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Feature Article

Bacteria in Insect Pest Management in Agriculture: The Past, Present, and Future

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Abstract

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Insect pests have plagued agriculture throughout history, and management of crop pests requires continuous innovation. Bacteria and other microbes are important tools for insect pest control through pathogenic activity, production of toxic secondary metabolites, and promotion of plant defenses. Additionally, bacteria present in agricultural environments often possess the ability to metabolize agricultural chemicals and can therefore be used to mitigate environmental impacts of agriculture. Only a small percentage of bacteria from plant and insect sources have been studied however, while there is a wealth of microbial diversity that is still unused. As the need for agricultural productivity increases and climate change shifts patterns of pest and disease, it is important to explore a wider range of bacterial species with potential for biological pest control and bioremediation applications. This review outlines some of the history of bacterial biological control, use of bacteria-derived agrochemicals, bacteria-mediated insecticide resistance, and current understanding of bacteria-insect-plant interactions. Suggestions are also provided for further research in this area to broaden the range of sustainable pest control options.

Key words: Insecticides, Biological control, Agriculture, Beneficial bacteria, Pest management.

BACKGROUND: BACTERIA AS PART OF INSECT PEST MANAGEMENT

Plant pests and pathogens have a significant impact on food security (Flood 2010). Although it is challenging to estimate across diverse crops and agricultural systems, insect pests in general and invasive insects in particular cost billions of dollars in losses and management investments globally (Bradshaw *et al*. 2016). For centuries, crop production has relied on the use of insecticidal compounds of various types, the first ones based on metals and elements or botanical extracts (Oberemok *et al*. 2015). In the early 1900s, discovery of insecticidal activity from bacteria and bacterial products led to a series of microbial-based insect pest management strategies that continues today (Starnes *et al*. 1993; Federici 2005; Wend *et al*. 2024). With increasing use of synthetic chemical insecticides on crop plants in the last 70 years, insecticide resistance and environmental damage emerged as concerning issues (Forgash 1984; Geiger *et al*. 2010; Brühl & Zaller 2019; Sparks *et al*. 2021b). Advancements in biotechnology have kept bacteria-based insec-

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ticides relevant in pest management throughout this trajectory in the form of modified natural products (Kirst 2010), biological controls (Faria *et al*. 2023), and bacterial genes expressed in plants (Gassmann & Reisig 2023). Although not exempt from concerns over resistance and environmental impact (Tabashnik *et al*. 2013), the diverse bacterial species that interact with insects and insecticidal compounds remain an abundant resource for new and improved pest management strategies. In addition to direct uses as biological control, bacteria interface with agricultural systems in many ways including through soil and plant microbial communities, contamination of food products, and remediation of the environmental impacts of agriculture. Understanding the role and potential of bacteria in all these areas will contribute to development of more sustainable and resilient crop management practices. The goal of this review is to highlight some of the important roles of bacteria in insect pest management systems of the past and present, and to discuss methods and future directions for research in this area.

INSECTICIDES DERIVED FROM BACTERIA

Many potent insecticidal compounds commonly used in agricultural pest management are natural products produced by bacteria. These compounds can be produced and extracted from the bacteria themselves, produced transgenically in plants, or modified and chemically synthesized. Although these are not the only bacterial-derived insecticides, Bt, abamectin, and spinosyns are discussed here as examples of widely used commercial insecticide products of bacterial origin.

Long history of Bt toxin

One of the most widely used bacterial insecticides is a group of toxins produced by the diverse bacterial species *Bacillus thuringiensis* (Bt). *B. thuringiensis* includes several subspecies of gram-positive spore-forming bacteria that can be found in the environment (Nester *et al*. 2002). Crystals produced by the bacteria during the spore formation process are highly toxic to certain insects if ingested. Additional toxins can also be produced as the bacterial spores germinate and reproduce within insects (Li *et al*. 2024). Insecticidal properties of Bt were first identified over 100 years ago, and Bt products have been used in agriculture since the 1930s (Lambert & Peferoen 1992). One of the advantages of Bt toxins is their specificity for certain insects and limited toxicity to mammals (de Maagd *et al*. 2001). This specificity allows Bt to be used in integrated management programs and in combination with biological controls. Although impacts on non-target organisms are generally limited, there may still be some risks for sub-lethal or secondary impacts on specific non-target insects such as parasitoids (Yu *et al*. 2011). Many of the insect pests most effectively targeted belong to the lepidopteran, dipteran, and coleopteran orders, although uses against other insect orders such as hemipterans, and some nematode species are still being explored (Federici *et al*. 1990; Baum *et al*. 2012; Domínguez-Arrizabalaga *et al*. 2020; Ramalakshmi *et al*. 2020; Pinheiro & Valicente 2021).

