rubiginosa</i> (Coleoptera)	<i>Stammera</i> (foregut organ)	Pectin digestion of leaf tissue	Salem <i>et al.</i> , (2020) ^[24]
<i>Odontotaenius disjunctus</i> (Coleoptera)	Gut community (compartmentalised)	Atmospheric nitrogen fixation	Ceja-Navarro <i>et al.</i> , (2014) ^[6]
<i>Bactrocera dorsalis</i> (Diptera)	<i>Morganella morganii</i> , <i>Klebsiella oxytoca</i>	Nitrogenous waste recycling into amino acids	Ren <i>et al.</i> , (2022) ^[23]
<i>Riptortus pedestris</i> (Hemiptera)	<i>Burkholderia insecticola</i>	B-vitamin supplementation on soy diet	Ohbayashi <i>et al.</i> , (2019) ^[19]
<i>Dolichoderus</i> spp. (Hymenoptera)	<i>Bartonellaceae</i>	Essential amino acid and vitamin biosynthesis	Bisch <i>et al.</i> , (2018) ^[11]
<i>Anoplophora glabripennis</i> (Coleoptera)	Diverse midgut consortium	Host-plant-responsive lignocellulose processing	Scully <i>et al.</i> , (2014) ^[9]
<i>Hypothenemus hampei</i> (Coleoptera)	<i>Pseudomonas</i> spp.	Caffeine detoxification and utilisation	Ceja-Navarro <i>et al.</i> , (2015)
<i>Hylobius abietis</i> (Coleoptera)	Gut bacterial consortium	Diterpene acid degradation and use as carbon source	Berasategui <i>et al.</i> , (2017) ^[3]
<i>Psylliodes chrysocephala</i> (Coleoptera)	Gut bacterial consortium	Isothiocyanate detoxification	Shukla and Beran (2020) ^[26]
<i>Plutella xylostella</i> (Lepidoptera)	<i>Enterococcus</i> sp.	Chlorpyrifos tolerance enhancement	Xia <i>et al.</i> , (2018) ^[36]
<i>Bactrocera dorsalis</i> (Diptera)	<i>Citrobacter</i> sp.	Trichlorophon hydrolysis	Cheng <i>et al.</i> , (2017) ^[8]
<i>Bombyx mori</i> bioassay system	<i>Rhodococcus</i> sp. BCH2	Acetamiprid degradation	Phugare and Jadhav (2015) ^[21]
<i>Bombyx mori</i> bioassay system	<i>Klebsiella pneumoniae</i> BCH1	Imidacloprid degradation	Phugare <i>et al.</i> , (2013) ^[22]

Table 2: Comparative cases of gut microbiota involvement in insecticide susceptibility, illustrating context-dependent outcomes

Insect	Insecticide	Bacterium implicated	Direction of effect	Reference
<i>Plutella xylostella</i>	Chlorpyrifos	<i>Enterococcus</i> sp.	Increases resistance	Xia <i>et al.</i> , (2018) ^[36]
<i>Plutella xylostella</i>	Chlorpyrifos	<i>Serratia</i> sp.	Reduces resistance	Xia <i>et al.</i> , (2018) ^[36]
<i>Plutella xylostella</i>	Chlorpyrifos	<i>Enterobacter</i> sp.	No measurable effect	Xia <i>et al.</i> , (2018) ^[36]
<i>Bactrocera dorsalis</i>	Trichlorophon	<i>Citrobacter</i> sp.	Increases resistance via hydrolysis	Cheng <i>et al.</i> , (2017) ^[8]
<i>Blattella germanica</i>	Indoxacarb	Native gut consortium	Bioactivates proinsecticide, increasing toxicity	Wolfe and Scharf (2022) ^[33]
<i>Diabrotica virgifera virgifera</i>	Bt Cry toxin	Altered field bacterial community	Interferes with toxin activation	Paddock <i>et al.</i> , (2021) ^[20]
<i>Nilaparvata lugens</i>	Imidacloprid	<i>Wolbachia</i> sp.	Increases NICYP4CE1 expression, aiding metabolism	Cai <i>et al.</i> , (2021) ^[5]
<i>Nilaparvata lugens</i> (field strains)	Multiple insecticides	Strain-variable microbiome	Correlated with susceptibility but temperature-dependent	Zhang <i>et al.</i> , (2023) ^[38]
<i>Riptortus pedestris</i>	Fenitrothion	<i>Burkholderia</i> sp. (soil-acquired)	Confers resistance, causally confirmed	Kikuchi <i>et al.</i> , (2012) ^[37]
<i>Plutella xylostella</i>	Chlorpyrifos (midgut survey)	Enterobacteriales, <i>Pseudomonadales</i> consortia	Correlated with resistant phenotype	Xia <i>et al.</i> , (2013) ^[35]
<i>Spodoptera frugiperda</i> (field larvae)	Multiple insecticides	Field-derived bacterial isolates	Greater metabolic activity than lab-selected strains	Gomes <i>et al.</i> , (2020) ^[16]

Conclusion

The gut microbiota of agricultural insect pests is best understood not as a fixed accessory organ but as a flexible, context-sensitive extension of host metabolism whose contribution shifts with diet, insecticide chemistry, temperature and geography. Three points emerge with reasonable confidence from the body of work surveyed here. Nutritional symbiosis, spanning cellulose and pectin digestion, nitrogen fixation, waste recycling and vitamin provisioning, is mechanistically well supported and reasonably consistent across the taxa where it has been examined closely. Detoxification is equally well supported in outline but far less predictable in direction, since the same bacterial process that neutralises one compound can activate another into a more dangerous metabolite, and the same genus can raise resistance in one host species while lowering it in a close relative. Third-trophic-level and

immune effects add a further layer of ecological contingency that resists reduction to a simple protective or harmful label.

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