In addition to Bt sprays and bacterial spore formulations, the genes which produce the toxic crystal proteins were introduced transgenically into several different crop plants, successfully conveying resistance to insect damage (Dively *et al*. 2018). Plant modification with Bt improved efficacy since Bt sprays and external products break down quickly in the environment. In the United States, adoption of Bt modified crops started in the late 1990s, and is currently at 80–90% of planted acres for some crops such as cotton and corn (USDA-ERS 2024). There is also significant commercial use of Bt crops in South America (Brookes 2018; Páez Jerez *et al*. 2023) and Asia (Kathage & Qaim 2012; Zhang & Dong 2024). Although field crops such as corn, soybean, and cotton are the most widely used Bt plants, Bt modified vegetables such as eggplant are also produced in some areas (Ahmed *et al*. 2024). However, key insect pests rapidly developed resistance to the first generation of Bt crops, prompting development of a second generation of the technology that includes multiple toxin genes instead of a single toxin. Combined with appropriate management practices such as use of non-Bt refuge plants alongside the Bt crop, resistance development can be slowed but not eliminated completely (Tabashnik *et al.* 2013).

Despite the long history of Bt in agricultural pest management, only a few bacterial strains out of the diverse *B. thuringiensis* species have been used and developed into pest control products. New strains continue to be characterized, including many that target new pest species. However, there is potentially many significant and diverse Bt products have not been explored yet for agricultural use. *B. thuringiensis* and related species can be found in soil, associated with insects, growing on plant surfaces, and as an endophyte in wild and cultivated plants (Espinoza-Vergara *et al.* 2023). There is also evidence for beneficial traits beyond insecticidal capacity including plant growth promotion and pathogen suppression for some members of the *B. thuringiensis* species (Cherif-Silini *et al.* 2016).

Bacterial chemistry solutions- avermectins and spinosyns

Many bacterial species, particularly those found in soils, produce a wide range of secondary metabolites with antimicrobial and insecticidal properties. Several important chemical insecticides used in agriculture have emerged from this niche. The genus *Streptomyces* is well known for its secondary metabolite production and is the source of many antibacterial and antifungal compounds (Kemung *et al.* 2018). The species *S. avermitilis* also produces a group of chemicals called avermectins which were originally identified as nematicides against animal parasites (Burg *et al.* 1979). Avermectins and similar natural products from *S. avermitilis* have a wide range of insecticidal activities and are effective as a foliar spray against pest insects of plants, as well as mites and nematodes (Putter *et al.* 1981; Bull 1986). These compounds belong to the family of macrocyclic lactones, which have relatively safe profile for humans and vertebrate animals (Bai & Ogbourne 2016). Ivermectin, of the same chemical family, is even used extensively as a pharmaceutical in veterinary and human medicine (Õmura & Crump 2004). Synthetic derivatives have also been produced from avermectin compounds with improved properties such as water solubility and thermal stability. The derivative salt, emamectin benzoate, is one of these synthetic derivatives with improved efficacy against lepidopteran pests (Ishaaya *et al.* 2002).

Another macrocyclic lactone produced by bacteria and extensively used in pest control is spinosad. Products made from spinosad have been sold in several commercial formulations since the 1990s and were originally identified from the actinomycete bacterial species *Saccharopolyspora spinosa* (Mertz & Yao 1990; Kirst 2010). Spinosad, which contains major and minor fermentation products spinosyn A and spinosyn D, is extremely potent against a wide range of insects including key agricultural pests such as thrips, fruit flies, European corn borer, fall armyworm, and leafminers (Biondi *et al.* 2012). Additional spinosyn variants, the butenyl-spinosyns, were identified from related bacterial species *Saccharopolyspora pogona* (Lewer *et al.* 2009). Generally considered safe for non-target species, the spinosyns are registered for use on organic crops in multiple countries (USDA-AMS 2022; Micheloni *et al.* 2023). These original bacterial products also became the basis for synthetic modification to create improved chemical variants. Use of artificial neural networks and quantitative structure activity relationships led to development of spinetoram, a compound with improved and longer lasting insecticidal activity (Dripps *et al.* 2008; Sparks *et al.* 2021a). Spinosad and spinetoram have been used in commercial agriculture since 1997 and 2007 respectively, generally with great success. However, overuse can lead to generation of resistant pest populations, and this has been observed for diamondback moth in *Brassica* crops, olive fruit fly, and beet armyworm among others (Moulton *et al*. 2000; Zhao *et al*. 2002; Kakani *et al*. 2010). More recent evidence also suggests that although acute toxicity to pollinators and beneficial insects is limited, sublethal exposure can have negative impacts (Biondi *et al*. 2012; Martelli *et al*. 2022).

Avermectins and spinosad are just some of the bacterial secondary metabolites with potential for pest control use. As with other chemical control strategies, development of resistance in insect populations does occur with these natural products and it is important to continue to investigate novel solutions. Like antibiotic discovery for human medicine, analyzing bacteria from extreme and unusual environments could be a path to identification of new bacterial products for pest control (Quinn & Dyson 2024).

BACTERIA FOR BIOLOGICAL CONTROL

Aside from purifying, modifying, and synthesizing bacteria-derived metabolites, in many cases it can be very successful to use the bacteria themselves to infect or inhibit insect pests. One advantage of using the biological organism is that it can replicate on its own and potentially persist in the environment for longer periods of time. On the other hand, living organisms must remain viable to be effective, and are strongly influenced by environmental conditions and selective pressures.

Insect-pathogenic bacteria

Like other animals, insects are threatened by a wide range of pathogens including fungi, viruses, and bacteria. Entomopathogenic bacteria can infect insects by ingestion and cause systemic infection or disruption of feeding that leads to insect starvation (Ruiu 2015). Some of these are free-living opportunistic bacteria that colonize insects causing lethal infections (Flury *et al*. 2016). *Pseudomonas fluorescens* strains Pf-5 and CHA0 are two such soil-dwelling bacteria that can colonize and kill the larvae of *Galleria mellonella* and *Manduca sexta* (Péchy-Tarr *et al*. 2008). Other related species such as *Ps. chlororaphis* and *Ps. protegens* are also pathogenic to lepidopteran larvae (Flury *et al*. 2016). The genus *Bacillus* includes many bacteria with biological control potential against insects. For example, longevity of the sorghum pest Southern green stink bug, *Nezara viridula*, was reduced after feeding on *B. velezensis* (Esquivel *et al*. 2022). In addition to free-living soil bacteria, plant endophytes can also have insect-pathogenic traits. Although more endophytic fungi were studied extensively, reduced pest damage was observed in rice plants colonized by an entomopathogenic strain of the bacterial species *Serratia marcescens* (Niu *et al*. 2022). However, the effectiveness of entomopathogenic bacteria for pest control is complex in many cases as it depends on insect life stage, as well as whether the bacteria are used in combination with other compatible pest control products (El Fakhouri *et al*. 2023). Pathogenic mechanisms of bacteria infecting insects often include production of enzymes such as proteinases and chitinases which facilitate invasion of insect tissues. Production of these enzymes can be used as a screening tool to identify entomopathogenic bacteria with biological control potential (Dai *et al*. 2024).

In addition to the generalist species living in soil and plant environments, other entomopathogenic bacteria have highly specialized lifestyles, such as those associated with predatory nematodes. *Photorhabdus luminescens* is one such bacterial species which forms a symbiotic relationship with nematodes of the genus *Heterorhabditis* (Dunphy & Webster 1988). When the nematodes invade an insect larva, *Ph. luminescens* is injected into the insect hemocoel where it causes infection and death of the insect (Rajagopal & Bhatnagar 2002). This infection process occurs through secretion of bacterial toxins and virulence factors that facilitate decomposition of the larval body so that the bacteria can acquire nutrients (Rodou *et al*. 2010). Some of these toxins produced by *Ph.*

luminescens are also toxic to adult insects via ingestion and have been explored for targeting agricultural pests such as white flies (*Bemisia tabaci*) and Colorado potato beetle (*Leptinotarsa decemlineata*) (Blackburn *et al*. 2005).

Although several bacterial species have been identified for biological control of various insect pests, few of them enter the market as commercial products. In many jurisdictions, microbial pesticides such as entomopathogens and biological control products are subject to specific and rigorous regulatory processes like chemical pesticides (Wend *et al*. 2024). In other areas, farmers may take it on themselves to produce microbial cultures for pest control directly on their farms (Faria *et al*. 2023). Quality of on-farm biopesticide production varies depending on expertise and equipment, however. In most places, widespread adoption of bacterial insect control products requires commercialization and production at large scale. This can be more challenging for microbial products than for chemical products since the organisms must remain viable under storage and transport conditions, and efficacy is highly reliant on appropriate environmental conditions (Teixidó *et al*. 2022; Koul 2023).

Protective effects of phytobiomes-bacterial community interactions

Although more commonly associated with plant pathogen suppression, beneficial components of the phytobiome, or microbial communities associated with plants, can impact insect feeding and therefore pest damage. The phytobiome encompasses microbes living on plant surfaces both above and below ground, as well as endophytes within the plant. Bacteria from all these niches can impact insect pests in different ways, but often involve plant defense responses. Disease-suppressive soils containing strains of *Ps*. *protegens*, were able to protect wheat plants from the cereal leaf beetle *Oulema melanopus* (Almario *et al*. 2014; Harmsen *et al*. 2024). This effect was attributed to plant defense priming and possibly reduced insect fitness due to disruption of the insects' beneficial symbiotic bacteria (Harmsen *et al*. 2024). Likewise, *Arabidopsis* plants grown in soil with different microbiome compositions were found to have changes in chemical metabolites which correlated with reduced feeding of cabbage looper (*Trichopulsia ni*) larvae (Badri *et al*. 2013). In some cases, the impact of rhizosphere microbiome composition can be greater than plant genetic variability in determining resistance to herbivorous insects (Hubbard *et al*. 2019). What distinguishes microbiome-mediated resistance to insect pests from direct pathogenesis by entomopathogenic bacteria, is that it typically occurs indirectly through physiological and metabolic changes in the plant. In addition to phytohormone signaling and production of secondary metabolites, presence of certain bacteria can trigger structural changes such as reinforcement of cell walls that also deters insect feeding (Underwood 2012). Because of the systemic nature of plant-microbe and plant-insect interactions, insect pest feeding and damage can be influenced by microbial interactions that occur in the soil as well as above-ground plant parts (Reverchon & Méndez-Bravo 2021). In some cases, soil microbial communities can impact the plant nutritional value and palatability to insects through influence on nutrient uptake (Poveda *et al*. 2005). Nitrogen-fixing bacteria such as *Rhizobium* are essential for optimal plant growth and performance of many plant species in the legume family. Nitrogen content in leaf tissues is also important for production of alkaloid compounds which are components of the plant defense response to herbivore feeding (Irmer *et al*. 2015; Liu *et al*. 2020). Cultivation of lima bean plants with rhizobia increased production potential of these secondary metabolites and in turn reduced feeding of beetles (Thamer *et al*. 2011). Soil treatment with plant growth-promoting *Bacillus* sp. also reduced infestation of cabbage aphid (*Brevicoryne brassicae*) in *Brassica oleracea* plants (Gadhave *et al*. 2016). Although less well-studied for plant health promotion than rhizosphere colonizing bacteria, there are also some species of phyllosphere bacteria that are correlated with reduced insect damage (Humphrey *et al*. 2014). Many of these beneficial bacterial benefits are effective in a field scenario, and not just under strictly controlled plant growth conditions (Heinen *et al*. 2018).

BACTERIAL DEGRADATION OF INSECTICIDE COMPOUNDS

Two of the main challenges of insecticide use in agriculture are development of resistant insects and lasting environmental impacts of agrochemicals. Diverse bacterial species present in the environment can metabolize many natural and synthetic agrochemicals. This ability can be exploited for remediation of environmental contaminants in both agricultural and industrial processes. However, capability of bacteria to digest insecticidal compounds can also contribute to insect tolerance to these chemicals, in some specific cases that have been studied.

Insecticide tolerance facilitated by symbiotic bacteria

Like other animals, insects harbor a range of microorganisms within and on their bodies (Douglas 2015). Some of these are obligate intracellular symbionts, but many others are acquired from the environment and reside in open niches such as the outer cuticle and digestive system. Bacterial species found in the gut of insects have been implicated in detoxification of plant compounds, and more recently research has identified bacteria that also detoxify pesticides used in agriculture (Table 1) (Adams *et al*. 2013; Douglas 2015; Wang *et al*. 2022). The dynamics and mechanisms behind these interactions of insects, bacteria, and pesticides are still largely under investigation, but there is enough existing evidence from specific insect-bacteria relationships to consider this possibility when insecticide tolerance is observed in agricultural pests.

Bacteria capable of metabolizing insecticidal chemicals are found in plant and soil environments and can colonize insects in a stable manner throughout the lifecycle. In multiple different pest species, symbiotic associations with these bacteria have been shown to convey resistance to specific insecticides. Bean bug (*Riptortus pedestris*) acquires symbiotic *Burkholderia* that can degrade the organophosphate insecticide fenitrothion (Kikuchi *et al*. 2012). These bacteria can accumulate in soil where fenitrothion is used extensively in agriculture and be naturally acquired by pest insects. Similar dynamics were also observed in the rice stinkbug (*Cletus punctiger*) when studied under laboratory conditions (Ishigami *et al*. 2021). In the brown planthopper (*Nilaparvata lugens*), different variants of the symbiont bacterium *Arsenophonus* provided different levels of resistance of the insects to imidacloprid (Pang *et al*. 2018). In this case, some specific *Arsenophonus* strains decreased resistance in the insects in laboratory studies, suggesting that there may be potential to increase pest control efficacy through dissemination of specific bacteria in the environment (Pang *et al*. 2018). Diamond-back moth (*Plutella xylostella*) harbors several different bacterial species which affect tolerances to the commonly used insecticide chlorpyriphos (Xia *et al*. 2018). Particularly some strains of *Enterococcus* were able to increase resistance, in this case through effects on the insect immune system and production of antimicrobial peptides in addition to direct degradation (Xia *et al*. 2018). Likewise, in *N. lugens*, *Wolbachia* symbionts increased insect stress response to sublethal doses of imidacloprid and may help the insects adapt to this chemical exposure (Cai *et al*. 2021). Although specific details of these interactions have mostly been characterized in laboratory experiments, in some instances there is evidence of bacterial populations with insecticide degradation ability acquired through selection of an insect population in agricultural settings. For example, selection in the field of *Spodoptera frugiperda* larvae led to more diverse bacterial populations with increased capabil-

Table 1. Major insecticide classes for which bacterial degradation has been identified.

Insecticide class[z]	Bacteria-mediated resistance in insects	Source of bacteria	Bacterial genera	Reference
Carbamate (carbaryl, isoprocarb, fenobucarb, carbofuran)	Unknown	Wastewater, landfill, soil	*Pseudomonas*, *Cupriavidus*, *Paracoccus*, *Rhizhobium*, *Sphingomonas*, *Achromobacter*, *Novosphingobium*	Tomasek & Karns (1989); Feng *et al*. (1997); Hashimoto *et al*. (2002); Yan *et al*. (2007); Peng *et al*. (2008); Trivedi *et al*. (2016); Gupta *et al*. (2019)
Neonicotinoid (Acetamiprid, imidacloprid, thiamethoxam)	Yes	Soil, water, plant, wastewater, insect	*Pigmentiphaga*, *Acinetobacter*, *Sphingomonas*, *Stenotrophomonas*, *Ensifer*, *Bacillus*, *Pseudomonas*, *Mycobacterium*, *Leifsonia*, *Klebsiella*, *Hymenobacter*, *Enterococcus*	Anhalt *et al*. (2007); Pandey *et al*. (2009); Wang *et al*. (2011); Tang *et al*. (2012); Phugare *et al*. (2013); Wang *et al*. (2013); Zhou *et al*. (2013); Sharma *et al*. (2014); Kandil *et al*. (2015); Rana *et al*. (2015); Guo *et al*. (2020); Sivakumar *et al*. (2022); Lv *et al*. (2023)
Organochlorine (lindane, chlordane)	Unknown	Soil, water	*Streptomyces*, *Micromonospora*	Fuentes *et al*. (2010); Raimondo *et al*. (2020)
Organophosphate (dimethoate, fenitrothion, chlorpyrifos, Trichlorpho)	Yes	Insect	*Serratia*, *Burkholderia*, *Enterococcus*, *Citrobacter*, *Pseudomonas*	Boush & Matsumura (1967); Kikuchi *et al*. (2012); Cheng *et al*. (2017); Xia *et al*. (2018); Ishigami *et al*. (2021); Xia *et al*. (2023)
Pyrethrins and pyrethroids (Bifenthrin, Deltamethrin, Cypermethrin)	Yes	Soil, wastewater, insect	*Serratia*, *Acinetobacter*, *Brevibacillus*, *Sphingomonas*, *Sphingobium*, *Achromobacter*, *Pseudomonas*, *Bacillus*, *Streptomyces*, *Ochrobactrum*, *Paracoccus*, *Enterococcus*, *Lactococcus*	Maloney *et al*. (1988); Guo *et al*. (2009); Lin *et al*. (2011); Zhai *et al*. (2012); Cycoń *et al*. (2014); Akbar *et al*. (2015); Pankaj *et al*. (2016); Tian *et al*. (2018); Yang *et al*. (2018); Gur Ozdal & Algur (2022); Zeng *et al*. (2024)
Macrocyclic lactone (abamectin, spinosad)	Unknown	Soil	*Stenotrophomonas*	Wang *et al*. (2015)

[z] Classified by chemical relatedness for regulatory purposes (US EPA 2013).

ities for degradation of multiple insecticides (Gomes *et al*. 2020).

Since insecticide-degrading bacteria can be selected for in the environment even in the absence of the pest, resistance can develop much more rapidly in an insect population that acquires these bacteria as symbionts compared with genetic resistance that may take extended periods of time to develop in an insect population (Kikuchi *et al*. 2012).

Bioremediation of agricultural environments

In some areas where pesticides have been used heavily, there is concern about toxicity in soil and water, and the impacts this may have on human health and biodiversity in the environment. Pesticide use overall is highest in the Americas and Asia, with insecticides being the second highest class of products used (Raffa & Chiampo 2021). Bioremediation involves use of biological organisms, often microbes, to degrade and metabolize these contaminants.

Bioremediation strategies include addition of beneficial organisms and stimulating growth of already present microorganisms with desirable metabolic properties (Gonçalves & da Silva Delabona 2022). There is evidence that soils can naturally accumulate higher degradation capacities after extended use of specific chemical inputs due to enrichment for bacterial species that degrade those chemicals (Jablonowski *et al*. 2013). Additionally, several decades of microbiology research has identified specific bacteria that can break down commonly used pesticides (Chaudhry & Ali 1988). Multiple bacterial genera have been identified for bioremediation capacity including *Pseudomonas*, *Burkholderia*, *Bacillus*, *Stenotrophomonas*, *Staphylococcus*, and *Streptomyces*. Many of these organisms were originally isolated from heavily contaminated environments (Fuentes *et al*. 2010). In some cases, genetic capability for insecticide degradation is carried on plasmids and can be horizontally transferred between different bacterial species rather than being associated with a single organism (Feng *et al*. 1997; Hayatsu *et al*. 2000; John *et al*. 2020). Many insecticide-degrading bacteria do so through production of specific enzymes which can also be utilized in a purified form for bioremediation efforts (Gangola *et al*. 2018; Jaffar *et al*. 2022). The benefit to using purified degradation enzymes rather than the original source bacteria, is that purified enzymes can be used for applications such as degrading pesticide residues on food (Fan *et al*. 2017).

One of the largest challenges to implementation of bacterial bioremediation is scaling up from small-scale experiments to field applications (Gonçalves & da Silva Delabona 2022). Like the challenges of bacteria in biological control, various factors in the field can impact results such as soil types and environmental conditions (Raimondo *et al*. 2020). Since many pesticide compounds are complex hydrocarbon molecules, full degradation often requires multiple different microbial species which can facilitate breakdown of various components and intermediate breakdown products (Ghazali *et al*. 2004; Yılmaz *et al*. 2022). In some cases such as neonicotinoids, complete breakdown is important as some of the initial breakdown intermediates are just as toxic as the original compound, and this may require facilitation by multiple microbial species (Dai *et al*. 2006; Ma *et al*. 2014; Pang *et al*. 2020). It is also likely that contaminated agricultural soils contain more than one chemical of concern, and that the environmental and microbial process needed for bioremediation will be complex.

METHODS FOR IDENTIFICATION OF BACTERIA WITH BIOLOGICAL CONTROL AND BIOREMEDIATION POTENTIAL

Although many beneficial bacteria have been identified for uses in insect pest control and agriculture, there is still significant bacterial diversity remaining untapped. General techniques for isolation and identification of novel bacteria with useful traits are described here, many of which can be employed in low resource settings with only basic microbiology laboratory capacity (Fig. 1).

Direct culturing followed by screening

When the goal is to isolate a diverse range of bacterial species from a specific sample type such as insect or plant materials, direct culturing on rich and complex media can be used.

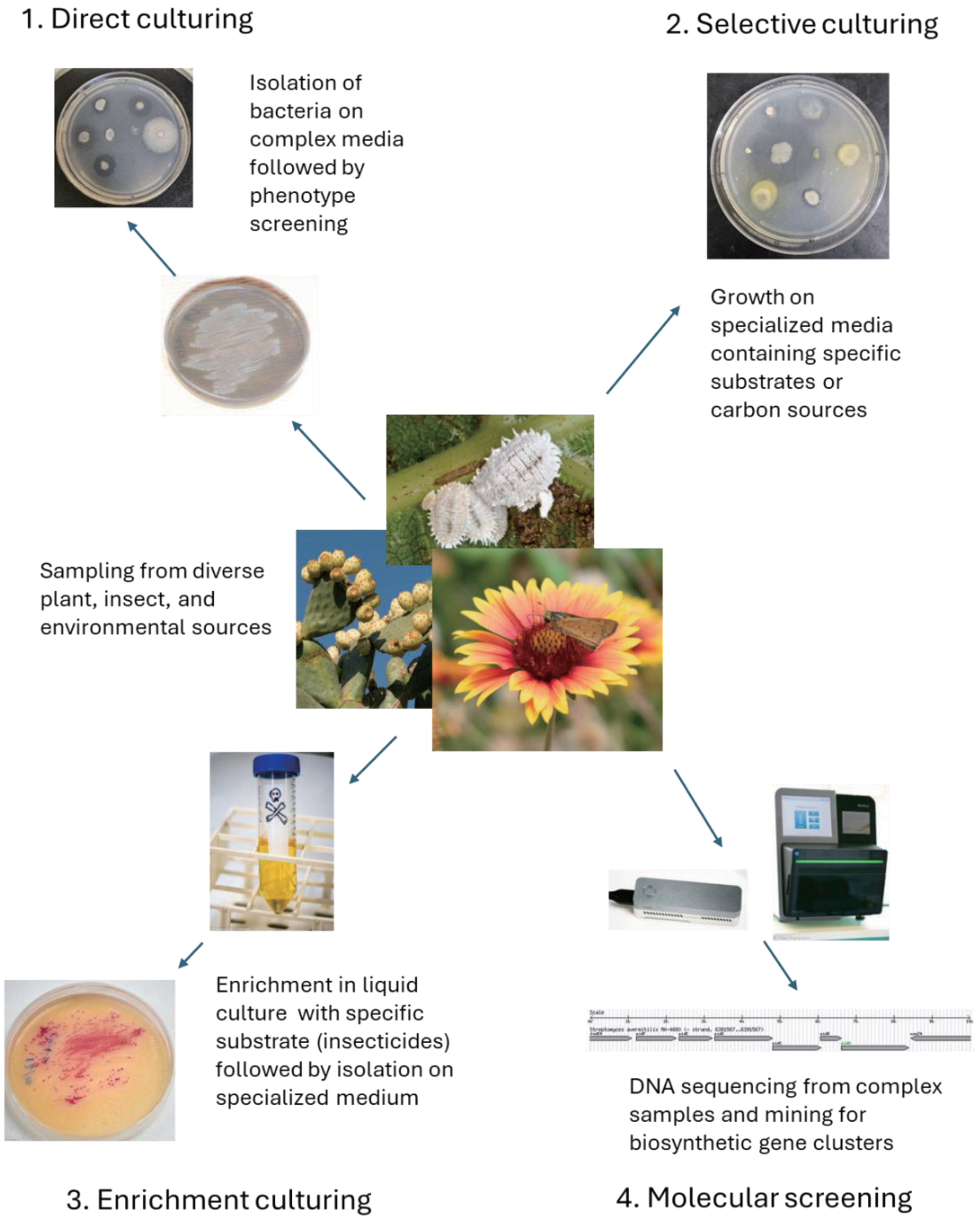

Fig. 1. Methods for identification of bacteria with biological control and bioremediation potential.

For direct culture experiments, samples of soil, plant, or insect materials are homogenized in sterile water or buffer and diluted onto a variety of complex culture media in Petri plates. Incorporating a range of media types, incubation temperatures, and atmospheric conditions, can yield more diverse bacterial isolates (Song *et al.* 2024). Once pure bacterial isolates have been obtained, these isolates can be screened for a variety of desirable traits such as production of antibiotics, chitinases, and carbohydrate-degrading enzymes (Pino-Hurtado *et al.* 2024; Zhang *et al.* 2024). However, direct culturing approaches will favor faster growing and more abundant organisms, and screening for desirable traits can be very time consuming. To address this challenge, various approaches to improving the diversity of organisms cultured from complex samples have been developed. Simple modifications to culture media can have significant impacts (Kato *et al.* 2018; Nishioka & Tamaki 2022), as can use of more complicated matrices instead of traditional Petri dish culture (Liu *et al.* 2021). Overall, the direct culturing approach typically needs to be tailored to the specific sample type, environment, and type of bacterial isolate desired.

Selective culturing

To selectively target bacterial isolates from a specific genus or with a specific growth trait or phenotype, growth media can be designed to target that trait or background. For example, sample pretreatments like desiccation, addition of selective antibiotics, and specific growth media can improve isolation of the genus *Streptomyces* (Oskay 2009; Antido & Climacosa 2022). For the genus *Pseudomonas*, there are also several semi-selective media formulations (Johnsen & Nielsen 1999), and other bacterial groups can be targeted if there are common chemical tolerances (Kini *et al.* 2019; Bonnet *et al.* 2020). Selecting for ability to utilize a specific carbon source can be done by plating dilutions of complex samples directly on minimal salt media including only that carbon source. This method has been used for isolation of chitinase producing organisms by using chitin as the sole carbon source (Saima *et al.* 2013), and for insecticide-degrading organisms by using a specific pesticide as the sole carbon source (Benimeli *et al.* 2007). The benefit to selective culturing is that bacteria of interest can be more quickly identified from complex samples. The drawback is that organisms may be excluded if they require supplemental nutrients, or if they are outliers for genus-specific growth requirements.

Enrichment culture

From complex samples such as soil or wastewater, enrichment culturing can increase the population of bacteria with the desired metabolic properties within the sample prior to isolating individual bacterial colonies. For this process, samples are typically mixed with minimal medium supplemented with the target chemical for degradation. Sequential culturing, sometimes with increasing concentrations of the target chemical, will select for species able to utilize the target as a carbon source (Akbar *et al.* 2015; Asamba *et al.* 2022). After several rounds of sequential culturing selection, samples are plated on minimal medium supplemented with the target chemical for isolation and identification of individual bacterial colonies. Benefits to this method are that rare species with the desired metabolic properties can be more easily identified, and minimal screening needs to be carried out afterwards if the selection process is robust. However, organisms that need a consortium of other bacteria or supplemental carbon or other nutrients to grow may be eliminated over the course of the selection process.

Molecular screening

Regardless of the growth medium and methods used, many bacterial species still cannot be cultured directly (Steen *et al.* 2019). Among the unculturable organisms, there is likely a significant number that have important biological traits that can be utilized indirectly. Metagenomic sequencing from a broader range of samples and locations can identify new bacterial species and biosynthetic gene clusters (Medema *et al*. 2011). For many pesticide degradation pathways, the functional genes are known, and homologs can be identified from sequences. Novel degradation pathways can also be identified by cloning metagenomic DNA into libraries expressed in a model bacterial system and screening for activity (Ufarté *et al*. 2017), or by bioinformatic prediction (Jeffries *et al*. 2018; Malla *et al*. 2022). Although easily culturable bacteria can be more directly used as biological control organisms, the diversity of natural products and novel activity that is present in the non-culturable bacteria should not be overlooked.

FUTURE DIRECTIONS FOR RESEARCH

Around the world there has been increasing research investment and adoption of biological control and biopesticides in agriculture, and in mitigation of insecticide impacts (Gelernter 2007; van Lenteren & Cock 2020; Wyckhuys *et al*. 2020; Helepciuc & Todor 2022; Lopes *et al*. 2023; Pioneering proposals to restore Europe's nature by 2050). All this innovation is based on fundamental research identifying new biological control organisms, characterizing plant-microbe-insect interactions, and developing a detailed understanding of microbial products. There are still several areas where this research can be expanded, including identification of more diverse biological control organisms in general, focusing on locally adapted organisms for specific settings, and utilization of existing microbial collection resources. Over the last few decades, reduced costs and increased accessibility of microbial sequencing has significantly increased knowledge of bacterial species from different environments. Technological advancements in screening and identifying natural products have also facilitated discovery of new microbial compounds. However, samples from insect and plant sources are underrepresented in databases and collections compared with other sources such as human samples (Fig. 2). There is also significant bias in research investments towards known pest organisms, major crops, and high-resource countries (Manners & van Etten 2018; Bebber *et al*. 2019; Skaldina & Blande 2025). Increasing sampling diversity could uncover novel bacterial species with important biological traits. One of the most common reasons for biological control failure is influence of environmental conditions (Quesada-Moraga *et al*. 2024). Organisms that are not adapted to local climate may not survive well or provide adequate stability. A more specific focus on isolating organisms from the local area where they will be used has the potential to facilitate implementation and improve outcomes (Ningthoujam *et al*. 2009; Harman *et al*. 2010). It may also be necessary to re-assess organisms that were isolated many years ago, as the climate conditions where they were initially effective may have shifted. In addition to isolating new and more geographically targeted bacteria, there is a wealth of existing microbial resources in culture collections around the world. The World Federation of Culture Collections lists more than twenty formal collections (World Federation for Culture Collections, https://wfcc.info/sites/), and there are countless informal collections maintained by individual researchers globally. Organisms from these collections

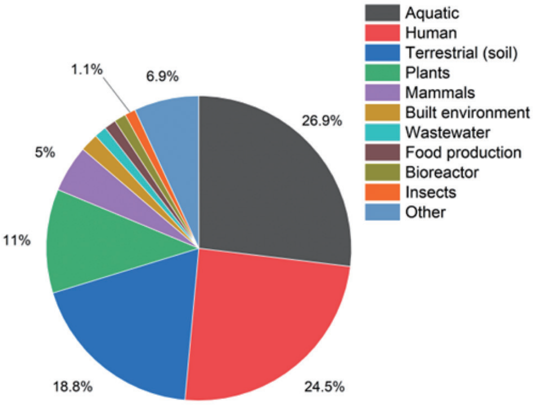

Fig. 2. Biosample type for all samples in Joint Genome Institute (JGI) Genomes Online Database (accessed December 2024).

can also be screened for relevant traits beyond the purpose they were collected and preserved for (Díaz-Rodríguez *et al*. 2021). The utility of repurposing organisms for more than one use is highlighted by the fact that bacteria identified for one biological control or bioremediation trait often show additional phenotypes such as antibacterial or antifungal activities or plant growth promotion (Akbar *et al*. 2015).

Bacteriology research over decades has provided a wide range of tools to increase agricultural productivity. In the relationships between pest insects and crop plants, bacteria are a key part of the equation and can be used to promote plant health in various ways. Continuing to focus resources on microbial solutions will facilitate further development in this area for a sustainable future of agriculture.

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細菌於農業害蟲防治的應用：過去、現在與未來

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摘要

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自古以來害蟲一直困擾著農業，農作物害蟲管理需隨之不斷創新。細菌與其他微生物透過發揮致病活性、產生有毒次級代謝物及提升植物防禦等能力，而成為防治害蟲的重要工具。此外，農業環境中的細菌通常具備代謝農業化學品的能力，故可用來減輕農業對環境的影響。然而，目前僅有小部分來自植物與昆蟲的細菌已被研究，還有大量的微生物多樣性尚未被運用。隨著對農業生產力需求的增加與氣候變遷改變病蟲害模式，探索更多具有害蟲生物防治與生物修復應用潛力的細菌種類至關重要。本綜述概述了細菌生物防治的一些歷史、細菌衍生農業化學品的使用、細菌導致殺蟲劑抗性以及目前對細菌-昆蟲-植物相互作用的理解。本文也進一步提出該領域的研究建議，以拓寬永續害蟲防治方案的範圍。

關鍵詞：殺蟲劑、生物防治、農業、有益細菌、害蟲管理。

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